

Bryophyte diversity on tree trunks in montane forests of Central Sulawesi, Indonesia

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Abstract: Previous studies have shown that submontane forests of Sulawesi harbor a very rich bryophyte flora, with more than 150 species occurring on eight canopy trees. We explore the relationships of trunk base bryophyte communities with elevation and tree characteristics (tree diameter, bark roughness) in montane forests of Sulawesi. The study showed that submontane, lower montane and upper montane forests of Sulawesi are characterized by very different bryophyte taxa. Calymperaceae, Fissidentaceae, Hypopterygiaceae, Lejeuneaceae, Leucobryaceae, Lophocoleaceae, Meteoraceae, Neckeraceae, Porellaceae, Pterobryaceae, Radulaceae and Thuidiaceae are mainly found at low elevations, while Herbertaceae, Lepidoziaceae, Mastigophoraceae, Scapaniaceae, Schistochilaceae and Trichocoleaceae predominate at high elevations. Lejeuneaceae are the most important family in submontane and lower montane forests in terms of number of species, and Lepidoziaceae in upper montane forest. Plagiochilaceae are prevalent in lower montane forest. In general, species richness of liverworts increases towards higher elevation whereas moss richness decreases. Similar trends are observed elsewhere in the Tropics. Trunk community similarity decreases with distance and is about 25% between Sulawesi and Borneo, and virtually nil across continents. A few species showed a significant preference for rough bark but none for smooth bark. In general, trees with rough bark had more species than those with smooth bark. Trunk diameter correlated with the distribution of a few species but not with community composition or species richness. Our data are first statistically-supported evidence for bark roughness and trunk-diameter specificity of bryophyte diversity in tree-species rich tropical forest.

Keywords: bark roughness, epiphytic bryophyte diversity, Indonesia, Sulawesi, tropical montane forest, trunk diameter.

Introduction

Bryophytes are an important component of moist tropical montane forests and may play a significant role in the water balance and nutrient cycling of these forests (Pócs 1980, Nadkarni 1984, Frahm 1990, Hofstede et al. 1994; but see Hölscher et al. 2004). The great variety of microhabitats and the permanently humid microclimate of these forests favor the growth of bryophytes and of other organisms, resulting in high species diversity and biomass (Gradstein et al. 2008). Much work has been done on the diversity and ecology of tropical montane forest bryophytes, especially in tropical America and Africa (e.g., Pócs 1982; Frahm & Gradstein 1991; Wolf 1993a, b, c, Frahm 1994, Kürschner 1995, Kürschner & Parolly 1998, Gradstein et al. 2001, Holz et al. 2002, Acebey et al. 2003, Parolly & Kürschner 2005, León-Vargas et al. 2006, Mandl et al. 2008). In contrast, studies from Southeast Asia are few; Frahm (1990) and Kürschner (1990) studied biomass resp. community composition of bryophytes along an elevational gradient on Mt. Kinabalu

(Sabah), and Ariyanti et al. (2008) and Sporn et al. (2009a, b) analysed the bryophyte diversity of submontane rain forests and cacao plantations of central Sulawesi, Indonesia. These studies have shown the overriding importance of microclimate as a driver of epiphytic bryophyte distribution. In addition, tree bark features play a role although this has rarely been demonstrated in tropical forests (e.g., Frahm, 1990), most evidence coming from temperate forests (e.g., Barkman 1958, McCune et al. 2000, Szövényi et al. 2004).

This paper deals with the diversity of trunk-inhabiting bryophytes in montane forests of central Sulawesi, Indonesia. With a total land surface of about 182,870 km² (Whitten et al. 2002), Sulawesi is the fourth largest island of Indonesia. Phytogeographically it is part of the Eastern Malesian Province, together with the Moluccas and New Guinea. The island has a rich flora and fauna, and more than 5000 species of flowering plants have been recorded of which about 15% are endemic (Roos et al. 2004). Much of Sulawesi's rich biodiversity is seriously threatened by

deforestation, which has resulted in an 80% loss of primary forest (Cannon et al. 2007). Only a small part of Sulawesi's forests remain, mostly at higher elevation in the mountains, and are preserved in protected areas.

For bryophytes, Sulawesi is one of the least explored major islands of the Malesian archipelago. A recent checklist (Gradstein et al. 2005) listed 476 species, which was significantly less than had been recorded from Sumatra, Java, Borneo, the Philippines or New Guinea. Since the appearance of the catalogue, the first author and his students did considerable collecting in central Sulawesi in the framework of the "STORMA" project of the university of Göttingen and the universities of Bogor (IPB) and Palu (UNTAD), Indonesia (Ariyanti & Gradstein 2007, Ariyanti et al. 2008, 2009, Sporn et al. 2009a, b). In addition, Eggers (2006) collected bryophyte species on Sulawesi, most of them epiphylls. These recent activities have raised the number of species known from Sulawesi by almost 40%, to 653 (414 mosses, 239 liverworts). We expect a further increase when other parts of the island are explored.

The bryophyte flora of the montane forests of Sulawesi is very rich. Sporn et al. (2009b) recorded 146 species on eight trees in a submontane forest at 1000 m, which is the highest number recorded in submontane tropical forest. Unusually high species richness in these forests has also been recorded for trees and terrestrial herbs (Kessler et al. 2005, Culmsee & Pitopang 2009, Ciczuzza et al. in press), and underlines the importance of the Malesian region as a global biodiversity hotspot (Myers et al. 2000). The mossy cloud forests of Sulawesi, above 2000 m, stand out by the high concentration of eastern Malesian liverwort species, about seven times more than western Malesian ones (Ariyanti & Gradstein 2007). The commonness of eastern Malesian taxa in these forests reflects the position of Sulawesi east of Wallace's line, and lends bryological support to this classical biogeographical boundary in the Malesian archipelago.

The goal of this study was to investigate the bryophyte diversity on tree trunks in montane rain forest of Sulawesi. We explore the relationships with elevation and tree characteristics (tree diameter, bark roughness) in order to increase our understanding of the bryophyte diversity of the mountain forests of Southeast Asia.

Materials and Methods

Study area. The study site was in an old-growth, lower montane rain forest at 1400 m a.s.l. in Lore Lindu National Park, near Bariri village, Sulawesi, 1°39.5' S, 120°10.4' E (Fig. 1). The site is located on

a level plateau near a 70 m tall meteorological tower. Mean annual temperature is 19.1°C and annual rainfall is about 1975 mm, with a short season of about two months with less than 100 mm rainfall (Fig. 2). The forest is largely undisturbed except for some minor disturbance near the tower. The forest canopy is on average 25 m high and very dense, with canopy closure exceeding 90%. The most important tree families are Fagaceae, Myrtaceae, Eleocarpaceae and Lauraceae; rattan palms are common in the understory. Tree richness is about 55 species per 0.25 hectare (Culmsee & Pitopang 2009).

Bryophytes occur on bark, living leaves and dead wood but lack on the soil, which is covered by a dense layer of dead leaves. The forest is not very mossy, bryophyte cover on trunk bases averaging 20–30% (to 75% max.). Thick branches in the tree crowns are covered by mats of *Macromitrium*, *Herbertus piliferus*, *Chandonanthus hirtellus*, *Thysananthus convolutus* and *Schiffneriolejeunea tumida*.

Sampling. Bryophytes were collected on the trunk bases (0–2 m high; whole trunk base sampled) of eighteen randomly selected trees in an area of about 0.72 ha of forest. Number of trees sampled follows Ariyanti et al. (2008; 18 trees >20 dbh). The forest area consisted of three adjacent 40 x 60 m² plots established for the purpose of a tree inventory by the second author (Culmsee & Pitopang, 2009). Trunk

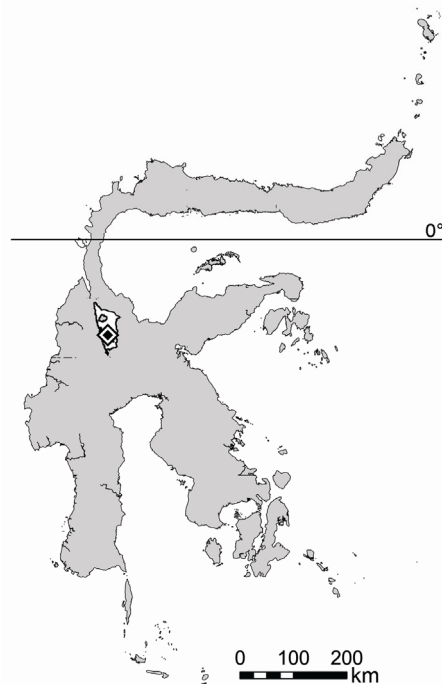


Figure 1. Location of the Bariri forest study site (diamond) in Lore Lindu National Park, Central Sulawesi, Indonesia (Universal Transverse Mercator projection 51 South).

Table 1. Characteristics of sampled trees in the investigated lower montane forest near Bariri, Central Sulawesi.

Tree species number	Species name	Family	Sample number	dbh (in cm)	Bark
1	<i>Calophyllum</i> sp.	Clusiaceae	8, 17	26.5, 39.0	rough
2	<i>Canarium trigonum</i> H.J.Lam	Burseraceae	2	92.0	rough
3	<i>Castanopsis acuminatissima</i> (Blume) Rheder	Fagaceae	4, 5	33.2, 38.8	rough
4	<i>Chionanthus polygamus</i> (Roxb.) Kiew	Oleaceae	3, 9	44.5, 14.4	smooth
5	<i>Elaeocarpus culminicola</i> Warb.	Elaeocarpaceae	10	53.2	smooth
6	<i>Gastonia serratifolia</i> (Miq.) Philipson	Araliaceae	15, 16	21.2, 20.3	smooth
7	<i>Lithocarpus elegans</i> (Blume) Hatus. ex Soepadmo	Fagaceae	18	23.7	rough
8	<i>Lithocarpus menadoensis</i> (Koord.) Soepadmo	Fagaceae	6, 13	50.3, 30.0	rough
9	<i>Macadamia hildebrandii</i> Steenis	Proteaceae	7	35.9	smooth
10	<i>Persea rimosa</i> Zoll. ex Meisn.	Lauraceae	1	68.0	smooth
11	<i>Pouteria firma</i> (Miq.) Baehni	Sapotaceae	11	56.7	smooth
12	<i>Streblus glaber</i> (Merr.) Corner subsp. <i>glaber</i>	Moraceae	12	32.5	smooth
13	<i>Syzygium</i> sp.	Myrtaceae	14	25.0	smooth

diameter at breast height (dbh) of the sampled trees varied between 14 and 92 cm. We did not distinguish between small trees (10-20 cm) and large trees (>20 cm) (Ariyanti et al., 2008) because the latter authors found no correlations between bryophyte diversity and the two size classes. To maximize information on species diversity, we sampled tree species that differed in bark texture (rough, smooth). The 18 sampled trees belonged to 13 different species, including eight with smooth bark and five with rough bark (Table 1).

On each sampled trunk we estimated total bryophyte cover and relative species abundance (dominant, frequent, rare). Bryophyte specimens were identified using recent taxonomic treatments (see Gradstein et al. 2005) and herbarium material. Vouchers were deposited in BIOT, CEB and GOET. Nomenclature follows the catalogue of the bryophytes of Sulawesi (Gradstein et al. 2005, Ariyanti et al. 2009).

Data analysis. We tallied species richness for all bryophytes and for mosses and liverworts separately. Commonness of bryophyte species was determined based on the number of trees on which the species was present. We constructed accumulation curves for observed and estimated species richness to assess the completeness of our sampling, using *vegan* (Oksanen et al. 2008) implemented in *R* (R Development Core Team 2008). Estimated species richness was calculated with *EstimateS* (Colwell 2005).

Classification of the trunk samples was performed by TWINSpan analysis (Hill 1979, Hill & Šmilauer 2005) using three pseudospecies cut-levels with equal weight, two divisions in maximum and with seven as the minimum group size. Principal Component Analysis (PCA) was applied because length of gradient in DCA was 3.128 (including all species). Number of samples was 18, total number of species 58 and number of active species 42 (sixteen rare

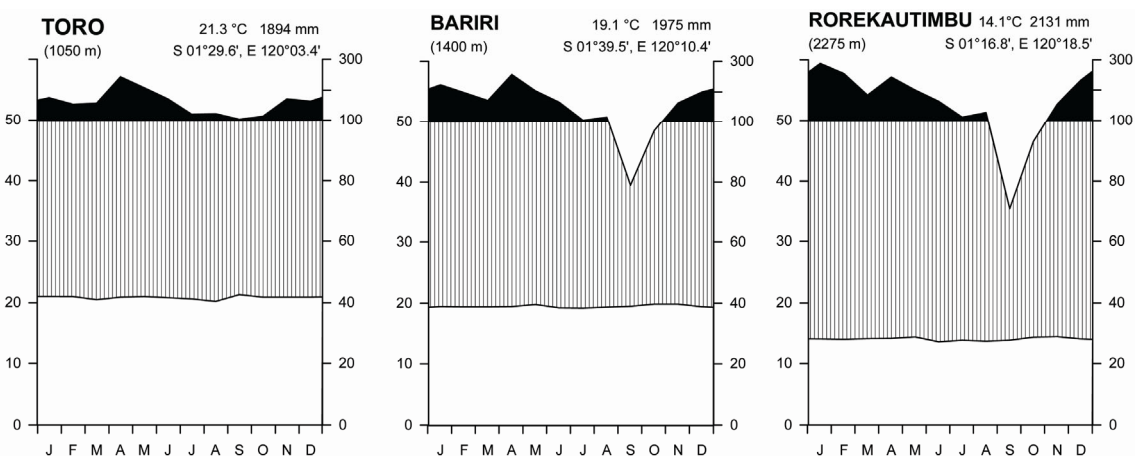


Figure 2. Climate diagrams of submontane forest (Toro village), lower montane forest (Bariri village) and upper montane forest (Mt. Rorekautimbu) in Lore Lindu National Park, Central Sulawesi. Climate data extracted from the WorldClim model (Hijmans et al. 2005; WorldClim 2006).

Table 2. TWINSPAN community classification of bryophyte samples from 18 tree bases in the investigated lower montane forest near Bariri, Central Sulawesi. Assemblage characteristic species in bold face. Tree species number as in Table 1. * species new to Sulawesi.

Bryophyte assemblage	<i>Syrrhopodon tristichus</i> - <i>Bazzania vittata</i> assemblage					<i>Homaliodendron exiguum</i> assemblage								<i>Schistochila</i> <i>aligera</i> assemblage				
Sample number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Tree species	10	2	4	3	3	8	9	1	4	5	11	12	8	13	6	6	1	7
Bark characteristics (rough, smooth)	s	r	s	r	r	r	s	r	s	s	s	s	r	s	s	s	r	r
Tree d.b.h. (in cm)	68	92	45	33	39	50	40	27	14	53	57	33	30	25	21	20	39	24
Bryophyte cover (in %)	?	?	15	25	20	30	?	40	60	15	?	?	?	25	30	70	15	40
No of bryophyte species	12	10	15	9	21	10	17	20	18	17	16	11	16	16	10	12	10	17
<i>Lejeunea obscura</i> Mitt.	1	.	1	2	.	2	1	.	2	.	.	1	.	.
<i>Cheilolejeunea ceylanica</i> (Gottsche) R.M. Schust. &	1	.	1	2	2	.	.	.	1
<i>Drepanolejeunea ternatensis</i> (Gottsche) Steph.	1
<i>Isocladia</i> sp.	1
<i>Lepidolejeunea bidentula</i> (Steph.) R.M. Schust.	1
<i>Plagiochila javanica</i> (Sw.) Dumort.	2
<i>Plagiochila</i> sp. A	2	2	3
<i>Plagiochila</i> sp. C	2
<i>Plagiochila</i> sp. D	2
<i>Trachyloma indicum</i> Mitt.	1
<i>Exostratum sullivantii</i> (Dozy & Molck.) L.T. Ellis	2	2
<i>Homaliodendron exiguum</i> (Bosch. & Sande Lac.) M.	1	1	1	2	2	2	2	1	1	2
<i>Leucobryum albidum</i> Dozy & Molck.	1
<i>Lopidium struthiopteris</i> (Brid.) M. Fleisch.	1	.	.	2	.	.	1
<i>Plagiochila</i> sp. B	3
* <i>Psiloclada clandestina</i> Mitt.	1
<i>Radula javanica</i> Gottsche	1	.	.	.	1	.	1
* <i>Syrrhopodon spiculosus</i> W.J. Hook. & Greville	2
<i>Metzgeria leptoneura</i> Spruce	.	1	1	.	.	.	1
<i>Trichocolea tomentella</i> (Ehrh.) Dumort.	1	1	.	1	1
* <i>Acromastigum divaricatum</i> (Gottsche et al.) A. Evans	.	1	1	1	1
<i>Chiloscyphus muricatus</i> (Lehm.) R.M. Schust. & J.J. Engel	.	.	1	.	1	.	.	.	1	.	.	1	1
<i>Spruceanthus polymorphus</i> (Sande Lac.) Verd.	1	.	.	.	1
<i>Bazzania</i> sp.	.	.	1
<i>Bazzania tridens</i> (Reinw. et al.) Trevis.	2	2	1	1
<i>Leucobryum aduncum</i> Dozy & Molck.	1	1	1	.	1	.	1	1
<i>Syrrhopodon aristifolius</i> Mitt.	.	.	.	2
<i>Syrrhopodon tristichus</i> Nees ex Schwaegr.	1	2	2	2	2	2	3	.	.	1
<i>Acroporium diminutum</i> (Brid.) M. Fleisch.	2	.	1	2	2	.	.	1	.	.	.	2	2	1	1	.	.	.
<i>Pyrrhobryum spiniferum</i> (Hedw.) Mitt.	2	.	1	.	1	3	.	2	1
* <i>Bazzania intermedia</i> (Lindenb. & Gottsche) Trevis.	.	1	.	.	3	3	.	.	1	3	1	1	3	1	2	2	.	.
<i>Heteroscyphus coalitus</i> (Hook.) Schiffn.	.	.	.	1	.	.	1	.	1	.	.	1	1
<i>Leucobryum javense</i> (Brid.) Mitt.	1	1	1	.	.	1	1
<i>Leucoloma molle</i> (Müll.Hal.) Mitt.	3	.	1	1	2	.	2	2	1	3	1	.	3	.	1	.	3	.
<i>Leucophanes octoblepharoides</i> Brid.	.	1	2	2	2	3	.	2	.	2	1	1	2	2	1	.	2	.
<i>Pelekium</i> sp.	1	.	.	.	1	1	1	1	1	.	1	.	1	.	1	.	.	.
<i>Trismegistia rigida</i> (Mitt.) Broth.	1	1	1	1	.	.	.	1
<i>Bazzania vittata</i> (Gottsche) Trevis.	.	.	2	2	1	2	.	.	1	1
<i>Plagiochila frondescens</i> (Nees) Lindenb.	2	.	2	3	2	.	2	1	.	2	.	.	.	1	.	.	1	1
<i>Symphysodontella cylindracea</i> (Mont.) M. Fleisch.	3	3	3	.	2	3	.	2	3	.	2	.	.	1	.	2	1	3
<i>Lejeunea discreta</i> Lindenb.	1	.	2	2	.	.	1	.	.	.	2	2
<i>Lejeunea sordida</i> (Nees) Nees	1	.	.	.	1	.	.	1	.	.
<i>Metalejeunea cucullata</i> (Reinw. et al.) Grolle	1	.	1	1	1	1	2
<i>Plagiochila sandei</i> Dozy ex Sande Lac.	1	1
<i>Acroporium</i> sp.	1	1	.	1	1	1	1	.	1
<i>Harpalejeunea filicuspis</i> (Steph.) Mizut.	.	2	1	.	2	.	.	.	1	.	.	.	1	1	.	.	2	2
* <i>Kurzia gonyotricha</i> (Sande Lac.) Grolle	1	.	1	1	.
<i>Thysananthus spathulistipus</i> (Reinw. et al.) Lindenb.	.	.	1	.	2	1	1	2	.	.
<i>Plagiochilium oppositum</i> (Reinw. et al.) S. Hatt.	.	.	1	1	.	.	1	2	1	1	.	2
<i>Schistochila aligera</i> (Nees & Blume) J.B. Jack & Steph.	3	.	1	.	.	.	1	.	2	1	2	2
<i>Chiastocaulon dendroides</i> (Nees) Carl	2	3	.	.
<i>Dicranoloma brevisetum</i> (Dozy & Molck.) Paris	2	.	.	1	.	2	2	3
<i>Dicranoloma reflexum</i> (Müll.Hal.) Renaud	1	.	.
<i>Heteroscyphus argutus</i> (Reinw. et al.) Schiffn.	2	2	.	1	.
<i>Heteroscyphus splendens</i> (Lehm. & Lindenb.) Grolle	1	.	.
<i>Sematophyllaceae</i> sp.	1
<i>Ectropothecium</i> sp.	1	2
<i>Zoopsis liukiensis</i> Horik.	1	2

species with only one occurrence were omitted). In order to optimally show dissimilarities between the species compositions of different samples, scaling was focused on inter-sample distances. Indirect gradient analysis was performed using CANOCO 4.5 (Ter Braak & Šmilauer 2002).

Results

Species diversity. In total 58 bryophyte species (35 liverworts, 23 mosses) were collected on the trunk bases of eighteen sampled trees (Fig. 3; Table 2). Five species, *Acromastigum divaricatum*, *Bazzania intermedia*, *Kurzia gonyotricha*, *Psiloclada clandestina* and *Syrrhopodon spiculosus*, were new to Sulawesi and one, *Bazzania vittata*, was previously considered a doubtful record. The number of species per trunk base ranged from 9-21, with an average of 15. The accumulation curve of observed species richness showed little evidence of levelling off (Fig. 3), indicating that we did not sample the total species richness on trunk bases in the study site. Estimated species richness using the incidence-based coverage estimator was 98 species, indicating that sampling completeness was 60%. The rather low sampling completeness is evidenced by the large number of species (36%) collected only once or twice (Table 2). Lejeuneaceae (10 spp.), Plagiochilaceae (9 spp.) and Lepidoziaceae (8 spp.) were the most species-rich groups and accounted for almost half (45%) of the bryophyte flora. The most important moss families were Calymperaceae and Sematophyllaceae, each represented by 5 species. While liverworts were more species-rich than mosses in the study site, mosses were more frequent in terms of number of records per species. *Leucoloma molle* and *Leucophanes octoblepharoides* were the most common species and occurred on 70% of the trees, often with high abundances (Table 2). They were followed by the *Symphysodontella cylindracea* (often with high abundancy), *Homaliodendron exiguum*, *Pelekium* sp., *Acroporium diminutum* and *Syrrhopodon tristichus*. The most common liverworts were *Bazzania intermedia*, *Plagiochila frondescens* and *Harpalejeunea filicuspis*. Scarce species included many liverworts (Table 2).

Species assemblages. Twinspan analysis of the data resolved three species assemblages, the *Syrrhopodon tristichus*-*Bazzania vittata* assemblage (sample nrs. 1-5), the *Homaliodendron exiguum* assemblage (nrs. 6-14) and the *Schistochila aligera* assemblage (nrs. 15-18) (Table 2). The latter two assemblages were recovered upon the first division of the samples, the first one upon the second subdivision. The *Homaliodendron exiguum* assemblage was the most common species assemblage (9 trees) and had 50 species, the other two assemblages were recovered on only 4-5 trees each contained fewer species (ca. 30

each). We found no abiotic characteristics for the three species assemblages; statistical analysis revealed no significant correlations with tree dbh and bark roughness (results not shown).

Species diversity and tree parameters. Ordination by PCA showed that community richness was more or less independent from trunk diameter and correlated only weakly with bark roughness (Fig. 4). Thus, trees

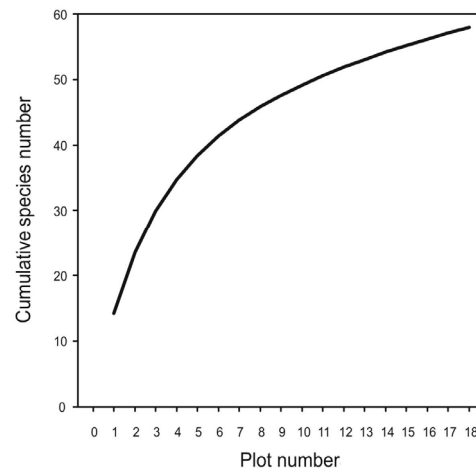


Figure 3. Plot-based species accumulation curve of bryophytes in lower montane rain forest near Bariri in Lore Lindu Park, Central Sulawesi.

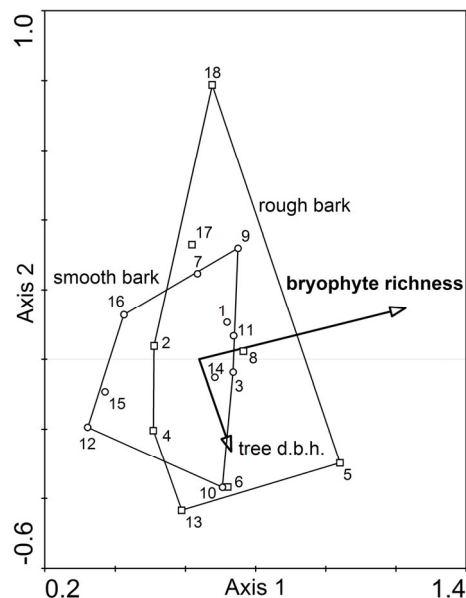


Figure 4. Indirect gradient analysis (PCA) diagram showing the dissimilarity between the species compositions of different samples whereas rare species were omitted from the analysis. Increasing bryophyte richness is indicated. Tree traits (environmental variables) passively projected into the resulting ordination space. Samples on trees with rough bark displayed by quadrates and on trees with smooth bark by circles. d.b.h. = diameter at breast height. Eigenvalues: Axis 1 = 0.436; Axis 2 = 0.087.

with rough (fissured) bark tended to be richer in bryophyte species than those with smooth bark (Fig. 4: envelopes drawn around the two bark type classes). At species level, however, several significant correlations with tree parameters were detected using regression analysis (Figs. 5, 6). The liverworts *Kurzia gonyotricha* and *Harpalejeunea filicuspis*, and the moss *Leucophanes octoblepharoides* showed significant preferences for rough bark, four bryophyte species (*Bazzania tridens*, *Leucobryum aduncum*, *Metzgeria leptoneura*, *Syrrhopodon tristichus*) had a significant preference for large trunks (dbh 30-90 cm), and one species, the liverwort *Lejeunea sordida*, was restricted to small trunks (dbh 15-25 cm). Species with a preference for smooth bark were not detected.

Discussion

Tree bases because of their relatively favorable moisture conditions are a suitable habitat for bryophytes. They are the transition zone between the forest floor and the tree trunk, and may show greater similarity to logs and soil than to the rest of the tree in terms of bryophyte diversity (e.g., Holz et al. 2002, Parolly & Kürschner 2005). Since trunk bases can be studied relatively easily and do not require tree climbing, they have received more attention than the rest of the tree (e.g., Kürschner & Parolly 1998, Drehwald 2005, Ariyanti et al. 2008).

Species richness. In a study of trunk base communities in submontane and lower montane rain forests of Peru and Bolivia, Drehwald (2005) collected on average 45 bryophyte species on ten trees, which agrees quite well with the figures obtained in our study. Significantly higher species richness was recorded in submontane rain forest near

Toro, Lore Lindu National Park, Sulawesi, by Ariyanti et al. (2008 and pers. com.), who found 86 species on the bases of eighteen trunks (>20 cm dbh) in four study plots of about 0.25 ha each. These findings coincide with the unusually high species richness at this site reported by Sporn et al. (2009; 146 spp. on eight whole trees). The high number of species recorded by Ariyanti et al. is surprising because the average number of species per tree was lower than in our study (12 vs. 15) and inventorying was done by analysis of small sample plots (see Gradstein et al. 2003) rather than whole trunk bases. One explanation might be the rather large distance between the study plots of Ariyanti et al. (>500 m), which could have increased habitat heterogeneity and thus species richness. In contrast, our study plots at Bariri were laying directly adjacent to each other and were quite similar in terms of the forest vegetation. Another explanation might be the somewhat different rainfall regimes at the two sites (Fig. 2). Rainfall at Bariri is characterized by a short period of about two month with less than 100 mm rainfall; at Toro, however, rain is rather evenly distributed throughout the year with lack of a drier period. The more permanently rainy conditions at Toro as compared with those at Bariri may have been more beneficial to the bryophyte flora, and may have enhanced the unusually high bryophyte diversity in the submontane forest at the former location. It should be noted that sampling completeness was rather low in both studies, viz. ca. 65% in Toro (Ariyanti et al. 2008 and pers. com.; based on 18 large trees) and 60% in Bariri (this study). These percentages are lower than those recorded from neotropical lowland and montane rain forests, where 5 trees in one hectare may yield a sampling completeness of ca. 80% (Gradstein et al. 2003).

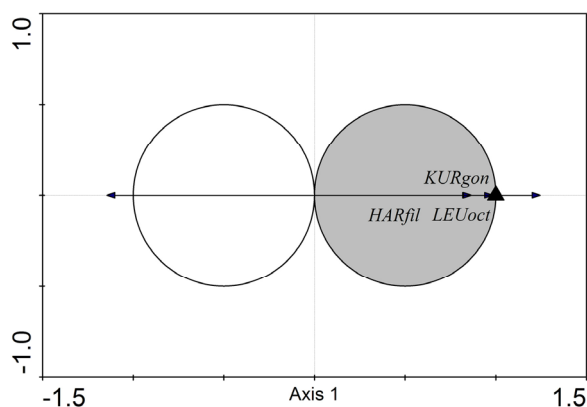


Figure 5. Bryophyte species having significantly positive correlation with rough bark (grey circle area) demonstrated in a t-value biplot (regression analysis, RDA). *KURgon* = *Kurzia gonyotricha*; *HARfil* = *Harpalejeunea filicuspis*; *LEUoct* = *Leucophanes octoblepharoides*. Open circle: smooth bark correlation area. Axis 1: t-value of regression coefficient = 4.551.

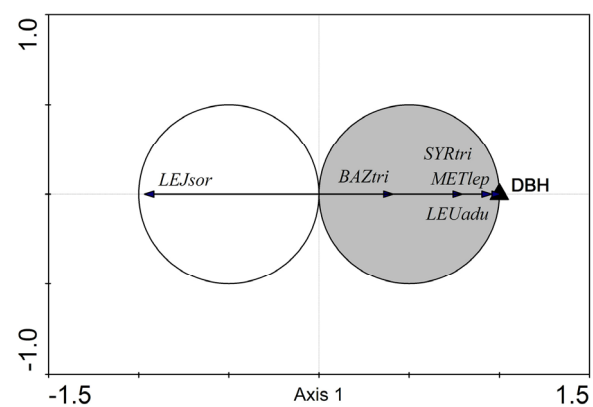


Figure 6. Bryophyte species having a significantly positive (grey circle area) or negative (open circle) correlation with tree d.b.h. as demonstrated in a t-value biplot (regression analysis, RDA). *LEJsor* = *Lejeunea sordida*; *BAZtri* = *Bazzania tridens*; *SYRtri* = *Syrrhopodon tristichus*; *METlep* = *Metzgeria leptoneura*; *LEUadu* = *Leucobryum aduncum*. Axis 1: t-value of regression coefficient = 6.735.

Elevational trends. A comparison of the trunk communities in lower montane forest near Bariri with those in submontane rain forest (Ariyanti et al. 2008, Sporn et al. 2009b) and upper montane rain forest (Gradstein, unpubl.) of Lore Lindu National Park, Sulawesi, shows marked differences in composition (Table 3). In the submontane forest, mosses (55%) are more species-rich than liverworts (45%) in spite of the abundance of Lejeuneaceae, and total species richness is higher (see above). This forest has a much higher canopy than the lower montane forest and a very different tree flora, which is also richer in species (Culmsee & Pitopang 2009). In the lower montane forest, in contrast, liverworts are more species-rich (60%) than mosses (40%). Moreover, the composition of the bryophyte communities in the investigated submontane and lower montane forests is quite different. Only 40% of the species recorded on trunk bases in the lower montane were also found in the

submontane forest, in spite of the higher diversity in the latter forest type, and only two species, *Homaliodendron exiguum* and *Symphysodontella cylindracea*, were common in both forest types.

Major differences are also observed between lower montane and upper montane rain forest of Lore Lindu National Park (Table 3). The canopy in the latter forest type is only little lower than in the lower montane forest, and Fagaceae and Myrtaceae are prominent tree families in both forest types. Bryophyte abundance, however, is much higher in the upper montane forest, with trees, shrubs and the ground being densely carpeted by thick mats of bryophytes and with long garlands of bryophytes hanging from twigs and branches. The bryophyte vegetation of the upper montane forest is strongly dominated by liverworts (*Bazzania* spp., *Lepidozia* spp., *Mastigophora diclados*), and species richness of

Table 3. Importance of bryophyte families in terms of number of species recorded on trunk bases in submontane, lower montane and upper montane forest of Lore Lindu National Park, Central Sulawesi. Study sites are given in brackets.

	Submontane forest (Toro)	Lower montane forest (Bariri)	Upper montane forest (Rorekautimbu)
Reference	N.S. Ariyanti (2008 and pers. com.)	this study	this study
Elevation	1000 m	1400 m	2350 m
Canopy height	45 m	25 m	20 m
Important tree families	Meliac., Sapotac., Myristic.	Fagac., Myrtac., Eleocarp., Laurac.	Podocarpaceae, Myrtac., Fagac.
Number of trunk bases sampled	18	18	1
Number of bryophyte species recorded	86	58	20
Mosses (% of all species)	55%	40%	30%
Liverworts (% of all species)	45%	60%	70%
Mosses			
Sematophyllaceae	8 species	5 species	2 species
Leucobryaceae	3	3	1
Dicranaceae	1	3	1
Brachytheciaceae	1	-	-
Entodontaceae	1	-	-
Prionodontaceae	1	-	-
Fissidentaceae	2	-	-
Meteoriaceae	6	-	-
Hypopterygiaceae	5	1	-
Neckeraceae	6	1	-
Calymperaceae	6	5	-
Pterobryaceae	4	2	-
Thuidiaceae	4	1	-
Hypnaceae	1	1	-
Rhizogoniaceae	-	1	1
Pilotrichaceae	-	-	1
Liverworts			
Lejeuneaceae	24	10	1
Lophocoleaceae	4	4	1
Plagiochilaceae	4	9	1
Porellaceae	1	-	-
Radulaceae	3	1	-
Metzgeriaceae	1	1	-
Lepidoziaceae	-	8	5
Trichocoleaceae	-	1	1
Schistochilaceae	-	1	2
Herbertaceae	-	-	1
Mastigophoraceae	-	-	1
Scapaniaceae	-	-	1

the latter is more than two times higher than of mosses (70% vs. 30%). *Dicranoloma blumei* is the only epiphytic moss reaching high abundance here. The "mossy" aspect of the upper montane forests in Lore Lindu Park is presumably explained by the prevalence of fog and the cooler temperatures since rainfall at these elevations is little different from that at lower elevations (Fig. 2). The elevational trends observed in the montane rain forests of Lore Lindu National Park may be summarized as follows:

- 1) Trunk base communities of submontane, lower montane and upper montane forests are dominated by very different bryophyte taxa.
- 2) Calymperaceae, Fissidentaceae, Hypopterygiaceae, Lejeuneaceae, Leucobryaceae, Lophocoleaceae, Meteoriaceae, Metzgeriaceae, Neckeraceae, Porellaceae, Pterobryaceae, Radulaceae and Thuidiaceae are mainly found at low montane elevations, while Dicranaceae, Herbertaceae, Lepidoziaceae, Mastigophoraceae, Plagiochilaceae, Scapaniaceae, Schistochilaceae and Trichocoleaceae predominate at high elevations (Table 3; lesser important families represented by only one species omitted).
- 3) Plagiochilaceae attain high species richness in lower montane forest are rather scarce in submontane and upper montane forest.
- 4) Liverwort species richness increases towards higher elevation whereas moss richness decreases.

Phytosociology. The three tree base assemblages found in the study area (*Syrrhopodon tristichus-Bazzania vittata* assemblage, *Homaliodendron exiguum* assemblage, *Schistochila aligera* assemblage) belong to the "Thysanantho-Bazzanietea" described by Kürschner & Parolly (1998), which encompass all bryophyte communities on tree trunks in Southeast Asian rain forests, from sea level to the forest line. The three assemblages appear to share floristic affinities with the communities from lowland and submontane elevations, alliance "*Lepidolejeunion bidentulae*" (0-1300 m), as well as with those of higher elevations, alliance "*Bazzanion uncigeriae*" (1500-3500 m). Species found in this study characteristic of the "*Lepidolejeunion bidentulae*" include *Cheilolejeunea ceylanica*, *Lepidolejeunea bidentula*, *Metalejeunea cucullata* and *Thysananthus spathulistipus*, those characteristic of the "*Bazzanion uncigeriae*" are *Acroporium diminutum*, *Plagiochila oppositum* and *Psiloclada clandestina* (Kürschner & Parolly 1998). All occur in the *Homaliodendron exiguum* assemblage and four in the other two assemblages. The data indicate that the species assemblages found in the study area are transitional between South East Asian trunk communities of lower elevation (to 1300 m) and of higher elevation

(1500 m and above), which agrees with the intermediate elevation (1400 m) of the study area.

Across-tropics comparison. The family composition of the tree trunk communities of the lower montane rain forest appears to be remarkably similar throughout the tropics. Lejeuneaceae and Plagiochilaceae are pantropically the most important groups in terms of species richness, as shown by studies in North Borneo (Kürschner 1990), East Africa (Kürschner 1995), Costa Rica (Gradstein et al. 2001, Holz et al. 2002) and South America (Gradstein 1995). Lepidoziaceae (*Bazzania*, *Lepidozia*) may also be species-rich even though the optimum of this family is in the upper montane and subalpine forests. Gradstein & Pócs (1989) suggested that mosses are more prominent in Asiatic rain forest while liverworts prevail in neotropical forests, but our findings and those of others indicate that liverworts generally dominate over mosses in tropical montane forests in all continents except in the submontane forest.

At the species level, community similarities across the tropics are more limited (Kürschner & Parolly 1998). Trunk base communities of central Sulawesi have only 7 bryophyte species (25%) in common with those of lower montane forest of Mt. Kinabalu (Kürschner 1990) and species similarity on trunk bases in lowland forests of French Guiana and Guyana, lying >600 km apart, is ca. 20% (Mota et al. 2009). Across continents, similarities at species level are very low or non-existent; trunk base communities in lower montane forest of East Africa (Kürschner 1995) and northern Peru (Kürschner & Parolly 1998) had only one species *Pyrrhobryum spiniforme* in common with those of central Sulawesi.

Species diversity and tree parameters. Several studies have shown relationships between epiphytic bryophyte communities and trunk diameter in temperate forests (McGee & Kimmerer 2004 and references therein). In our study, diameter of host trees correlated with distribution of a few individual species (Fig. 6) but not with community composition or species richness. To the best of our knowledge this is the first demonstration of a relationship between trunk diameter and bryophyte diversity in a tree species-rich tropical forest. Ariyanti et al. (2008) found no correlation in trunk diameter with bryophyte composition in the submontane forest of central Sulawesi. Their negative result, however, might have been influenced by separating between trees with trunks larger and with smaller than 20 cm dbh. Analysis of the dataset without recognition of trunk diameter classes might have lead to a different result.

The underlying causes of the trunk diameter–epiphyte community relationships remain unclear although several explanations have been proposed such as age-related changes in bark conditions and establishment

limitation of protonemata (McGee & Kimmerer 2004). Bark may become more roughened with the age of the tree and thus conditions for establishment of bryophytes become enhanced. As to bark roughness, our study confirmed that trees with rough, fissured bark are usually richer in species than those with smooth bark (Fig. 4). Presumably this is because diaspores may hold more easily on rough bark than on smooth bark (flaking bark is also not a good substrate for epiphytic bryophytes). While this may be generally true, some trees with very rough bark have been observed to be almost devoid of epiphytes, e.g. the lowland tree *Fagraea fragrans* (B.C. Ho, pers. com.). Probably other properties of tree bark not measured in this study, such as chemical composition, water retention or porosity, play a role here.

In addition, we found that three species (*Kurzia gonyotricha*, *Harpalejeunea filicuspis*, *Leucophanes octoblepharoides*), representing 5% of all the species sampled, had a significant preference for trees with rough bark; no species were significantly associated with smooth bark (Figs. 5, 6). The results support the notion that bark roughness plays a role in shaping the epiphytic bryophyte distributions even though our statistical evidence was only minor. However, the possibility should be taken into account that our results were biased by recognition of only two bark roughness classes, which may not have accounted for the variation in bark roughness present in our sample. It should be noted that the importance of bark roughness as a factor shaping epiphytic bryophyte distribution has mostly been shown in forests with very few (2-5) tree species (Barkman 1958, Cornelissen & ter Steege 1989, Frahm 1994, Kürschner 1995, Holz 2003). Evidence from tree species-rich tropical forests (>50 per ha) is very scarce. Kürschner (1990) recorded a preference for smooth bark of the smooth-mat forming Lejeuneaceae and Radulaceae in lowland dipterocarp forest of Borneo, and this has also been observed elsewhere. Our data are the first statistical evidence of bark-specificity in a tree-species rich tropical forest. The low percentage of species with preference for rough (5%) or smooth (0%) bark in our study may have been biased by the recognition of only two bark roughness classes; clearly, more work is needed to substantiate these results.

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