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Bryophytes on tree trunks in natural forests, selectively logged forests and cacao agroforests in Central Sulawesi, Indonesia

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ABSTRACT

Forest disturbance and transformations into agricultural land alter tropical landscapes at drastic rates. Here, we investigate bryophyte assemblages on trunk bases in natural forest, selectively logged forest and cacao agroforests that are shaded by remnants of natural forest in Central Sulawesi. Overall, bryophyte richness per site did not differ between forest types. However, mosses and liverworts reacted differently in that moss richness was lowest in cacao agroforests, whereas liverwort communities were equally rich in all forest types. In terms of cover, mosses remained unaffected while liverwort cover decreased significantly in disturbed forest. Species composition of bryophytes clearly changed in cacao agroforests as compared to natural forests and selectively logged forests. In particular some drought-sensitive species were rare or absent in cacao agroforests and were replaced by drought-tolerant ones, thus underlining the importance of microclimatic changes. Moreover, differences in bryophyte species composition between large and small trees were only pronounced in cacao agroforests, presumably due to concomitant changes in stemflow of precipitation water. In conclusion, the bryophyte assemblages of selectively logged forests and cacao agroforests were as rich as in natural forest, but species turn-over was particularly high towards cacao agroforests probably due to microclimatic changes. Maintenance of shade cover is crucial to the conservation of the drought-sensitive forest species.

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1. Introduction

Over 5 million hectares of pristine tropical forests are disturbed and transformed into agricultural land each year (Achard et al., 2002) and the majority of remaining tropical forests undergo frequent disturbance by human activities, such as timber extraction and agriculture. These large scale rapid habitat changes pose a major threat to tropical tree species (Kessler et al., 2005) and associated flora and fauna, such as epiphytes, birds, butterflies and beetles (Krömer and Gradstein, 2004; Schulze et al., 2004; Gray et al., 2007; Bos et al., 2007).

Agricultural activities that involve forestry techniques (agroforestry) are used in cultivating perennial tree crops such as coconut, rubber, coffee and cacao (Schroth et al., 2000, 2004). In terms of heterogeneity, such cultivated forests range

from small scale coffee and cacao agroforests that are shaded by forest remnants, to regional homogeneous land cover by corporate palm plantations. Whereas non-intensive agroforestry systems such as shaded coffee and cacao agroforests can still support levels of species richness that resemble that of natural forests, large scale plantations that are dominated by single crop and tree species can cause drastic declines in associated species richness (Perfecto et al., 1997; McNeely, 2004; Schulze et al., 2004; Gradstein et al., 2007; Steffan-Dewenter et al., 2007).

Anthropogenic changes in the structure of forest habitats generally involve canopy-thinning activities that are accompanied by increases in air circulation and solar radiation in lower vegetation layers, with consequent microclimatic changes (Green et al., 1995; Thomas et al., 1999). By decreasing the projected crown area, thinning may also result in changed stemflow of precipitation water (Ford and Deans, 1978; Dietz et al., 2006), with possible consequences for the epiphytic flora on tree trunks.

Bryophytes are the most common corticolous epiphytes, of which indicator values for environmental changes have been evaluated in a wide variety of landscapes (Holz and Gradstein, 2005; Drehwald, 2005; Larsen et al., 2007). Because of their sensitivity to environmental changes, occurrences of bryophyte species have been related to microclimatic changes that relate to vegetation type (Vellak and Paal, 1999; Newmaster and Bell, 2002; Gonzalez-Mancebo et al., 2004; Pharo et al., 2004; Holz and Gradstein, 2005). Furthermore, the richness and composition of bryophyte communities may indicate forest quality in terms of forest structure and resource availability (Frego, 2007). In tropical America, no less than 30–50% of the occurring bryophyte species was lost after deforestation (Sillett et al., 1995; Acebey et al., 2003; Nöske et al., 2008).

With less drastic forest changes, bryophyte richness and community structure have been related to forest management (Pharo and Blanks, 2000; Pharo and Beattie, 2001; Fenton and Frego, 2005; Humphrey et al., 2002; McGee and Kimmerer, 2002; Ross-Davis and Frego, 2002) and land use intensity in agricultural landscapes (Zechmeister and Moser, 2001; Andersson and Gradstein, 2005). However, no studies have included the bryophyte flora of Southeast Asia in relation to human forest use, despite the fact that disturbed forests increasingly dominate Southeast Asian forest cover. Moreover, we are not aware of any study on bryophyte diversity in selectively logged tropical forest.

Here we investigate bryophyte communities on tree trunks and compare between trees in natural forests and trees in selectively logged forests and cacao agroforests in the margin of a large national park in Central Sulawesi, Indonesia. The impact of forest disturbance and cacao agroforestry on tree diversity in the region has been well documented (Kessler et al., 2005; Gradstein et al., 2007), yet studies on other groups of plants including bryophytes are lacking. A recent checklist of bryophytes in Sulawesi (Gradstein et al., 2005; Ariyanti et al., in press) includes less than half the number of species recorded from Borneo, New Guinea and the Philippines most likely because of the very incomplete inventory of Sulawesi. Our objectives are to increase our understanding of bryophyte dynamics in relation to human forest alterations in the tropics and to contribute to the knowledge of the bryophytes of Sulawesi.

2. Materials and methods

2.1. Study sites

The study was conducted in and around the Toro village (120°1′–120°3′30″E 1°29′30″–1°32′S, 800–1100 m a.s.l.), about 100 km South of Palu, the capital city of Central Sulawesi, Indonesia. Study sites were selected along the western border of the Lore Lindu National Park where the mean annual relative air humidity was 85% and mean annual temperature 23.4 °C. Annual rainfall was 2000–3000 mm, without pronounced seasonality (Gravenhorst et al., 2005).

Bryophytes were studied in a total of 12 study sites with a minimum distance of 500 m from each other. The 12 sites belonged to the following forest types (four sites in each type).

2.1.1. Natural forest (NF)
The investigated sites were situated in non-fragmented, protected submontane forest of Lore Lindu National Park. Human activities were restricted to collecting of medicinal plants and extensive hunting; rattan palms were present.

2.1.2. Selectively logged forest (SLF)
The investigated sites were part of a continuous forest band along the margin of the park where selective logging by inhabitants of Toro Village was allowed. The sites contained small to medium sized gaps and underwent disturbance of ground vegetation by the removal of rattan. Abundance of lianas was increased as compared to natural forest as a consequence of selective extraction of canopy trees 1–2 years previous to this study.

2.1.3. Cacao agroforest (CAF)
The investigated sites were part of a continuous band of cacao plantations bordering the park. Shade was provided by natural shade trees (=remaining forest cover). Boundaries between agroforests were arbitrary based on ownership. The types of shade tree stands used in the area differed between agroforests (Bos et al., 2007). Therefore, we marked core areas of 50 × 30 m with uniform shade tree stands. The age of the agroforests was 6–8 years.

Natural forests were dominated by Meliaceae, Lauraceae and Sapotaceae, selectively logged forests by Rubiaceae, Fagaceae and Myristicaceae, and cacao agroforests by Moraceae, Myristicaceae and Melastomataceae (Gradstein et al., 2007). Tree species richness was similar in natural forest and selectively logged forest (ca. 50 spp. per 0.25 ha), but significantly lower in cacao agroforests (ca. 20 spp. per 0.25 ha). Stem density, basal area and canopy cover were highest in the natural forests and lowest in the cacao agroforests. The microclimate, measured at 10 cm above the ground, became drier from the natural forest to the cacao agroforest (Table 1).

2.2. Bryophyte sampling

Sampling followed the general recommendations of Gradstein et al. (2003) for corticolous bryophytes. In each site, core areas of 0.25 ha were marked within which bryophytes were collected from five trees with a diameter of more than 20 cm dbh ("large trees") and 10 trees of 10–20 cm dbh ("small trees").

Table 1 – Vegetation structure and microclimate (air humidity) in the three different forest types studied in Central Sulawesi

	Natural forest	Selectively logged forest	Cacao agroforest
[a]Number of tree species (0.25 ha^{-1})	55.8 ± 5.5^a	48.3 ± 4^a	20.8 ± 7.8^b
[a]Stem density dbh >10 cm (0.25 ha^{-1})	140.5 ± 17.3^a	129 ± 10.3^a	77.5 ± 21.1^b
[a]Basal area (m^2 ha^{-1})	56.7 ± 18.2^a	33.7 ± 9.3^{ab}	20.5 ± 8.4^{bc}
[b]Canopy cover (%)	90.3 ± 0.4^a	81.9 ± 0.3^b	78.7 ± 0.4^c
[c]Mean daytime air humidity (%)	97.6 ± 3.1^a	94.7 ± 4.3^a	89.5 ± 7.8^a

Statistical significance indicated by lower case letters (Tukey HSD post hoc tests, $p < 0.01$).

Air humidity was measured at 10 cm above the ground in two sites per forest type over a period of 100 days (December 2004–March 2005), using data loggers (Migge, pers. comm.).

a After Gradstein et al. (2007).
b After Hertel et al. (2007).
c After Migge (unpublished).

We distinguished between these two classes of trees because they seemed to be inhabited by different bryophyte species, especially in the cacao agroforests. To maximize information on species richness, we sampled tree species standing well apart and differing in bark texture (rough, smooth). The majority of the species were rough-barked. In all, we sampled 58 different tree species (14 smooth-barked) in natural forest, 54 species (13 smooth-barked) in selectively logged forest and 23 species (2 smooth-barked) in cacao agroforest. On the large trees, five small plots of 20 × 30 cm were positioned between 0 and 2 m height on the trunks. From the small trees, bryophytes were collected from two or three 600 cm^2 plots such that the total equaled 25 plots per site. Cover of bryophyte species was recorded in percent of 600 cm^2.

Bryophyte specimens were identified using recent taxonomic treatments (see Gradstein et al., 2005) and reference collections of Herbarium Bogoriense (BO), the Herbarium of the University of Göttingen (GOET) and the Herbarium of the National University of Singapore (NUS). Vouchers were deposited in BO.

2.3. Data analysis

We tallied species richness for all bryophytes and for mosses and liverworts separately (hornworts were not recorded in this study). Commonness of bryophyte species was determined based on the number of trees on which the species was present. Species were considered common when they occurred on 10% or more of all trees. We constructed accumulation curves for observed and estimated species richness to assess the completeness of our sampling in each forest type. On a per site basis, species-saturation was assessed by comparing the observed and estimated species richness. For species richness estimation, we chose the incidence-based coverage estimator (ICE) as implemented in EstimateS 7.0 (Colwell, 2004), which is recommended for taxonomic groups of which abundance is difficult to quantify (Chao et al., 2000).

Effects of forest type on observed and estimated species richness per 0.25 ha^2 study sites ($n = 4$ per habitat type) were tested in general linear models (GLMs) with type I variance decomposition. In the models, forest type was entered first, followed by replication of study sites. To test whether effects of forest type were site-dependent, the interaction effect between forest type and site replication was entered.

The effects of forest type on species richness and bryophyte cover (%) per 600 cm^2 plot ($n = 200$ per forest type) were tested with GLMs with type I variance decomposition, forest type entered first, followed by tree size (large and small) and its interaction effects with forest type and tree size to test whether effects of habitat or tree type were site-dependent. Cover data were arcsine square-root transformed before analyses in order to achieve normal distribution of the data. The same model was used to compare the cover per plot of the most common bryophyte species.

To test for the effects of forest type on the structure of bryophyte communities, we calculated shared and unshared species between natural forest, selectively logged forest and cacao agroforest. In addition, we calculated the Sørensen similarity index from presence–absence data for each pairwise comparison between sites and tree sizes. We used the multidimensional scaling (MDS) to visualize the similarity matrix. The number of dimensions was chosen based on the percentage of raw stress reduced calculated with the first five dimensions. For each scaling, stress values below 0.20 were considered as a good fit to the similarity matrix. Analyses of similarity (ANOSIM) were carried out to test for statistical significance of differences between community structure of the investigated forest types and tree size.

General linear models and multidimensional scaling were carried out using Statistica 6.0 (StatSoft Inc, 2001) and analyses of similarity using PRIMER 5.0 (© 2000 PRIMER-E Ltd.).

3. Results

3.1. Species richness and abundance

In total, 168 species of bryophytes were recorded in the twelve 0.25 ha sites, including 88 species of mosses (19 families) and 80 species of liverworts (8 families) (Appendix; hornworts were not recorded). Lejeuneaceae were the most species-rich family, being represented by 41 species. Neckeraceae (10 species) were the overall most commonly observed moss family, Leucobryaceae and Lepidoziaceae were only found in natural and selectively logged forests, and Frullaniaceae (7 species) were the most common and species-rich family in cacao agroforests (Appendix).

The accumulation curves of observed species richness showed little evidence of approaching an asymptote (Fig. 1),
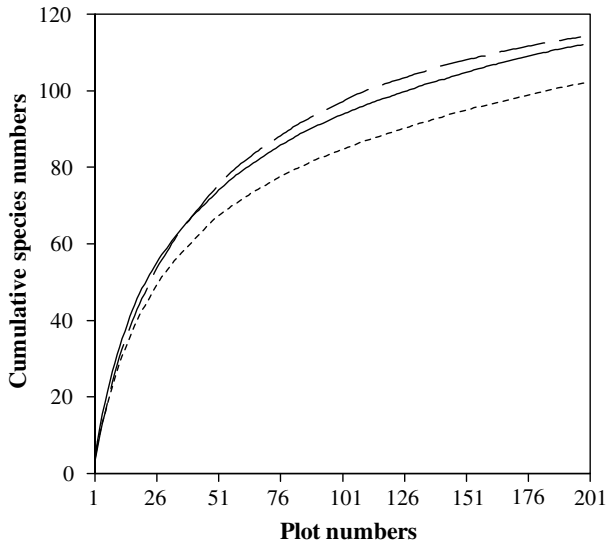
Fig. 1 – Plot-based species accumulation curves of bryophytes in natural forest (continuous line), selectively logged forest (dashed line), and cacao agroforest (dotted line) in Central Sulawesi. Size of the plots is 30×20 cm.

suggesting that we did not sample total species richness in the forest types. Overall observed species richness in natural forests, selectively logged forests and cacao agroforests were

112, 114 and 102, respectively (estimated richness: 131, 126, and 120, respectively).

Although estimated species richness was higher than observed species richness in all sites, neither observed richness (51–58 species per site, GLM: $F_{[2,6]} = 0.2$, $p = 0.82$) nor estimated richness (66–79 species per site, GLM: $F_{[2,6]} = 0.53$, $p = 0.61$) were significantly affected by forest type (Fig. 2). At the plot level (600 cm^2), however, species richness of mosses decreased significantly in selectively logged forests and cacao agroforests as compared to natural forests (GLM: $F_{[2,2]} = 39.32$, $p = 0.02$, Fig. 2). The species richness of liverworts per plot was not significantly affected by forest type (GLM: $F_{[2,2]} = 2.68$, $p = 0.27$, Fig. 2).

In terms of cover per plot (%), liverworts decreased significantly in the selectively logged forests as compared to natural forests and cacao agroforests (GLM: $F_{[2,2]} = 17.54$, $p = 0.05$), whereas cover of mosses was not significantly affected by forest type (GLM: $F_{[2,2]} = 2.73$, $p = 0.27$) (Fig. 2). Tree size affected neither species richness (mosses: 1.9–2.8, GLM: $F_{[1,2]} = 0.19$, $p = 0.71$; liverworts: 1.7–2.8, GLM: $F_{[1,2]} = 0.00$, $p = 0.97$) nor cover (mosses 11–16%, GLM: $F_{[1,2]} = 0.66$, $p = 0.50$; liverworts: 5–10%, $F_{[1,2]} = 3.14$, $p = 0.22$).

In total, 29 species occurred on 10% or more of the studied trees and were thus assigned "common" (Table 2, Appendix). Of these, *Caudalejeunea recurvistipula*, *Chaetomitrium lanceolatum*, *Lopholejeunea subfusca*, *Floribundaria floribunda* and *Mastigolejeunea auriculata* had highest abundance in cacao agroforests and *Acroporium rufum*, *Archilejeunea planiuscula*, *Homaliodendron exiguum*, *Metzgeria furcata*, *Mitthyridium undulatum* and
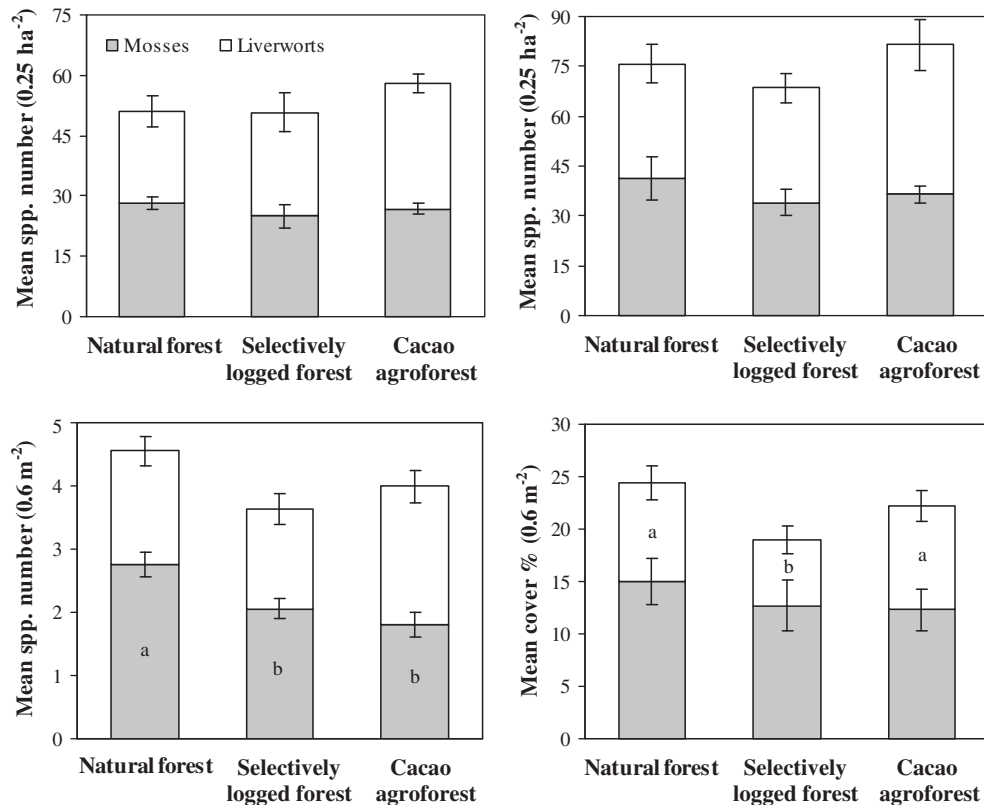
Fig. 2 – Species richness of bryophytes per site (top) and species richness and cover % of bryophytes per plot (bottom) in natural forest, selectively logged forest and cacao agroforest in Central Sulawesi. Top left: observed species richness. Top right: estimated species richness (ICE).
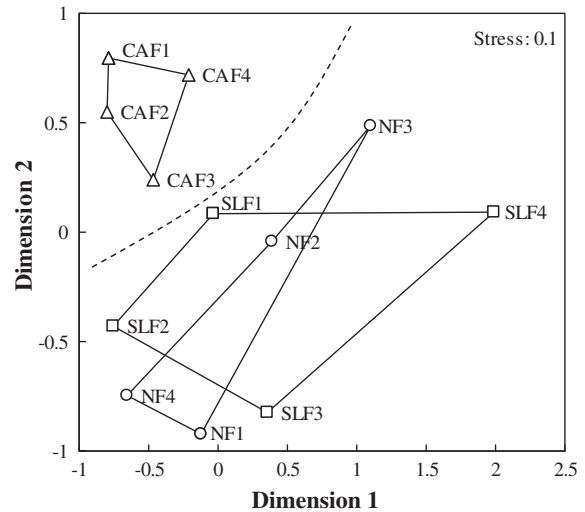
Table 2 – The most common bryophyte species, occurring on 10% or more of studied trees in natural forest, selectively logged forest and cacao agroforest in Central Sulawesi			
	Mean cover (%) (600 m^{-2})		
	Natural forest	Selectively logged forest	Cacao agroforest
Mosses			
Acroporium rufum	0.27	0.13	0.03**
Chaetomitrium lanceolatum	0.01	0.02	0.47***
Chaetomitrium leptopoma	0.17	0.15	0.44
Ectropothecium dealbatum	0.75	0.18	0.91
Floribundaria floribunda	0.32	0.26	1.7***
Himantocladium plumula	0.39	0.49	0.06
Homaliodendron exiguum	0.51	0.33	0**
Leucophanes octoblepharoides	0.39	0.77	0.09
Meteoriopsis squarrosa	0.16	0.27	0.13
Mitthyridium undulatum	1.14	0.97	0.05*
Neckeropsis lepineana	0.52	0.42	1.34
Pelekium velatum	0.19	0.19	0.45
Pinnatella kuehliana	0.95	0.74	0.08
Pinnatella mucronata	0.58	0.36	0.9
Symphysodontella cylindracea	0.35	0.11*	0.03**
Liverworts			
Archilejeunea planiuscula	1.03	0.47	0.2*
Caudalejeunea recurvistipula	0.01	0.04	0.42**
Cheilolejeunea vittata	0.42	0.09	0.12
Heteroscyphus argutus	0.54	0.33	0.18
Lejeunea anisophylla	0.33	0.31	0.25
Lejeunea obscura	0.59	0.01	0.4
Lepidolejeunea bidentula	0.5	0.33	+
Lopholejeunea subfusca	0.46	0.61	2.34***
Mastigolejeunea auriculata	0	0	1.27***
Metalejeunea cucullata	0.01	0.01	+
Metzgeria furcata	0.41	0.08**	0***
Plagiochila junghuhniana	0.11	0.21	0.13
Porella acutifolia	0.44	0.16	0.3
Stenolejeunea apiculata	0.09	0.02	0.18

Stars (* = p < 0.05; ** = p < 0.01; *** = p < 0.001) indicate significant differences based on GLM analysis and Tukey's HSD post hoc tests. Cross (+) indicates cover less than 0.01%.

Fig. 3 – Multidimensional scaling based on Sørensen's indices for similarity of bryophyte communities on tree trunk bases in three different forest types in Central Sulawesi. Because patterns were similar for mosses and liverworts, the graph is shown for overall bryophyte communities in natural forests (NF), selectively logged forests (SLF) and cacao agroforests (CAF). Lines connect sites of the same habitat type.

Symphysodontella cylindracea had lowest abundance in the agroforests (Table 2). Only two species, *Metzgeria furcata* and *Symphysodontella cylindracea*, had significantly lower cover values in selectively logged forests in comparison to natural forests; no species had highest cover in the selectively logged forests.

The first two dimensions of the multidimensional scaling of Sørensen's similarity index reduced 99.9% of the raw stress, with stress values lower than 0.20. This two-dimensional scaling of similarity between bryophyte communities shows distinct bryophyte compositions in cacao agroforests as compared to those in the natural and selectively logged forests (Fig. 3), which is confirmed by ANOSIM results (Table 3). Fifty-two species (30%) occurred in cacao agroforests as well as in natural and selectively logged forests. The ANOSIM results further confirm that bryophyte communities of the natural and selectively logged forests did not significantly differ (Table 3): of 145 bryophyte species that occurred in the natural and selectively logged forests, over half occurred in both for-

est types (Table 3). Lastly, these results confirm that bryophyte communities on small and large trees only differed in the cacao agroforests, and this difference was only significant for mosses (Table 3).

4. Discussion

The species richness of mosses and liverworts per site did not differ significantly between natural forests, selectively logged forests and cacao agroforests. This supports the notion that cacao agroforests can preserve rich bryophyte communities that may be almost as species rich as those in natural forests (Andersson and Gradstein, 2005). However, species turn-over was particularly high towards the cacao agroforests. Moreover, we found a marked difference between mosses and liverworts in their response to forest type. Mosses were most affected in terms of species richness, whereas liverworts were affected only in terms of cover.

Liverwort cover on tree stems was negatively affected by the logging activities, whereas cover of mosses remained unaffected. This is in accordance with Thomas et al. (2001), who found a similar effect on liverworts and mosses after thinning of temperate evergreen forests. Surprisingly, in the present study liverwort cover increased in the cacao agroforests. This may be due to the fact that the disturbance event (logging) in the selectively logged forests dated back 1–2 years before the study took place as compared to 6–8 years in the cacao agroforests. Acebey et al. (2003) found that re-establishment of Bolivian rainforest bryophytes in fallows following deforestation was faster for liverworts than for mosses. In 4-year-old fallows they found only liverworts (all of them members of Lejeuneaceae) and in 10–15-year-old fallows still three quarters of the bryophyte species were liverworts.

Table 3 – Similarity (ANOSIM) based on Sørensen's similarity index of overall bryophyte communities, communities of mosses and communities of liverworts on large (>20 cm dbh) and small (<20 cm dbh) tree trunks in natural forest (NF), selectively logged forest (SLF) and cacao agroforest (CAF) in Central Sulawesi

Pairwise comparison	All bryophytes			Mosses			Liverworts		
	R	P	Shared species	R	P	Shared species	R	P	Shared species
Between forest types									
NF vs. SLF	−0.05	0.724	55.9 %	0.019	0.318	58.4 %	−0.063	0.779	52.9 %
NF vs. CAF	**0.58**	**0.01**	41.7 %	**0.525**	**0.01**	39.5 %	**0.4**	**0.01**	44.3 %
SLF vs. CAF	**0.468**	**0.01**	43.1 %	**0.429**	**0.01**	37.3 %	**0.415**	**0.01**	48.7 %
Between large and small tree trunks									
NF	0.031	0.457		0.021	0.457		0.078	0.371	
SLF	−0.115	0.686		−0.146	0.886		−0.042	0.600	
CAF	**0.370**	**0.029**		**0.479**	**0.029**		0.120	0.343	

Values that are significant at the 5% level are given in bold.

However, species composition in the fallows differed significantly from that of the forest. Our observations are in general agreement with those of Acebey et al. (2003) and are suggestive of fast recovery of the liverwort communities in cacao agroforests in terms of abundance but not in species composition.

The pronounced differences between mosses and liverworts in their response to habitat changes may relate to their different adaptations to environmental drought. In general, bryophytes depend on environmental moisture to maintain turgor pressure (i.e., are poikilohydric; e.g., Proctor, 2000), which may explain their sensitivity to selective logging and cacao agroforestry. Most of the mosses in the study sites were turfs or large, feathery or tree-like plants growing exposed to the air with considerable risk of drying out. In contrast, most liverworts formed small mats adhering closely to bark or were growing thread-like among larger species (supporting Richards, 1984), thus decreasing the risk of desiccation. Moreover, the majority of these epiphytic liverworts, especially members of Lejeuneaceae and Frullaniaceae, possess 'water sacs' that are adaptations for water retention and thus decrease the risk of drying out (Gradstein and Pócs, 1989).

Of the 29 most common bryophyte species (i.e., species that occurred on 10% or more of all trees sampled), more than one third were affected by forest type. Almost equal numbers of species decreased and increased in cacao agroforests. The majority of the decreasing species (*Acroporium rufum, Homaliodendron exiguum, Mitthyridium undulatum, Symphysodontella cylindracea*) are known as desiccation-intolerant taxa characteristic of the shaded understory of tropical rainforests (Gradstein and Pócs, 1989). Those species that increased in cacao agroforests are all known as desiccation-tolerant species that are characteristic of open habitats (*Caudalejeunea recurvistipula, Lopholejeunea subfusca* and *Mastigolejeunea auriculata*) or have leaves densely covered by papillae that prevent desiccation (*Floribundaria floribunda* and *Chaetomitrium lanceolatum*) (Richards, 1984; Proctor, 2000; Gradstein et al., 2002). Other examples of drought-tolerant species in our collections are members of the genera *Frullania* and *Macromitrium*, all of which were exclusively found in cacao agroforests and have been categorized as "sun-epiphytes" (Gradstein et al., 2001).

Bryophyte assemblages of small and large trees differed only in the cacao agroforests. This may be due to the increased stemflow of precipitation water on small trees in cacao agroforest, as compared with the larger trees (Dietz et al., 2006; Dietz, 2007), stemflow having pronounced effects on corticolous bryophytes (Proctor, 1990).

Thus, although overall species richness per site did not significantly differ between the forest types, bryophyte assemblages on trunk bases changed clearly in composition towards the cacao agroforests, primarily because of the replacement of drought-intolerant species by drought-tolerant ones. The species assemblages of the selectively logged forest, however, were less different from the natural forest. These findings correlate with microclimate in the forest understory which tended to become dryer towards the cacao agroforest (Table 1). Work in progress (Sporn et al., in preparation) suggests that the bryophyte assemblages of the cacao agroforest are rather characteristic to this forest type. Our results also indicate that selectively logged forests can contribute to the conservation of the natural forest flora, confirming earlier findings for tree diversity of these forest (Gradstein et al., 2007), and for butterflies (Schulze et al., 2004; Veddeler et al., 2005) and bryophytes (Costa, 1999; but see Holz and Gradstein, 2005) of secondary forests. In addition, our results indicate that more intense forms of land-use, such as cacao agroforestry, may lead to drastic floristic changes in tropical forest landscapes.

In conclusion, overall bryophyte richness and abundance on trunk bases in selectively logged forests and cacao agroforest was not significantly different from that of natural forests. In terms of species composition, the assemblages in the natural forest remained largely unchanged in selectively logged forests, but clearly changed in the cacao agroforests. These floristic changes toward cacao-dominated agroforests possibly relate to the more open canopy and the resulting changes in microclimate and rainfall dynamics in these systems. Our results show that such environmental changes may affect species groups asymmetrically and thus drive changes in the bark-inhabiting bryophyte flora.

Floristic changes resulted primarily from adaptations to environmental drought, which differs between mosses and liverworts and thus explains their different response to habitat change. Liverworts seemed to be better capable of recovery in cacao agroforests than mosses. However, most community changes were explained by the changes in drought-tolerant versus drought-intolerant species. Whereas some typical drought-intolerant taxa almost disappeared in the cacao

agroforests, some typical "sun-epiphytes" flourished in the cacao agroforests, which is in general agreement with results from recent work on epiphyte dynamics along similar habitat gradients in tropical America (Acebey et al., 2003; Nöske et al., 2008).

Our study shows that selective logging activities in the margins of tropical rainforests do not necessarily conflict with the conservation of the bryophyte flora, which argues for the inclusion of moderately disturbed forests in conservation schemes. It suggests that moderately intensive forest use (rattan extraction, selective logging) in rainforest areas may not necessarily be in conflict with conservation of bryophyte diversity. A similar conclusion was reached for tree diversity in the study area (Gradstein et al., 2007). It indicates that future conservation policies may focus on developing measures aimed at moderate use of the rain forest rather than attempting to exclude human activities. Moreover, out study shows that cacao agroforests can support high bryophyte richness and thus contribute to the conservation of bryophyte flora outside protected areas. However, we conclude that in order to maximize the proportion of forest flora in cacao agroforests, management should aim at maintaining sufficient shade cover in these agroforests. Shade cover is crucial to maintain microclimatic conditions that are comparable to those in natural forests and can enhance the conservation of drought-intolerant, disturbance-sensitive forest species.

Acknowledgments

Appendix

Abundance of bryophyte species in three different forest types in Central Sulawesi, Indonesia. Taxonomic nomenclature is in accordance with Gradstein et al. (2005) and Ariyanti et al. (in press). Species in bold occurred on ⩾10% of trees sampled (Table 2). NF = natural forest; SLF = selectively logged forest; CAF = cacao agroforest; mc = mean species cover (%) in 0.6 m^2 plots (as based on total cover/number of plots); np = number of plots in which the species occurred (n = 200); nt = number of trees sampled on which the species occurred (n = 180); + = mean cover less than 1%; − = species absent.

Group/family/species	Natural forest		Selectively logged forest		Cacao agroforest		Overall forest types
	mc	np	mc	np	mc	np	nt
Mosses							
Brachytheciaceae							
Rhynchostegiella menadensis	–	–	–	–	16	4	2
Rhynchostegium celebicum	2	8	9	3	7	5	13
Calymperaceae							
Arthrocormus schimperi	14	2	11	8	–	–	5
Calymperes afzelii	4	2	6	5	–	–	5
Calymperes boulayi	–	–	–	–	1	4	3
Calymperes caugiense	–	–	–	–	2	1	1
Calymperes tuberculosum	1	1	3	7	16	5	9
Exostratum blumei	6	1	7	2	–	–	2
Leucophanes massartii	4	18	2	2	–	–	11
Leucophanes octoblepharoides	3	29	4	34	5	4	39
Mitthyridium jungquilianum	–	–	5	7	–	–	4
Mitthyridium undulatum	9	24	9	21	2	4	21
Syrrhopodon aristifolius	15	4	+	2	–	–	4
Syrrhopodon muelleri	6	1	–	–	–	–	1
Dicranaceae							
Campylodontium flavescens	–	–	–	–	2	1	1
Dicranoloma brevisetum	5	5	7	9	–	–	7
Entodontaceae							
Entodon bandongiae	9	2	–	–	13	13	9
Erytodontium julaceum	–	–	–	–	12	2	2
Fissidentaceae							
Fissidens ceylonensis	12	7	–	–	–	–	4
Fissidens crassinervis	–	–	+	2	–	–	2

Appendix – *continued*

Group/family/species	Natural forest		Selectively logged forest		Cacao agroforest		Overall forest types
	mc	np	mc	np	mc	np	nt
Fissidens hollianus	2	3	2	5	–	–	7
Fissidens papillosus	–	–	32	1	+	1	2
Hookeriaceae							
Chaetomitrium lanceolatum	1	2	4	1	3	27	24
Chaetomitrium leptopoma	5	7	4	8	5	19	26
Chaetomitrium massartii	20	1	–	–	–	–	1
Chaetomitrium orthorrhynchum	1	3	4	2	6	9	11
Chaetomitrium papillifolium	–	–	–	–	5	7	6
Chaetomitrium setosum	15	28	34	2	–	–	15
Hypnaceae							
Ectropothecium dealbatum	11	14	4	10	9	20	28
Ectropothecium ichnotocladum	–	–	–	–	17	2	2
Taxithelium instratum	10	1	7	3	3	2	5
Taxithelium nepalense	2	1	–	–	3	3	3
Vesicularia reticulata	7	6	1	7	6	2	12
Hypopterygiaceae							
Cyathophorella spinosa	12	1	–	–	–	–	1
Hypopterygium aristatum	1	2	–	–	4	1	3
Hypopterygium tenellum	+	8	2	1	5	5	11
Lopidium strupthiopteris	3	9	–	–	–	–	7
Leucobryaceae							
Leucobryum aduncum	–	–	6	1	–	–	1
Leucobryum boninense	5	2	–	–	–	–	2
Leucobryum javense	3	3	11	1	–	–	2
Leucobryum sanctum	–	–	5	2	–	–	1
Meteoriaceae							
Barbella trichophora	+	2	–	–	11	2	3
Floribundaria floribunda	3	20	2	23	11	31	44
Floribundaria pseudofloribunda	5	7	5	7	–	–	4
Floribundaria thuidioides	–	–	3	4	–	–	2
Meteoriopsis reclinata	11	1	–	–	11	13	8
Meteoriopsis squarrosa	2	13	7	8	3	8	21
Meteorium miquelianum	–	–	–	–	7	7	5
Papillaria fuscescens	1	1	–	–	–	–	1
Mniaceae							
Orthomnion dilatatum	–	–	–	–	6	8	6
Neckeraceae							
Caduciella mariei	–	–	2	10	–	–	7
Himantocladium plumula	5	16	5	19	2	7	31
Homaliodendron exiguum	3	32	4	18	–	–	30
Homaliodendron flabellatum	2	4	–	–	–	–	3
Neckeropsis gracilenta	3	6	9	6	4	4	11
Neckeropsis lepineana	5	22	6	13	9	31	42
Pinnatella alopecuroides	6	18	–	–	–	–	8
Pinnatella anacamptolepis	–	–	1	4	5	4	8
Pinnatella kuehliana	4	50	5	27	5	3	47
Pinnatella mucronata	3	44	2	30	6	31	66
Octoblepharaceae							
Octoblepharum albidum	2	4	+	1	–	–	2
Orthotrichaceae							
Macromitrium semipellucidum	–	–	–	–	30	1	1
Phyllogoniaceae							
Cryptogonium phyllogonioides	–	–	1	1	–	–	1
Prionodontaceae							
Neolindbergia rugosa	4	7	3	3	5	4	10

Appendix – *continued*

Group/family/species	Natural forest		Selectively logged forest		Cacao agroforest		Overall forest types
	mc	np	mc	np	mc	np	nt
Pterobryaceae							
Calyptothecium recurvulum	3	1	–	–	3	2	2
Calyptothecium urvilleanum	3	1	2	2	7	14	13
Garovaglia elegans	–	–	27	1	–	–	1
Garovaglia plicata	–	–	–	–	4	7	5
Jaegerina luzonensis	6	5	4	3	7	3	8
Symphysodontella cylindracea	3	24	2	10	2	4	25
Rhizogoniaceae							
Hymenodon angustifolium	–	–	62	3	–	–	1
Pyrrhobryum spiniforme	27	2	40	8	–	–	4
Sematophyllaceae							
Acanthorrhynchium papillatum	41	2	44	1	–	–	2
Acroporium diminutum	11	2	2	5	4	1	8
Acroporium falcifolium	2	2	7	5	–	–	3
Acroporium hemaphroditum	13	2	–	–	–	–	1
Acroporium rufum	5	11	2	13	3	2	18
Acroporium sigmatodontium	5	2	–	–	–	–	2
Clastobryum epiphyllum	2	1	–	–	–	–	1
Isocladiella sulcularis.	4	10	4	7	–	–	11
Mastopoma uncinifolium	1	1	+	1	–	–	2
Unidentified species	62	1	–	–	–	–	1
Thuidiaceae							
Pelekium gratum	–	–	–	–	3	11	10
Pelekium velatum	4	10	2	16	6	15	30
Pelekium versicolor	1	1	9	1	13	1	3
Thuidium assimile	5	3	–	–	–	–	1
Thuidium cymbifolium	13	1	2	2	–	–	3
Thuidium glaucinum	5	20	35	4	–	–	11
Liverworts							
Frullaniaceae							
Frullania ericoides	–	–	–	–	0	8	8
Frullania eymae	–	–	10	2	11	5	6
Frullania galeata	–	–	–	–	3	14	12
Frullania hampeana	–	–	–	–	3	1	1
Frullania intermedia	+	1	3	1	1	1	3
Frullania neosheana	–	–	+	2	–	–	1
Frullania reflexistipula	–	–	–	–	4	3	3
Geocalycaceae							
Chiloscyphus ciliolatus	–	–	3	2	–	–	1
Chiloscyphus muricatus	2	6	+	1	–	–	7
Heteroscyphus argutus	4	25	4	15	4	9	43
Heteroscyphus coalitus	19	3	5	3	3	1	7
Heteroscyphus succulentus	–	–	2	4	–	–	2
Heteroscyphus zollingeri	2	3	2	9	4	4	13
Lejeuneaceae							
Acrolejeunea pycnoclada	2	2	5	5	–	–	4
Archilejeunea planiuscula	8	27	7	14	3	14	41
Caudalejeunea recurvistipula	1	2	2	4	4	22	22
Cheilolejeunea celebensis	+	1	–	–	–	–	1
Cheilolejeunea ceylanica	6	4	6	9	2	3	11
Cheilolejeunea falsinervis	8	3	3	2	–	–	4
Cheilolejeunea imbricata	–	–	1	3	5	9	9
Cheilolejeunea meyeniana	+	1	2	4	5	7	10
Cheilolejeunea orientalis	2	4	–	–	3	17	14
Cheilolejeunea trifaria	8	2	12	3	4	2	6
Cheilolejeunea vittata	8	11	3	7	3	7	20
Cololejeunea planissima	–	–	–	–	+	1	1
Cololejeunea spinosa	1	5	+	5	1	6	13
Dendrolejeunea fruticosa	4	2	–	–	–	–	1

Appendix – *continued*

Group/family/species	Natural forest		Selectively logged forest		Cacao agroforest		Overall forest types
	mc	np	mc	np	mc	np	nt
Drepanolejeunea angustifolia	–	–	–	–	5	7	6
Drepanolejeunea ternatensis	4	9	1	5	2	11	16
Lejeunea anisophylla	3	21	4	16	2	21	43
Lejeunea discreta	–	–	4	2	–	–	2
Lejeunea eifrigii	–	–	+	5	–	–	5
Lejeunea exilis	–	–	3	4	+	2	4
Lejeunea flava	4	2	–	–	–	–	1
Lejeunea obscura	9	13	+	2	11	7	19
Lejeunea punctiformis	+	2	+	1	+	1	4
Lejeunea sordida	7	12	–	–	8	8	12
Lepidolejeunea bidentula	7	15	4	18	+	1	21
Leptolejeunea epiphylla	–	–	1	1	2	1	2
Leptolejeunea maculata	–	–	–	–	1	1	1
Lopholejeunea borneensis	–	–	1	6	4	4	7
Lopholejeunea eulopha	+	1	10	3	4	1	5
Lopholejeunea nigricans	–	–	3	10	–	–	5
Lopholejeunea subfusca	5	19	7	17	5	89	75
Lopholejeunea zollingeri	+	1	–	–	–	–	1
Mastigolejeunea auriculata	–	–	–	–	6	43	27
Mastigolejeunea virens	–	–	–	–	6	7	5
Metalejeunea cucullata	+	11	+	10	+	7	25
Ptychanthus striatus	5	6	4	5	10	1	11
Pycnolejeunea contigua	–	–	–	–	+	1	1
Spruceanthus polymorphus	4	3	2	2	6	16	17
Stenolejeunea apiculata	1	13	2	2	2	20	25
Thysananthus convolutus	10	4	1	1	9	1	4
Thysananthus spathulistipus	8	15	5	14	–	–	14
Lepidoziaceae							
Bazzania tridens	14	1	14	5	–	–	5
Lepidozia wallichiana	–	–	20	1	–	–	1
Metzgeriaceae							
Metzgeria furcata	4	20	2	8	–	–	21
Metzgeria leptoneura	–	–	3	4	2	1	4
Metzgeria lindbergii	–	–	1	1	–	–	1
Plagiochilaceae							
Plagiochila bantamensis	3	19	+	1	4	3	12
Plagiochila celebica	–	–	3	1	11	1	2
Plagiochila javanica	–	–	2	3	2	1	3
Plagiochila junghuhniana	3	8	3	14	3	8	18
Plagiochila longispica	–	–	14	3	15	1	3
Plagiochila obtusa	+	1	–	–	5	5	4
Plagiochila parvifolia	–	–	3	2	10	8	8
Plagiochila salacensis	3	5	–	–	1	5	9
Plagiochila sandei	–	–	6	9	–	–	4
Plagiochila sciophila	10	4	1	4	–	–	5
Porellaceae							
Porella acutifolia	4	22	3	9	5	12	23
Porella javanica	–	–	1	1	–	–	1
Porella perrottetiana	8	1	8	9	–	–	3
Radulaceae							
Radula acutiloba	4	4	1	4	–	–	7
Radula gedena	–	–	1	5	3	4	5
Radula javanica	17	10	6	6	–	–	11
Radula madagascarensis	4	2	–	–	–	–	1
Radula multiflora	–	–	3	2	–	–	2
Radula pinnulata	–	–	–	–	3	1	1
Radula retroflexa	10	7	–	–	3	1	6
Radula vanzantenii	–	–	–	–	3	1	1

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