

## Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia

Amparo Acebey\*, S. Rob Gradstein<sup>†1</sup> and Thorsten Krömer<sup>†</sup>

\*Herbario Nacional de Bolivia, Casilla 10077, La Paz, Bolivia

<sup>†</sup>Institute of Plant Sciences, University of Göttingen, 37073 Göttingen, Germany

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**ABSTRACT:** An analysis of corticolous bryophyte diversity on whole trees in primary rain forest and 4–15-y-old fallows at 500–650 m in the Alto Beni, Bolivia, showed a significantly decreased diversity of bryophyte families and moss species in the fallows. However, liverwort diversity was scarcely lower in the fallows, except in the very young (4 y old) ones. Fallows had a significantly higher percentage of smooth mat species (72%), which may reflect the warmer, drier microclimate in the fallows. About half of the bryophyte species of the rain forest had re-established in the 10–15-y-old fallows. The majority of these are ecological generalists and sun epiphytes; a small minority are shade epiphytes. Re-establishment of ecological specialists is slower than that of generalists. Species richness in the primary forest is highest in the canopy; in the fallows it is highest in the understorey due to striking shifts of species and specialized growth types (rough mats, fans, tails) towards lower heights on the trees in the fallows. These shifts correspond well with measured changes in air temperature and air humidity in the fallows as compared with the forest.

**KEY WORDS:** biodiversity, deforestation, ecological generalist, growth form, shade epiphyte, species richness, succession, sun epiphyte, vertical distribution

### INTRODUCTION

The conservation of the biodiversity of tropical rain forests is of worldwide concern. It is generally considered that human exploitation of tropical rain forests causes major changes in biodiversity but rather few research data are available. Recent work on vascular plant diversity in neotropical rain forests indicates that forest degradation does not always lead to reduction of species richness. In Amazonian lowland forests, Fujisaka *et al.* (1998) found that secondary forests supported only slightly fewer species of vascular plants than primary ones and in Costa Rican montane rain forests, Kappelle (1996) recorded more species in secondary than in primary forest. Only the conversion of forest to pasture land led to a considerable loss of total species richness. However, both studies found that many secondary forest species were lacking in the primary forests.

The majority of plant diversity studies have been limited to selected plant groups, especially to structurally dominant and economically important trees. Herbs, shrubs, lianas, epiphytes, and cryptogamic plants such as bryophytes and lichens have frequently been neglected (Gradstein 1992a, Whitmore & Sayer 1992). Data on the impact of human activities on plant diversity in tropical

forests ecosystems must therefore be interpreted with caution and are often discussed controversially (Mooney *et al.* 1995).

This paper focuses on bryophytes (mosses, liverworts) in tropical rain forests and deals with the question of how deforestation and forest regeneration affect the diversity of these organisms. Recent studies have indicated the importance of bryophytes as ecological indicators, especially of humidity conditions, in tropical rain forests (e.g. Frahm 1990, 1994; Frahm & Gradstein 1991, Kürschner & Frey 1999). It has also been shown that bryophytes are not evenly distributed within the forest and that the canopy of the dense, primary forest may have many more species than the understorey (Cornelissen & ter Steege 1989, Wolf 1993a, b). Another important finding of these studies was that species density of epiphytic bryophytes in rain forests is high and minimum areas for sampling relatively small. Complete sampling of 4–5 trees, from base to outer canopy, may yield over 75% of the flora of a homogeneous forest stand.

Deforestation is generally considered to have a deleterious effect on the bryophyte flora of the primary forest and may lead to a considerable loss of species (up to 50% or more), especially of the desiccation-intolerant ‘shade epiphytes’ (Costa 1999, Equihua & Gradstein submitted, Gradstein 1992a, Hyvönen *et al.* 1987, Sillet *et al.* 1995).

<sup>1</sup> Corresponding author.

Those surviving in clearings and secondary forests are mainly the desiccation-tolerant 'sun epiphytes' of the forest canopy and weedy 'generalists'.

The above conclusions as to the effects of deforestation were based on uneven sampling of the forest, with a bias to the understorey (Costa 1999) or the canopy (Silllett *et al.* 1995). In this study we analyse for the first time bryophyte diversity in primary forest and young secondary ones (= fallows), based on sampling of plots on whole standing trees, from the base of the trees to the outer canopy. The main research question posed is how species richness, species composition and habitat preferences of species differ in primary forest and in fallows of different ages.

## METHODS

The study was conducted on the south-eastern slope (550–650 m asl) of the Serranía Marimonos, 15° 31'–32'S, 67° 20'–21'W, along the Alto Beni River near Sapecho, Sud Yungas Province, La Paz Department, Bolivia (Figure 1). Fieldwork was carried out during May–August 1999. Temperatures at *c.* 450 m average about 24–25 °C during the day, with a maximum of 34 °C and a minimum of 16 °C. Annual rainfall varies from 1300–1600 mm in the valley (*c.* 450 m) to over 2000 mm higher up the slopes. The rainy season lasts from October to May, alternating with a dry period of about 4(–5) mo, during June–September (CUMAT-COTESU 1985, Elbers 1995).

The forest of the slopes of the Serranía Marimonos is an evergreen submontane forest with a well-developed shrub layer. The forest is made up of 30–40-m-tall trees, with

trunks measuring over 100 cm dbh, frequently buttressed, and lowermost branches at about 20–25 m height. Common tree species are *Poulsenia armata* (Miq.) Standley, *Pseudolmedia laevis* (Ruíz & Pavón) Macbr., *Clarisia racemosa* Ruíz & Pavón and *Brosimum lactescens* (Moore) Berg (Moraceae), *Otoba parvifolia* (Markgr.) Gentry (Myristicaceae), *Leonia racemosa* Mart. (Violaceae) and *Tetragastris altissima* (Aublet) Swart (Burseraceae) (Seidel 1995).

Since the 1960s the population of the Alto Beni region has increased considerably due to colonization by immigrants from the country's harsh altiplano regions. The increased population has led to the conversion of large tracts of forest into agricultural fields. As a result, the lower slopes of the Serranía Marimonos are mainly covered by a mosaic of arable fields and fallow land up to 15 y in age (Seidel 1995). The vegetation of the young fallows consist mainly of grasses and shrubs (Asteraceae, Melastomataceae, *Piper* spp.), while trees gain in importance in older fallows. The most common pioneer trees of the fallows are *Cecropia* spp., *Ochroma pyramidale* (Cav. ex Lam.) Urb. and *Inga* spp. Tree height in the fallows is 5–15 (–18) m.

Bryophytes were sampled in six sites (Figure 1): two forest sites (PI, PII) and four fallow sites of different ages (4, 10, 12 and 15 y). The forest sites are 1-ha plots installed in 1990 by R. Seidel (Instituto de Ecología, La Paz) together with staff of Proyecto de Investigaciones Agroecológicas y Forestales (PIAF) of the Cooperativa EL CEIBO in Sapecho (Seidel 1995). Forest site 1 (PI) is located *c.* 3.5 km W of Sapecho at an elevation of about 600 m (inclination 15–20°, exposure SW). Forest site 2

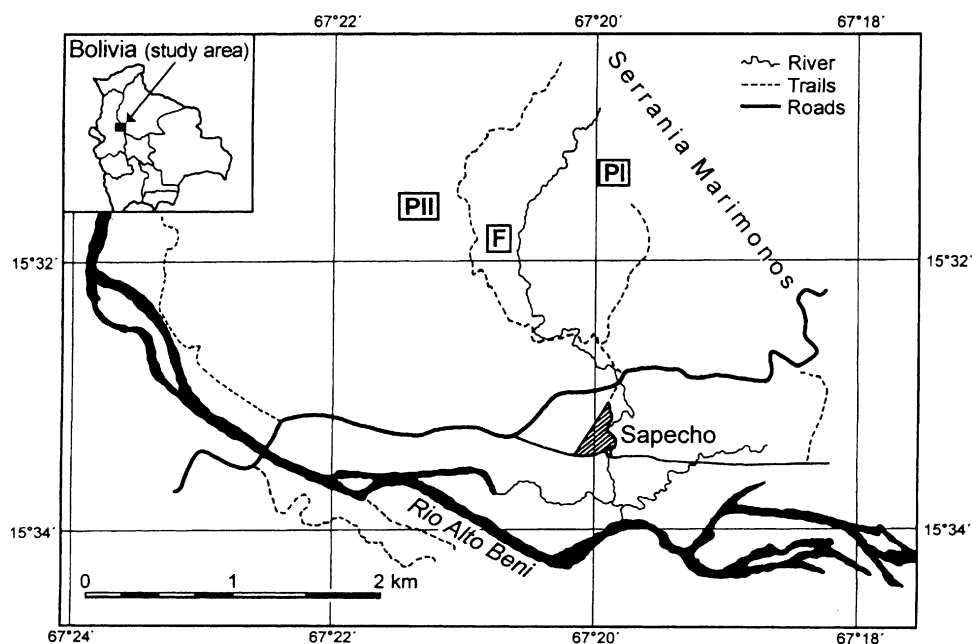


Figure 1. Study area. PI, PII, rain-forest sites; F, fallows.

(PII) is c. 2 km SW from the village at an elevation of 600–650 m (inclination 10 °, exposure SE). The four fallow sites, c. 1000–2000 m<sup>2</sup> in size and about 200–300 m distant from each other, were located c. 1.5 km from PI and c. 1 km from PII, at an elevation of about 550 m.

In each site corticolous (= bark-inhabiting) bryophytes were sampled from three whole trees, from the base of the trunk to the outer part of the crown. Host trees included *Ficus killipii* Standl., *Poulsenia armata*, *Pseudolmedia laevis* and *Tetragastris altissima* (three trees) in the forest, and *Cecropia* sp. (four trees), *Inga* sp. (three trees), *Ochroma pyramidale* (two trees), *Schizolobium* sp. and an unidentified species each of Asteraceae and Euphorbiaceae in the fallows. All trees had smooth bark with exception of *Inga* sp. (rough bark) and *Tetragastris altissima* (flaking bark). Trees were climbed using rope techniques as described by Perry (1978) and ter Steege & Cornelissen (1988) except for fragile trees in young fallows, which were cut. Trees were divided into five vertical zones following Johansson (1974; see also Gradstein *et al.* 1996): (1) trunk base (0–2 m), (2) trunk, (3) lower canopy, (4) middle canopy and (5) outer canopy. One plot was sampled in each Johansson zone; sample plot size was 500 cm<sup>2</sup> on trunks and 200–250 cm<sup>2</sup> on branches. Sampling of thin branches included the upper and lateral sides, not the underside of the branch.

Completeness of the sampling was estimated using the Chao 1 formula (Chao 1984):

$$S_1 = S_{\text{obs}} + (a^2/2b)$$

where  $S_1$  is the estimated number of species;  $S_{\text{obs}}$  the observed species number;  $a$ , the number of species registered only once (singletons); and  $b$ , the number of species recorded twice (doubletons). Individual trees (six in primary forest, 12 in secondary forest) were treated as independent samples.

Six types of bryophyte growth-form (= life-form) were recognized: fan, smooth mat (including threads), pendant, rough mat, tail and turf (Kürschner & Frey 1999, Kürschner & Parolly 1998, Richards 1984). Fan and tail were sometimes difficult to distinguish and were therefore combined in the analysis.

Presence–absence was scored for all species and growth-form type detected. Voucher specimens were deposited in the Herbario Nacional de Bolivia (LPB) with duplicates in the Herbarium of the University of Göttingen (GOET). Floristic similarities between forest and fallows in terms of bryophyte assemblages were calculated using the Sørensen Index (Bray & Curtis 1975).

Air temperature and relative humidity in forest and fallows were measured continuously for 40 d during December 2000 and January 2001 (rainy season), using data loggers (HOBO Pro RH/Temp, Onset) installed at 2-m and 25-m height in the forest plots, at 2-m height in 15-y-old fallow, and at 2-m height in an open area in

Sapecho village. From these values vapour pressure deficit (vpd) was calculated. Light environment in the different strata was not quantified.

Nomenclature follows Churchill & Linares (1995) for mosses and Uribe & Gradstein (1998) for liverworts. Family classification of bryophytes is according to Gradstein *et al.* (2001a).

## RESULTS AND DISCUSSION

### Forest

**Species richness** In total, 80 species of corticolous bryophyte (48 of liverwort, 32 of moss) in 26 families were recorded on six trees in the forest (Tables 1, 2). Sampling included 85% of the estimated total number of species in the forest (see below). Lejeuneaceae (liverworts; 32 species) were the largest family, representing 40% of all the bryophyte species recorded. Next in importance were Jubulaceae (5 spp.), Plagiochilaceae (5 spp.), Pterobryaceae (5 spp.), Calymperaceae (3 spp.) and Meteoriaceae (3 spp.). All of these belong to the 15 most important bryophyte families of the tropical rain forest (Gradstein & Pócs 1989).

The number of species on whole trees in the submontane forests of the Alto Beni is rather similar to that recorded from lowland rain forests of Guyana (150 m) (Table 2). It is lower than in lowland rain forest of Central French Guiana (150 m), however, and higher than in lower montane forest of Colombia at 1500 m. These findings support the notion that trees in lowland and submontane forests may harbour more bryophyte species than those in lower montane forests (but not upper montane ones) (Gradstein 1995, Wolf 1993a, b). We propose that the greater habitat complexity of the lowland forests, having a taller and structurally more complex canopy, is the reason why epiphytic species diversity may be higher in lowland forests than in lower montane forests. Opposed to this, Richards (1984, 1988) and other authors (e.g. Frahm & Gradstein 1991) have documented higher species numbers in montane forests than lowland forests. The latter studies were biased to the forest understorey, however. We speculate that due to the lower and more open forest canopy, species diversity in the understorey of montane forests is usually much higher than in lowland forests. It is thus not surprising that inventories focusing on the understorey record higher species numbers in montane forests.

**Growth forms** About half of the growth-form records in the forest are smooth mats, followed by fans and tails (21%) and rough mats (14%) (Tables 1 and 3). Turfs and pendants are scarce, totalling less than 10% each. Smooth-mat species, the majority of them Lejeuneaceae, are well adapted to smooth bark and their dominance is

**Table 1.** Occurrence, vertical distribution and growth form of corticolous bryophytes in submontane rain forest and fallows in Bolivia. PI: rain forest site 1. PII: rain forest site 2. F4: 4-y-old fallow. F10: 10-y-old fallow. F12: 12-y-old fallow. F15: 15-y-old fallow. Vd: vertical distribution (numbers refer to Johansson zones). Growth forms: f, fan and tail; m, smooth mat; p, pendant; r, rough mat; t, turf.

| Taxa                                   | PI | PII | F4 | F10 | F12 | F15 | Vd<br>P (I, II) | Vd<br>F (4–15) | Growth<br>form |
|----------------------------------------|----|-----|----|-----|-----|-----|-----------------|----------------|----------------|
| <b>Liverworts</b>                      |    |     |    |     |     |     |                 |                |                |
| <b>Geocalyceae (= Lophocoleaceae)</b>  |    |     |    |     |     |     |                 |                |                |
| <i>Leptoscyphus porphyrius</i>         |    | +   |    |     |     |     | 4               |                | m              |
| <i>Lophocolea bidentata</i>            |    |     | +  | +   |     |     |                 | 1              | m              |
| <b>Jubulaceae (= Frullaniaceae)</b>    |    |     |    |     |     |     |                 |                |                |
| <i>Frullania brasiliensis</i>          | +  | +   |    | +   |     |     | 4,5             | 2,3            | r              |
| <i>Frullania ericoides</i>             | +  |     |    |     |     |     | 2               |                | m              |
| <i>Frullania kunzei</i>                |    |     |    | +   |     |     |                 | 2              | m              |
| <i>Frullania mucronata</i>             | +  |     |    |     | +   |     | 3               | 2              | r              |
| <i>Frullania riojaneirensis</i>        | +  | +   |    | +   | +   | +   | 3,4,5           | 1,2,3,4,5      | m              |
| <b>Jungermanniaceae</b>                |    |     |    |     |     |     |                 |                |                |
| <i>Anastrophyllum piligerum</i>        | +  |     |    |     |     |     |                 | 4              | m              |
| <b>Lejeuneaceae</b>                    |    |     |    |     |     |     |                 |                |                |
| <i>Amphilejeunea reflexistipula</i>    | +  | +   |    |     |     | +   | 1,2,3,4         | 1,2            | m              |
| <i>Anoprolejeunea conferta</i>         |    | +   |    | +   |     |     | 4               | 2              | m              |
| <i>Aphanolejeunea camillii</i>         |    |     | +  | +   | +   | +   |                 | 1,4,5          | m              |
| <i>Aphanolejeunea clavatopapillata</i> | +  | +   |    |     |     |     | 1               |                | m              |
| <i>Archilejeunea auberiana</i>         |    | +   |    |     | +   | +   | 5               | 1,2            | m              |
| <i>Bryopteris diffusa</i>              | +  | +   |    |     |     |     | 3,4,5           |                | f              |
| <i>Bryopteris filicina</i>             | +  | +   |    | +   |     |     | 1,2,3,4,5       | 1,2            | f              |
| <i>Caudalejeunea lehmanniana</i>       |    | +   | +  |     |     |     |                 | 1,2            | m              |
| <i>Ceratolejeunea cornuta</i>          | +  | +   |    | +   | +   | +   | 3,4,5           | 1,2            | m              |
| <i>Ceratolejeunea cubensis</i>         | +  | +   |    |     |     | +   | 1,2,3           | 1              | m              |
| <i>Cheilolejeunea clausa</i>           | +  | +   |    |     | +   | +   | 1,2,3,4,5       | 1,2,3          | m              |
| <i>Cheilolejeunea rigidula</i>         |    | +   | +  |     |     |     | 4               | 1              | m              |
| <i>Cheilolejeunea trifaria</i>         | +  | +   |    | +   | +   | +   | 1,2,3,4,5       | 1,2,3          | m              |
| <i>Cheilolejeunea</i> sp.              |    |     |    | +   | +   |     |                 | 3              | m              |
| <i>Cololejeunea cardiocarpa</i>        |    | +   | +  |     |     |     |                 | 2,3,4,5        | m              |
| <i>Cololejeunea lanciloba</i>          | +  |     | +  | +   | +   | +   | 5               | 1,2,3,4,5      | m              |
| <i>Cololejeunea minutissima</i>        |    | +   |    |     |     |     |                 | 3,4            | m              |
| <i>Colura cylindrica</i>               |    |     |    | +   |     |     |                 | 1,3            | m              |
| <i>Diplasiolejeunea cavifolia</i>      |    |     | +  |     |     |     |                 | 4              | m              |
| <i>Diplasiolejeunea rudolphiana</i>    |    | +   | +  |     |     |     |                 | 5              | m              |
| <i>Diplasiolejeunea unidentata</i>     | +  |     |    | +   |     |     |                 | 54             | m              |
| <i>Drepanolejeunea inchoata</i>        | +  |     |    |     |     |     |                 | 2,4            | m              |
| <i>Drepanolejeunea</i> sp.             |    | +   |    |     | +   |     | 3,4             | 3              | m              |
| <i>Frullanoides densifolia</i>         | +  | +   | +  | +   | +   | +   | 3,4,5           | 1,2,3,4,5      | r              |
| <i>Lejeunea caespitosa</i>             |    |     | +  | +   | +   | +   |                 | 1,2,3,4,5      | m              |
| <i>Lejeunea flava</i>                  |    |     |    | +   | +   |     |                 | 2,3            | m              |
| <i>Lejeunea laetevirens</i>            | +  | +   | +  | +   |     |     | 1,2,3,4         | 1              | m              |
| <i>Lejeunea phyllobola</i>             | +  | +   | +  | +   | +   |     | 1,3,4,5         | 1,2,3,4        | m              |
| <i>Lejeunea trinitensis</i>            |    |     | +  | +   |     |     |                 | 1,2,3,4,5      | m              |
| <i>Lejeunea (Heterolejeunea) sp. 1</i> | 1  | +   | +  | +   | +   |     | 1,2,3,4         | 1,2            | m              |
| <i>Lejeunea (Heterolejeunea) sp. 2</i> | +  | +   |    |     |     |     | 1               |                | m              |
| <i>Lejeunea sp. 3</i>                  |    |     | +  | +   | +   | +   |                 | 1,2            | m              |
| <i>Lepidolejeunea eluta</i>            | +  | +   | +  | +   | +   |     | 1,2,3,4,5       | 1,2,3          | m              |
| <i>Leptolejeunea elliptica</i>         | +  |     | +  | +   |     |     | 5               | 1,2,3,4,5      | m              |
| <i>Leptolejeunea exocellata</i>        | +  | +   | +  |     |     |     | 5               | 2,3            | m              |
| <i>Lopholejeunea subfusca</i>          | +  | +   | +  | +   | +   | +   | 1,2,3,4,5       | 1,2,3,4        | m              |
| <i>Marchesinia brachiata</i>           | +  |     |    |     |     |     | 1,5             |                | r              |
| <i>Marchesinia robusta</i>             |    |     | +  |     |     |     |                 | 2              | r              |
| <i>Mastigolejeunea auriculata</i>      | +  | +   |    |     |     | +   | 1,2,3,4         | 1,2            | m              |
| <i>Microlejeunea bullata</i>           | +  | +   | +  | +   |     |     | 3,4,5           | 1,2,4          | m              |
| <i>Odontolejeunea lunulata</i>         | +  | +   |    | +   |     | +   | 4,5             | 2,4            | m              |
| <i>Omphalanthus filiformis</i>         |    | +   |    |     |     |     | 4,5             |                | p              |
| <i>Rectolejeunea berteriana</i>        |    | +   |    |     | +   | +   | 1               | 1,2            | m              |
| <i>Symbiezidium transversale</i>       | +  | +   |    | +   | +   | +   | 2,3,4,5         | 1,2,3          | m              |
| <i>Taxilejeunea obtusangula</i>        |    | +   |    |     | +   | +   | 1,2,3           | 1,2            | m              |
| <i>Taxilejeunea cf. terricola</i>      | +  | +   |    |     |     |     | 2,3             |                | p              |
| <b>Lepidoziaceae</b>                   |    |     |    |     |     |     |                 |                |                |
| <i>Bazzania phyllobola</i>             |    | +   |    |     |     |     | 4               |                | r              |
| <b>Metzgeriaceae</b>                   |    |     |    |     |     |     |                 |                |                |
| <i>Metzgeria decipiens</i>             | +  | +   |    |     |     |     | 1               |                | m              |
| <b>Plagiochilaceae</b>                 |    |     |    |     |     |     |                 |                |                |
| <i>Plagiochila disticha</i>            | +  | +   |    |     | +   | +   | 1,4,5           | 1,2,3          | f(r)           |
| <i>Plagiochila montagnei</i>           | +  | +   |    | +   |     |     | 1,3,4,5         | 1,2            | f(r)           |

Table 1. continued

| Taxa                                               | PI | PII | F4 | F10 | F12 | F15 | Vd<br>P (I, II) | Vd<br>F (4–15) | Growth<br>form |
|----------------------------------------------------|----|-----|----|-----|-----|-----|-----------------|----------------|----------------|
| <i>Plagiochila raddiana</i>                        | +  | +   |    | +   | +   | +   | 1,2,3,4,5       | 1,2,4          | f(r)           |
| <i>Plagiochila</i> (sect. <i>Contiguae</i> ) sp. 1 | +  | +   |    | +   |     | +   | 1               | 1,2            | f(r)           |
| <i>Plagiochila</i> (sect. <i>Contiguae</i> ) sp. 2 | +  |     |    | +   |     |     | 2,3,4           | 2              | f(r)           |
| Porellaceae                                        |    |     |    |     |     |     |                 |                |                |
| <i>Porella swartziana</i>                          | +  |     |    |     |     |     | 1               |                | f              |
| Radulaceae                                         |    |     |    |     |     |     |                 |                |                |
| <i>Radula macrostachya</i>                         |    | +   |    |     |     |     | 4,5             |                | m              |
| <i>Radula</i> sp.                                  | +  | +   |    |     |     | +   |                 | 11             | m              |
| Mosses                                             |    |     |    |     |     |     |                 |                |                |
| Brachytheciaceae                                   |    |     |    |     |     |     |                 |                |                |
| <i>Rhynchostegium</i> sp.                          | +  |     |    |     |     |     |                 | 1              | m              |
| Bryaceae                                           |    |     |    |     |     |     |                 |                |                |
| <i>Bryum</i> sp.                                   |    | +   |    |     |     |     | 4,5             |                | t              |
| Calymperaceae                                      |    |     |    |     |     |     |                 |                |                |
| <i>Calymperes afzelii</i>                          | +  | +   |    |     |     |     | 1,2             |                | t              |
| <i>Syrrhopodon incompletus</i>                     |    | +   |    |     |     |     |                 | 1              | t              |
| <i>Syrrhopodon parasiticus</i>                     | +  | +   |    | +   |     |     | 5               | 2              | t              |
| Dicranaceae                                        |    |     |    |     |     |     |                 |                |                |
| <i>Holomitrium arboreum</i>                        |    | +   |    |     |     |     |                 | 3,4            | t              |
| Fissidentaceae                                     |    |     |    |     |     |     |                 |                |                |
| <i>Fissidens</i> sp.                               | +  | +   |    |     |     |     | 1               |                | t              |
| Helicophyllaceae                                   |    |     |    |     |     |     |                 |                |                |
| <i>Helicophyllum torquatum</i>                     |    | +   |    |     |     |     | 3               |                | r              |
| Hypnaceae                                          |    |     |    |     |     |     |                 |                |                |
| <i>Chrysohypnum diminutivum</i>                    | +  | +   |    | +   | +   | +   | 1               | 1              | m              |
| <i>Isopterygium tenerum</i>                        |    | +   | +  | +   |     |     | 3               | 1              | m              |
| Leptodontaceae                                     |    |     |    |     |     |     |                 |                |                |
| <i>Pseudocryphaea domingensis</i>                  | +  | +   |    |     |     | +   | 2,3,4,5         | 2              | r              |
| Leucobryaceae                                      |    |     |    |     |     |     |                 |                |                |
| <i>Octoblepharum albidum</i>                       |    | +   |    |     |     |     | 3,4             |                | t              |
| Macromitriaceae (= Orthotrichaceae)                |    |     |    |     |     |     |                 |                |                |
| <i>Groutiella tomentosa</i>                        | +  | +   |    |     |     |     | 3,4             |                | r              |
| <i>Macromitrium stellulatum</i>                    | +  |     |    |     |     |     | 3,4             |                | r              |
| Meteoriaceae                                       |    |     |    |     |     |     |                 |                |                |
| <i>Papillaria nigrescens</i>                       | +  | +   |    |     |     |     | 3,4,5           |                | r              |
| <i>Zelometeorium patens</i>                        | +  | +   |    |     |     | +   | 1,2,3,4,5       | 1,2            | p              |
| <i>Zelometeorium patulum</i>                       | +  | +   |    |     | +   |     | 1,2,3,4,5       | 1              | p              |
| Neckeraceae                                        |    |     |    |     |     |     |                 |                |                |
| <i>Neckeropsis disticha</i>                        |    | +   |    |     |     |     | 1               |                | f              |
| <i>Neckeropsis undulata</i>                        | +  | +   |    | +   | +   | +   | 1,2,3,4,5       | 1,2            | f              |
| Pilotrichaceae                                     |    |     |    |     |     |     |                 |                |                |
| <i>Actinodontium</i> cf. <i>sprucei</i>            | +  |     |    |     |     |     | 3               |                | r              |
| <i>Lepidopilum amplirete</i>                       | +  | +   |    |     |     |     | 1               |                | m              |
| <i>Jaegerina scariosa</i>                          |    | +   |    |     |     |     | 1,2             |                | f              |
| Pterobryaceae                                      |    |     |    |     |     |     |                 |                |                |
| <i>Henicodium geniculatum</i>                      | +  | +   |    |     |     | +   | 3,4,5           | 2              | f              |
| <i>Hildebrandtiella guyanensis</i>                 | +  | +   |    |     |     | +   | 2,3,4,5         | 2              | f              |
| <i>Orthostichopsis</i> cf. <i>tenuis</i>           | +  |     |    |     |     |     | 2               |                | f              |
| <i>Pirella pohlii</i>                              | +  | +   |    |     |     |     | 1,2,3           |                | f              |
| Racopilaceae                                       |    |     |    |     |     |     |                 |                |                |
| <i>Racopilum tomentosum</i>                        | +  | +   |    |     |     |     | 1,2,3           |                | m              |
| Sematophyllaceae                                   |    |     |    |     |     |     |                 |                |                |
| <i>Sematophyllum subpinnatum</i>                   | +  | +   |    | +   | +   | +   | 3,4,5           | 1,2,3          | m              |
| <i>Taxithelium planum</i>                          |    | +   |    |     |     |     |                 | 1              | m              |
| Thamnobryaceae                                     |    |     |    |     |     |     |                 |                |                |
| <i>Pinnatella minuta</i>                           | +  | +   |    |     |     |     | 1,2,3           |                | f              |
| <i>Porotrichum lindigii</i>                        | +  | +   |    |     |     |     | 3,5             |                | f              |
| Thuidiaceae                                        |    |     |    |     |     |     |                 |                |                |
| <i>Cyrtohypnum sharpii</i>                         | +  | +   |    | +   | +   |     | 1               | 1              | m              |

**Table 2.** Species richness of corticolous bryophytes in neotropical rain forests. (1) Cornelissen & ter Steege (1989); (2) Montfoort & Ek (1990); (3) Wolf (1993b); (4) this study.

|                                                 | Number of trees sampled | Mosses | Liverworts | Total (bryophytes) |
|-------------------------------------------------|-------------------------|--------|------------|--------------------|
| Guyana; lowland dry rain forest (1)             | 11                      | 28     | 53         | 81                 |
| Guyana; lowland moist rain forest (1)           | 5                       | 28     | 60         | 88                 |
| French Guiana; lowland moist rain forest (2)    | 4                       | 43     | 61         | 104                |
| Bolivia; submontane rain forest, 600–650 m (4)  | 6                       | 32     | 48         | 80                 |
| Colombia; lower montane rain forest, 1500 m (3) | 4                       | 22     | 36         | 58                 |

characteristic of tropical lowland and submontane rain forests (Cornelissen & ter Steege 1989, Kürschner & Frey 1999, Kürschner & Parolly 1998). The data on species richness and growth forms clearly indicate that the rain forests of the Alto Beni are similar to other tropical rain forests in terms of their bryophyte assemblages.

**Vertical distribution** Growth forms were rather evenly distributed over the trees with exception of rough mats which occurred almost exclusively in the canopy (Table 1). The preference of rough-mat species for canopy branches was also observed in earlier studies (e.g. Cornelissen & ter Steege 1989) and reflects their adaptation to well-illuminated substrates.

Based on their occurrence in the Johansson zones in primary forest, epiphytic species may be habitat specialists (occurring only in one or two zones, or in three continuous ones) or habitat generalists (occurring in three or more zones). Specialists may be further subdivided into 'sun epiphytes' (occurring in Johansson zones 3–5) and 'shade epiphytes' (largely restricted to the understory; Johansson zones 1–2).

About three-quarters of the bryophyte species in the submontane forests of the Alto Beni were specialists, the majority of them sun epiphytes (Table 1). *Archilejeunea auferiana*, *Cololejeunea lanciloba*, *Leptolejeunea exocellata*, *L. elliptica*, *Diplasiolejeunea unidentata* and *Syrhopydon parasiticus* grew exclusively on twigs in the outer canopy whereas *Leptoscyphus porphyrius* and *Bazzania phyllobola* were exclusive to the thicker canopy branches covered by organic material. Shade epiphytes included several mosses (most of them pleurocarps) growing exclusively on the trunk bases: *Chrysohypnum diminutivum*, *Cyrtohypnum sharpii*, *Fissidens* sp., *Lepidopilum amplirete* and *Rhynchostegium* sp. Among the generalists the most common ones, found in all five Johansson zones,

were the moss *Neckeropsis undulata* and the liverworts *Bryopteris filicina*, *Cheilolejeunea clausa*, *C. trifaria*, *Lepidolejeunea eluta* and *Lopholejeunea subfusca*.

Species richness was highest in the lower (43 spp.) and middle canopy (44 spp.). Nearly 45% of the species were sun epiphytes, 31% were shade epiphytes and 24% were generalists (Table 1). The high percentage of species restricted to the canopy is corroborated by earlier findings in lowland and montane rain forests of the Guianas and Costa Rica (Cornelissen & Gradstein 1990, Gradstein *et al.* 1990, 2001b).

#### Comparison between forest and fallows

**Species richness** Twelve trees in the fallow plots yielded a total of 61 species (50 liverworts, 11 mosses) in 13 families, as compared with 80 species (48 liverworts, 32 mosses) in 26 families occurring on only half the number of forest trees (Table 1). Using the Chao 1 formula, estimated total number of bryophytes is 94 species in forest and 75 species in fallows. Thus, sampling completeness was 85% for forest species and 81% for fallow ones, indicating that sampling had been reasonably representative.

Forest plots had many more species of moss than fallow plots while liverwort species richness in forest plots was only slightly higher than in 10–15-y-old fallows (Table 6). Very young, 4-y-old fallows were very poor in species. Less than half of the species (45%) were shared by the forest and fallows, 35 species were exclusive to the forest and 16 to the fallows. In conclusion, bryophyte species diversity in the forest was higher than in the fallows, especially in terms of mosses, but the fallows had some species that did not occur in the forest.

**Growth forms** The fallows are characterized by a significantly higher percentage of smooth-mat species (72%) as compared with the forest (52%), and by a decrease of other growth types (Table 3). The smooth-mat growth form of epiphytic bryophytes is usually interpreted as an adaptation to smooth bark. Since bark structure of the sampled trees was mostly smooth in forest as well as fallow sites, we propose that the increase of smooth mats in the fallows reflects the warmer, drier microclimate in these environments (see below). The increased tendency for bryophyte species to grow appressed to the substrate

**Table 3.** Distribution of growth-form types (in percentages) in submontane rain forest and fallows in Bolivia.

| Growth-form  | Forest | Fallows |
|--------------|--------|---------|
| Smooth mat   | 51     | 72      |
| Fan and tail | 21     | 15      |
| Rough mat    | 14     | 8       |
| Turf         | 9      | 2       |
| Pendant      | 5      | 3       |

in the fallows as compared with the forest, may thus be interpreted as a strategy to avoid desiccation.

**Vertical distribution.** Whereas species richness in the forest was highest in the canopy (zones 3–4), in the fallows it was highest in the understorey (zones 1–2). More than 90% of the species (57) in the fallows occurred in zones 1–2, less than 30% (18) occurred in zones 4–5. Bryophyte cover in the fallows is also much higher in the understorey than in the canopy, while in the forest it is highest in the canopy. On trunk bases (zone 1) cover was 15–20% in forest and 20–75% in fallows, on upper portions of trunks and on branches (zones 3–5) 20–60% in forest and less than 5% in fallows. Indeed, the upper portions of the fallow trees were almost devoid of epiphytes.

Looking at the vertical distribution of the forest species, 36 were sun epiphytes, 25 shade epiphytes and 19 generalists. Of these, 19 sun epiphytes, 7 shade epiphytes and 19 generalists occurred also in the fallows. Thus three-quarters (72%) of the shade epiphytes and almost half (46%) of the sun epiphytes, but none of the generalists were absent in the fallows. This result supports the hypothesis that the shade epiphytes of the forest are most

strongly affected by deforestation and have the least capability to re-establish in secondary vegetation, being particularly sensitive to desiccation (Costa 1999, Gradstein 1992a, b). Several sun epiphytes (e.g. *Holomitrium arboreum*, *Leptoscyphus porphyrius*, *Omphalanthus filiformis* and *Bazzania phyllobola*) were also affected although to a lesser extent than the shade epiphytes, whereas generalists were not affected. Apparently, species with smaller niches (= specialists) have less chance to survive deforestation and are more prone to local extinction than those with wider niches. It thus appears that niche width, as expressed by vertical distribution along the tree, may be a useful parameter to determine the vulnerability of corticolous bryophyte species to habitat change.

A comparison of the vertical distributions of species shared by the forest and the fallows shows a striking species shift towards lower relative heights on trees in the fallows (Figures 2, 3). Thus, sun epiphytes and generalists occurred in the fallows mainly on the tree bases and lower portion of the trunks (zones 1–3). Exceptions are the sun epiphytes *Frullania riojaneirensis*, *Frullanoides densifolia* and *Cololejeunea lanciloba*, and the generalists *Lopholejeunea subfusca* and *Plagiochila raddiana*, which

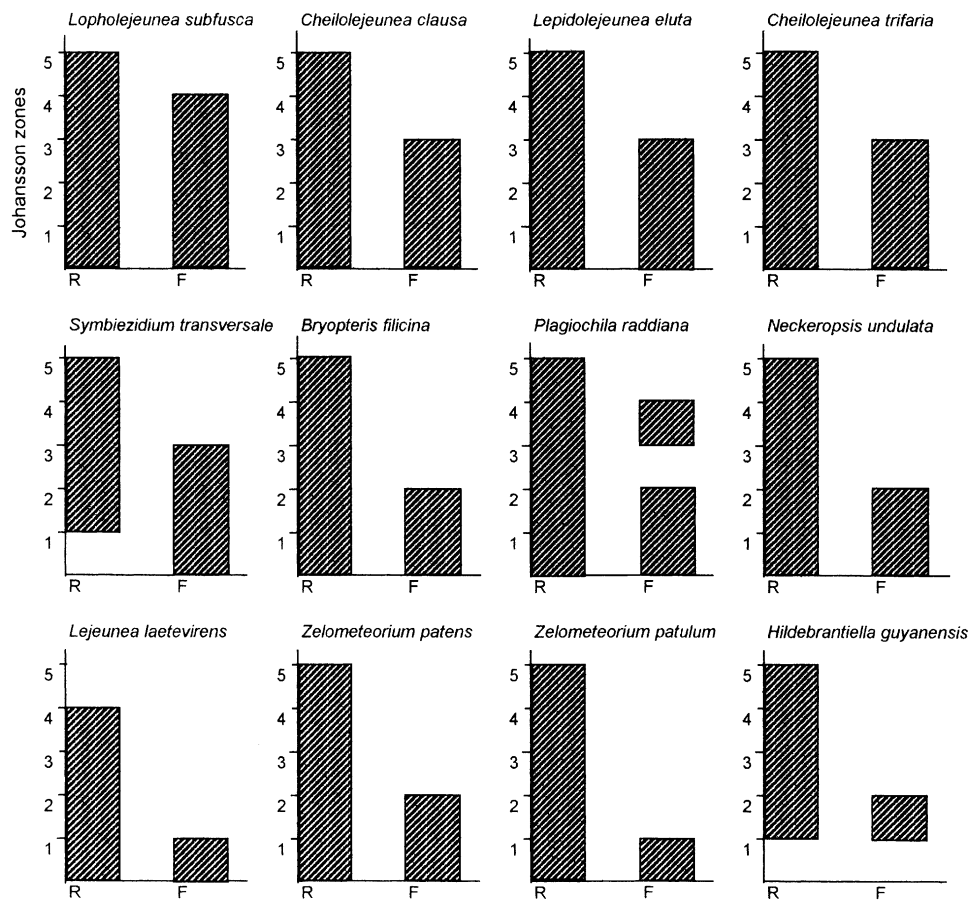


Figure 2. Vertical distribution of sun epiphytes in the submontane rain forest and fallows. R, rain forest; F, fallows; 1–5: Johansson zone.

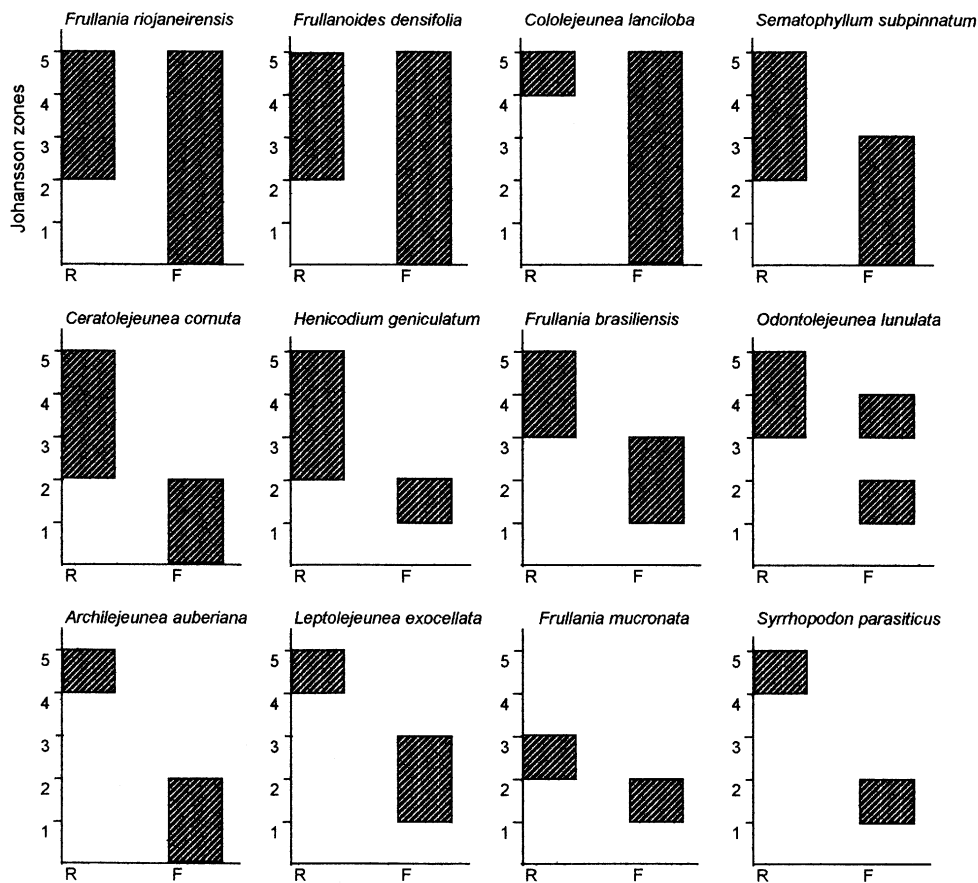


Figure 3. Vertical distribution of generalists in submontane rain forest and fallows. R, rain forest; F, fallows; 1–5: Johansson zone.

extend from the tree base to (almost) the outer canopy in the fallows. The latter five species appear to be the most drought tolerant among the forest species in the study area.

The shift of forest species to lower heights in the fallows is also evidenced by the prevalence of rough mats, fans and tails in fallow zones 1–2 and the high floristic similarity (0.4–0.5) between forest zones 3–5 and fallow zones 1–2 (Tables 1 and 4), and corresponds well with measured microclimatic conditions (Tables 4 and 5). Mean daily maximum air temperatures at 2 m height in the fallow was about 1.5 °C higher, mean minimum relative air humidity about 7.5% lower, and mean maximum vapour pressure deficit almost two times higher than in the forest. Microclimatological conditions at 25 m height in the forest, however, are rather similar to those at 2 m height in the fallow (Table 5). The drier and warmer microclimate in the fallows as compared with the forest, caused presumably by the lower and more open canopy, may explain why sun epiphytes and generalists occur at low heights in the fallows and why shade epiphytes are mostly lacking. The distributional shifts, already hinted at by Gradstein (1992b) and He (1999), are demonstrated here for the first time by comparative analysis of vertical

species distribution and microclimatic measurements in forest and fallows.

**Bryophyte succession in fallows** The selected trees in 4-y-old fallow had only 10 bryophyte species, all of them Lejeuneaceae (Tables 1 and 6). These pioneer species are characterized by small size, prostrate habit, growth in dense patches and frequent vegetative reproduction (Cornelissen & ter Steege 1989). Some of them occur also in the forest as sun epiphytes (*Frullanoides densifolia*, *Lopholejeunea subfusca*), others are apparently exclusive to young fallows (*Aphanolejeunea camilli*, *Lejeunea trinitensis*, *L. caespitosa*).

Ten-y-old fallows had four times more species (37)

Table 4. Sørensen index of corticolous bryophytes in submontane rain forest and fallows in Bolivia. R: Johansson zone in rain forest. F: Johansson zone in fallows.

| Johansson zone | 1F   | 2F   | 3F   | 4F   | 5F |
|----------------|------|------|------|------|----|
| 1R             | 0.41 | 0.24 | 0.12 | 0    | 0  |
| 2R             | 0.39 | 0.28 | 0.16 | 0.03 | 0  |
| 3R             | 0.43 | 0.37 | 0.20 | 0.04 | 0  |
| 4R             | 0.42 | 0.45 | 0.25 | 0.04 | 0  |
| 5R             | 0.39 | 0.50 | 0.23 | 0.05 | 0  |



**Table 5.** Comparison of microclimatological factors measured over 40 d (rainy season) in fallow, rain forests (lower trunk, lower canopy) and Sapecho village. t, mean daily maximum air temperature; RH, mean minimum relative air humidity; vpd, mean maximum vapour pressure deficit (hPa, hectoPascal; 1 hPa, 1 millibar).

| Site                     | t<br>(°C) | RH<br>(%) | vpd<br>(hPa) |
|--------------------------|-----------|-----------|--------------|
| Sapecho                  | 31.6      | 58.7      | 20.3         |
| Fallow 15-y-old          | 26.3      | 81.9      | 6.5          |
| Rain forest PI (trunk)   | 24.8      | 89.6      | 3.4          |
| Rain forest PI (canopy)  | 26.5      | 76.3      | 8.6          |
| Rain forest PII (trunk)  | 24.8      | 89.4      | 3.5          |
| Rain forest PII (canopy) | 26.2      | 78.3      | 8.4          |

**Table 6.** Species richness of corticolous bryophytes in submontane rain forest and fallows in Bolivia. For abbreviations see Table 1.

| Vegetation type | Mosses | Liverworts | Total |
|-----------------|--------|------------|-------|
| Rain forest PI  | 22     | 37         | 59    |
| Rain forest PII | 29     | 39         | 68    |
| Fallow 15-y-old | 8      | 31         | 39    |
| Fallow 12-y-old | 6      | 30         | 36    |
| Fallow 10-y-old | 5      | 32         | 37    |
| Fallow 4-y-old  | 0      | 10         | 10    |

than 4-y-old ones and were inhabited by numerous Lejeuneaceae (27), some Jubulaceae and Plagiogochilaceae, as well as the first mosses (*Syrrhophodon parasiticus*, *Neckeropsis undulata*, *Sematophyllum subpinnatum*, *Chrysohypnum diminutivum*, *Cyrtohypnum sharpii*). Forest species establishing in 10-y-old fallows include the generalists *Cheilolejeunea trifaria*, *Lejeunea phyllobola* and *Symbiezidium transversale* and common sun epiphytes such as *Anoplolejeunea conferta*, *Ceratolejeunea cornuta*, *Diplasiolejeunea unidentata* and *Frullania riojaneirensis*.

Species numbers did not increase significantly in the older fallows, 12-y-old fallow having 36 species and 15-y-old fallow 39 species. The latter had two further species of mosses (*Hildebrandtiella guyanensis* and *Pseudocrypaea dominguiensis*) and the liverwort *Marchesinia robusta*, a shade epiphyte characteristic of primary forest and old secondary forest (Gradstein 1994). The occurrence of the latter species is suggestive of the importance of older fallows as a habitat for vulnerable, desiccation-intolerant forest species.

Data on succession of epiphytic bryophytes in tropical rain forest are very scarce. Chapman & King (1983) showed that in subtropical rain forests of Australia few bryophytes could return after 25 y. Similar data were reported from south-eastern Brazil by Costa (1999). Sillett *et al.* (1995) found that on isolated, remnant forest trees only about 50% of the original species remained 30 y after clear felling. Our data indicate that about half of the rain-forest species, especially liverworts, may re-establish in 10–15-y-old fallows. The great majority of these are drought-tolerant specialists of the forest canopy and generalists, a small minority are shade epiphytes. The general

composition of the epiphytic bryophyte flora of the fallows thus differs considerably from that of the forest.

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