

Microclimate determines community composition but not richness of epiphytic understory bryophytes of rainforest and cacao agroforests in Indonesia

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Abstract. Management intensification in cultivated, tropical forests drives changes in the microclimate that can threaten native forest flora and fauna. In this study, we use epiphytic bryophytes, known to be sensitive to microclimatic changes due to their lack of a protective cuticle and the exposed habitat, to investigate the predictive power of microclimate for changes in species richness and composition. Bryophytes were sampled from understory trees in natural forest and cacao (*Theobroma cacao* L.) trees in two types of cacao agroforests (natural shade trees and planted shade trees) in Central Sulawesi, Indonesia. The microclimate in the agroforests was characterised by low air humidity and high air temperature during the afternoon. Bryophyte species richness did not differ between habitat types but species composition changed markedly from the natural forest to the cacao agroforests. Although no correlation between species richness and microclimate values could be found, a series of matrix-based analyses revealed a significantly positive relationship between similarities in species composition and in maximum values for temperature and minimum values for humidity, which suggests that microclimatic changes are a good predictor for high turnover of bryophyte community composition from natural forests to cacao agroforests.

Additional keywords: biodiversity, conservation, liverworts, mosses, tropical rainforest.

Introduction

The ongoing deforestation and habitat degradation in the tropics continue to cause losses of highly diverse flora and fauna (Myers *et al.* 2000; Achard *et al.* 2002; Laurance *et al.* 2002; Sodhi *et al.* 2004). Because timber plantations and agroforests may have a superficially similar structure to natural forests, such cultivated forests have been suggested to provide surrogate habitats serving as tools in tropical biodiversity conservation (Greenberg 1998; Barlow *et al.* 2007). Extensively managed cultivated forests with native vegetation consisting of local tree and herb species can offer sufficient habitats to harbour levels of species richness comparable with that of natural forests (Lamb 1998; Hietz 2005; Brockerhoff *et al.* 2008). Wide ranges of indigenous and endemic species may occur in these cultivated habitats, underlining their conservation value (Perfecto *et al.* 1997; Rice and Greenberg 2000; Schulze *et al.* 2004; Andersson and Gradstein 2005). Management intensification of these cultivated forests by, for example, removal of shade trees and cleaning of the understory, may again lead to depletion of biodiversity (Acebey *et al.* 2003; Steffan-Dewenter *et al.* 2007; Ariyanti *et al.* 2008; Bos *et al.* 2008). Such intensifications are usually associated with changes in microclimate because gaps in the canopy and the absence of an interceptive herb layer leads to rising temperatures, decreasing air humidity and increasing through-fall

of rainwater (Walsh 1996; Leigh 1999; Acebey *et al.* 2003; Nöske 2005; Dietz *et al.* 2006).

Bryophytes, due to their lack of a protective cuticle, have often been suggested to be highly sensitive to changes in microclimate, especially among the epiphytic species (Barkman 1958; Ataroff and Rada 2000; Frahm 2003; Léon-Vargas *et al.* 2006). Whereas terrestrial bryophytes may receive protection against desiccation through shading by herbs and leaf litter, epiphytic bryophytes are more directly exposed to the increased insolation and decreased humidity that follow the opening-up of the forest canopy. These human-induced changes in microclimate conditions may be associated with losses of up to one-third of native tropical forest bryophyte species (Acebey *et al.* 2003). Particularly affected are ecological ‘specialists’ such as the shade epiphytes of the forest understory (Gradstein 1992, 2008; Acebey *et al.* 2003). Sun epiphytes and ecological ‘generalists’, on the other hand, are usually less impacted by the disturbance.

In the present study, species richness and species composition of epiphytic bryophytes were investigated in natural rainforests and plantations of cacao (*Theobroma cacao* L., grown in agroforests) on the island of Sulawesi, Indonesia. Indonesia, after Ivory Coast and Ghana, is the most important cacao exporting country with the

majority coming from Sulawesi (ICCO 2008). With a world production that reached an annual 3.4 million tonnes in 2006–07, demands for dried cacao beans (from which cocoa is extracted) are steadily increasing. The flora of South-east Asia is characterised by high diversity and levels of endemism (Roos *et al.* 2004; Sodhi *et al.* 2004; Gradstein *et al.* 2005; Ariyanti *et al.* 2009), making it one of the world's hotspots in terms of biodiversity (Myers *et al.* 2000). However, the region is also characterised by some of the highest rates of rainforest loss (Achard *et al.* 2002), which on Sulawesi has resulted in an 80% loss of primary forest habitats (Cannon *et al.* 2007). Changes in biodiversity in the study area in relation to ongoing forest conversion have been well documented (Schulze *et al.* 2004; Steffan-Dewenter *et al.* 2007), but the correlations with microclimatic changes have not yet been studied. The purpose of the present study was to analyse the importance of microclimate as a predictor of differences in epiphytic bryophyte species richness and composition in the understory of rainforests and differently managed cacao agroforests in Sulawesi.

Materials and methods

Study sites

This study took place in and around Toro Village at the western border of the 231 000 ha Lore Lindu National Park, Central Sulawesi, Indonesia. The village is situated at ~800 m above sea level, has an overall annual temperature of 23.4°C, a relative humidity of 85% and an annual precipitation of 2000 to 3000 mm, without clear seasonal fluctuations (Gravenhorst *et al.* 2005). The vegetation of the park is largely made up of natural rainforest; near Toro village the park is bordered by an almost continuous band of cacao plantations. Within an altitudinal range of 800–1000 m, 11 study sites were selected in three different habitat types: four sites in natural forest, three in agroforests under natural shade and four in cacao agroforests under planted shade trees.

1. *Natural forests* (NF): Primary submontane rainforests that were part of the national park that surrounded the village and underwent only minor anthropogenic disturbance (e.g. minor rattan extraction, collection of medicinal plants, extensive hunting). Mature canopy trees were 30 to 50 m high.
2. *Cacao agroforests under natural shade* (CNS): Cacao-dominated agroforests at the margin of the national park, shaded by trees that remained from natural forest stands (described as 'rustic cacao' by Rice and Greenberg (2000)). Cacao trees were 10 to 15 years old and shading canopy trees were 15 to 30 m high.
3. *Cacao agroforests under planted shade trees* (CPS): Cacao-dominated agroforests shaded by a variety of planted fruit trees such as *Lansium domesticum* Corr., *Nephelium lappaceum* L. and *Syzygium aromaticum* (L.) Merr. and Perry, timber trees like *Bischofia javanica* Blume and *Aleurites moluccana* Willd., as well as the non-indigenous legume trees *Gliricidia sepium* (Jacq.) Walp. and *Erythrina subumbrans* Hassk. Cacao trees were between 4 and 10 years old and shading canopy trees were 15 to 25 m high.

Microclimate measurement

In each study site, air temperature (°C) and relative air humidity (%RH) at 2 m height were measured with 15-min intervals during February to March 2005, using data-loggers (type HOBO RH/Temp, SYNOTECH, Linnich, Germany). Average daily minimum and maximum values were calculated per site. Vapour pressure deficit (VPD = difference between measured absolute humidity and potential maximum absolute humidity) was determined using the equation $VPD = E - e$ (where $E = 6107 \times 10^{(17.27 \times T / (237.3 + T))}$ [hPa] and $e = E \times RH[\%] / 100$; Schulze *et al.* 2004). Because of daily rains, the minimum values of VPD approached zero in all study sites and were excluded from further analyses.

Bryophyte sampling

In each study site, two trees up to 7 m high, a diameter between 20–60 cm at breast height (1.4 m above forest floor) and at a minimum distance of 15 m from each other, were selected for collecting epiphytic bryophytes. All sampled trees in the agroforests were trees of *Theobroma cacao* L. (no other species were observed in the size class); those sampled in the forest belonged to different species each. All trees were similar in bark structure.

On each selected tree, epiphytic bryophytes were sampled from plots of 200 cm² positioned at each cardinal direction in three height zones: (1) trunk, from base to first ramification; (2) inner crown; and (3) outer crown. In total, 12 plots (2400 cm²) per tree were sampled.

The collected epiphytic bryophytes were identified using taxonomic literature and reference collections from the Herbarium at the University of Göttingen (GOET) and the National Herbarium of the Netherlands at Leiden (L) or were sorted to morphospecies. Vouchers were deposited in the Herbarium Bogoriense, Bogor (BO), the Herbarium Celebense, Palu (CEB), and in GOET and L.

Statistical analysis

We used the first order Jackknife estimator (applied previously in similar studies in the study area; Schulze *et al.* 2004) to assess sampling completeness at different spatial levels. Differences between habitat types in observed and estimated species richness per site were tested with one-way ANOVAs. Correlation between microclimate values and estimated and observed species richness per site were tested with Spearman Rank correlations.

We tested for the effect of habitat type on species richness per tree and per zone using general linear models (GLMs) with Type I hierarchical variance decomposition. 'Habitat type' was entered first, followed by 'study site', 'tree' and 'height zone'. We included the interaction effect between habitat type and height zone to detect possible habitat-dependence of differences between zones.

To analyse differences in species composition between the sites, Sørensen's similarity index was calculated for each pairwise site comparison followed by a multidimensional scaling (MDS) of the similarity matrix. Stress values below 0.20 were considered to indicate a good fit of the scaling to the matrix. The dimensions that reduced the majority of the 'raw stress' were chosen for the final scaling. To test whether differences in species composition

between habitat types were significant, analyses of similarity (ANOSIM) were carried out. To test whether microclimate changed along the axes of the scaling, we carried out Spearman Rank correlations between the microclimatic factors and the dimension values. We used Mantel tests to determine whether the similarity in species composition related to similarity in microclimatic data. As a control, Mantel tests were also carried out for differences in species richness relative to microclimate similarity.

All analyses were carried out for all bryophytes and for mosses (Bryophyta s. str.) and liverworts (Marchantiophyta) separately. Jackknife estimates were calculated using EstimateS (Colwell 2004), one-way ANOVAs, Spearman Rank correlations and GLMs with Statistica 7.0 (StatSoft Inc 2001), Sørensen's similarity index, MDS and ANOSIM with Primer 5.0 (PRIMER-E Ltd 2002) and Mantel tests using PC-ORD 5.0 (McCune and Mefford 1999).

Results

Species richness

In total, 119 bryophyte species were collected including 63 of liverwort and 56 of moss (Fig. 1). In NF sites, 84 species (72% of estimated species richness) were recorded, in CNS, 47 species (73% of estimate), and in CPS, 58 species (79% of estimate) (Fig. 1). At the per site level, neither observed nor estimated species numbers of all bryophytes, liverworts or mosses were affected by habitat type (Table 1, Fig. 2). Species richness also remained unaffected by habitat type at the level of site, tree and height zone (Table 1). Moreover, no significant differences between the three zones within trees could be found (Table 1).

Species composition

In terms of species composition, 48 species (40%) were exclusively found in NF sites, 14 species (12%) in CPS and 7

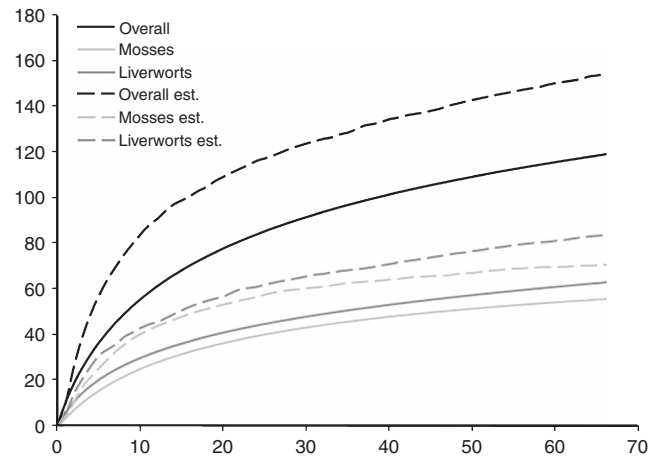


Fig. 1. Species accumulation curves for overall bryophytes (black lines), liverworts (dark shaded lines) and mosses (light shaded lines) on understory trees in 11 study sites in Central Sulawesi, Indonesia. Continuous lines are for observed species richness and dotted lines are for estimated species richness (first order Jackknife estimators). Height zones are taken as sampling units.

species (6%) in CNS. Thirty-five species were restricted to cacao agroforest sites in general. The first two dimensions of the multidimensional scaling of Sørensen's similarity matrices reduced 99.9% of the raw stress, showing stress values of 0.08 for all bryophytes, 0.05 for liverworts and 0.1 for mosses. The multidimensional scaling showed distinct differences in overall bryophyte community composition and moss and liverwort assemblages between the two types of cacao plantations and the NF sites (Fig. 3). ANOSIM showed that the differences between CPS and NF were significant for all bryophytes, liverworts and mosses, but between CNS and NF only for mosses (Table 2).

Table 1. The results of the ANOVA and general linear model analyses that were used to test for the effects of 'Habitat', 'Site', 'Tree' and height 'Zone' on observed and estimated species richness in natural forest sites and cacao (*Theobroma cacao*) agroforests in Central Sulawesi, Indonesia

CNS, cacao plantation under natural shade; CPS, cacao plantation under planted shade; est., first-order Jackknife estimated species richness; NF, natural forest; obs., observed species richness

| Effect | Habitat type | Site | Tree |
|-------------------|-------------------------------|---------------------------------|--------------------------------|
| Bryophytes | | | |
| Site | obs.: | ANOVA: F(2, 8) = 0.66, P = 0.54 | |
| | est.: | ANOVA: F(2, 8) = 1.79, P = 0.23 | |
| Tree | GLM: F(2, 8) = 0.24, P = 0.79 | GLM: F(8, 10) = 2.51, P = 0.09 | GLM: F(1, 10) = 0.03, P = 0.86 |
| Zone | GLM: F(2, 8) = 0.08, P = 0.92 | GLM: F(8, 52) = 2.87, P = 0.01 | GLM: F(1, 52) = 0.2, P = 0.66 |
| Liverworts | | | |
| Site | obs.: | ANOVA: F(2, 8) = 0.01, P = 0.99 | |
| | est.: | ANOVA: F(2, 8) = 0.19, P = 0.83 | |
| Tree | GLM: F(2, 8) = 0.09, P = 0.91 | GLM: F(8, 10) = 2.48, P = 0.09 | GLM: F(1, 10) = 2.22, P = 0.17 |
| Zone | GLM: F(2, 8) = 1.29, P = 0.33 | GLM: F(8, 52) = 2.10, P = 0.05 | GLM: F(1, 52) = 2.22, P = 0.14 |
| Mosses | | | |
| Site | obs.: | ANOVA: F(2, 8) = 1.65, P = 0.25 | |
| | est.: | ANOVA: F(2, 8) = 2.44, P = 0.15 | |
| Tree | GLM: F(2, 8) = 1.47, P = 0.29 | GLM: F(8, 10) = 1.97, P = 0.16 | GLM: F(1, 10) = 1.61, P = 0.23 |
| Zone | GLM: F(2, 8) = 0.52, P = 0.61 | GLM: F(8, 52) = 3.06, P = 0.007 | GLM: F(1, 53) = 1.20, P = 0.28 |

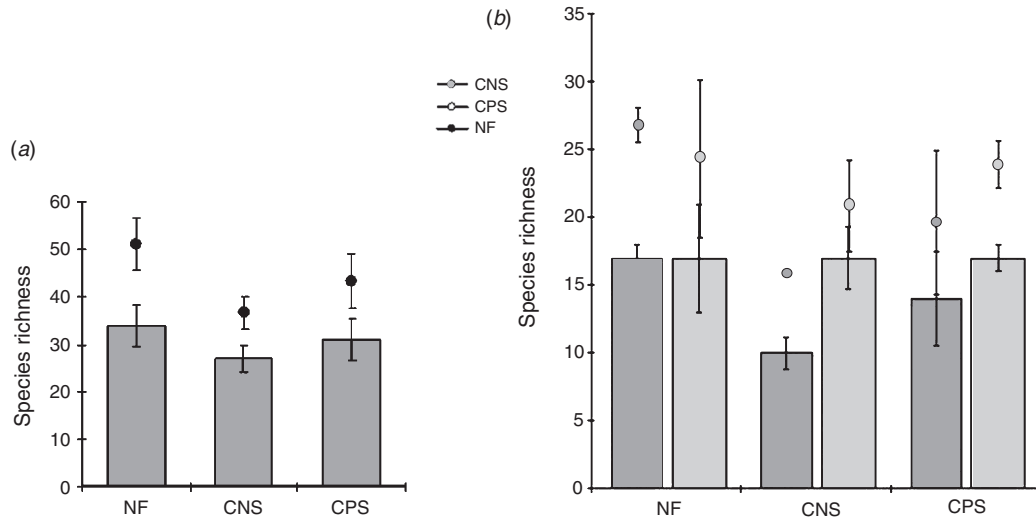


Fig. 2. Mean numbers of observed (grey bars) and estimated (black dots) species richness of (a) bryophytes and (b) liverworts and mosses on understory trees in natural forests (NF), cacao plantations under natural shade (CNS), and in cacao plantation under planted shade (CPS) in Central Sulawesi, Indonesia. Vertical bars indicate the standard error.

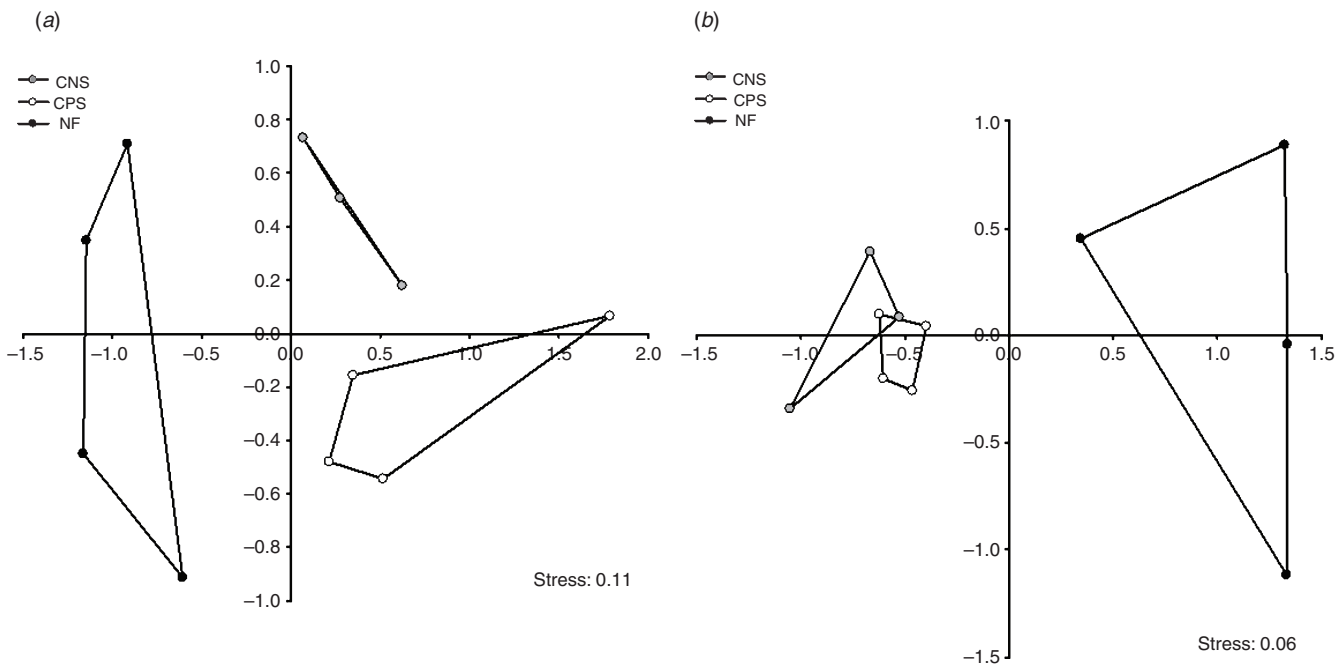


Fig. 3. Multidimensional scaling based on Sørensen's indices for similarity of species compositions of (a) mosses and (b) liverworts on understory trees in natural forests (NF), cacao agroforests under natural shade (CNS) and cacao agroforests under planted shade (CPS) in Central Sulawesi, Indonesia.

Microclimate and species richness

While overall air temperature and relative air humidity did not differ between habitat types, maximum temperature and minimum relative humidity differed significantly with highest respectively lowest values being measured in CPS (Table 3). Both overall and maximum values of VPD differed significantly between habitat types with highest values also in CPS (Table 3).

None of the species richness values per site (neither observed nor estimated) were significantly correlated with any of the microclimate variables (Table 4).

Microclimate and species composition

The first dimension of the multidimensional scaling of Sørensen's similarity matrices of overall bryophytes and liverworts was significantly correlated with maximum temperature and

Table 2. The results of analyses of similarity (ANOSIM) based on Sørensen's similarity index of overall bryophyte composition, liverwort and moss composition in three habitat types in Central Sulawesi, Indonesia

CNS, cacao (*Theobroma cacao*) plantation under natural shade; CPS, cacao plantation under planted shade; NF, natural forest. Asterisks indicate significance ($P < 0.05$)

| | NF v. CNS | | NF v. CPS | | CNS v. CPS | |
|------------|-----------|----------|-----------|----------|------------|----------|
| | <i>R</i> | <i>P</i> | <i>R</i> | <i>P</i> | <i>R</i> | <i>P</i> |
| Bryophytes | 0.806 | 0.057 | 0.865 | 0.029* | 0.333 | 0.114 |
| Liverworts | 0.722 | 0.057 | 0.698 | 0.029* | 0.222 | 0.171 |
| Mosses | 0.759 | 0.029* | 0.755 | 0.029* | 0.389 | 0.057 |

Table 3. The mean values of the microclimatic factors per habitat type in Central Sulawesi, Indonesia

CNS, cacao (*Theobroma cacao*) plantation under natural shade; CPS, cacao plantation under planted shade; max, maximum values; min, minimum values; NF, natural forest; RH, relative humidity; T, temperature; VPD, vapour pressure deficit. Statistical significance between habitat types are indicated by superscript letters based on Tukey's HSD post hoc tests after the ANOVA

| | NF | CNS | CPS | ANOVA results |
|---------|-------------------------|--------------------------|-------------------------|-----------------------------|
| T | 21.8 ± 0.4 | 22.8 ± 1.3 | 22.6 ± 0.1 | F(2, 8) = 0.8, $P = 0.5$ |
| T min | 19.4 ± 0.5 | 19.4 ± 1.1 | 18.6 ± 0.2 | F(2, 8) = 0.6, $P = 0.6$ |
| T max | 26.2 ± 0.6 ^a | 29.4 ± 1.5 ^{ab} | 30.6 ± 0.6 ^b | F(2, 8) = 8.1, $P = 0.01$ |
| RH | 93.2 ± 1.4 | 89.2 ± 2.0 | 89.5 ± 0.5 | F(2, 8) = 3.1, $P = 0.1$ |
| RH min | 74.6 ± 4.0 ^a | 59.9 ± 2.4 ^b | 55.6 ± 1.3 ^b | F(2, 8) = 12.7, $P = 0.003$ |
| RH max | 99.7 ± 0.2 | 98.7 ± 1.2 | 99.4 ± 0.3 | F(2, 8) = 0.8, $P = 0.5$ |
| VPD | 2.1 ± 0.4 ^a | 3.6 ± 0.3 ^b | 4.3 ± 0.1 ^b | F(2, 8) = 13.3, $P = 0.003$ |
| VPD max | 8.9 ± 1.7 ^a | 16.5 ± 1.2 ^b | 20.5 ± 1.2 ^b | F(2, 8) = 18.8, $P = 0.001$ |

maximum VPD, in that bryophyte are positively and liverworts negatively correlated for both values (Table 4). There was no correlation between microclimate values and the second dimension of the multidimensional scaling.

Sørensen's similarity matrices for overall bryophyte species, mosses and liverworts were not related to similarity matrices calculated from pairwise site comparisons of temperature and relative humidity. However, these matrices were significantly and positively related to minimum relative humidity and maximum temperature, and to overall and maximum VPD (Tables 4, 5). In contrast, none of the species richness similarity matrices correlated with microclimatic similarity (Table 5).

Discussion

Species richness

The results show that levels of bryophyte species richness on cacao trees in agroforests can be comparable to those found in the understory of pristine natural forests. Neither observed nor estimated species richness per site differed between the natural forest and the two types of cacao agroforests, a finding that is in line with recent studies on, for example, birds, lower canopy beetles and ants, trees and bryophytes in South America (da Costa 1999; Acebey *et al.* 2003; Nöske 2005; Harvey and González Villalobos 2007) and South-east Asia (Schulze *et al.* 2004; Bos *et al.* 2007; Steffan-Dewenter *et al.* 2007; Ariyanti *et al.* 2008).

Species richness of epiphytic bryophytes in the understory of natural forests in Central Sulawesi with 84 species on eight understory trees exceeds that recorded from submontane rainforest of Bolivia (80 spp. on 6 mature canopy trees; Acebey *et al.* 2003) and in montane rainforests in Ecuador (72 spp. on 10 mature canopy trees; Nöske 2005). The high bryophyte richness on forest understory trees in the study area is also reflected in that of adjacent cacao agroforests where 71 species were recorded on 14 cacao trees. In comparison, Andersson and Gradstein (2005) found only 44 species on 116 cacao and 29 shade trees in Ecuadorian cacao agroforests, even though these plantations were older (20–50 years) than those in Indonesia (4–15 years). Moreover, the bryophyte flora of Ecuador with almost 1500 reported species (Léon-Vargas *et al.* 2006) is richer than that of Sulawesi (597 species recorded; Ariyanti *et al.* 2009).

Species composition

In terms of species composition, the present study revealed a significant turnover from the natural forest sites to the cacao agroforests. Only 30% of the species recorded on understory trees in the natural forest also occurred in the agroforests. Turnover between the two types of agroforests was not significant, however, and within the habitat types, turnover was lower than between forest sites.

High turnover of epiphytic bryophytes in response to human-induced habitat changes has also been documented in other studies. For example, only 45% of bryophyte species on Bolivian forest trees also occurred in adjacent fallows (Acebey *et al.* 2003). Ariyanti *et al.* (2008) found 40% similarity between the bryophyte floras of forest trunk bases and agroforests in the study area in Central Sulawesi. Taken together, these data do not support the assumption of Andersson and Gradstein (2005) that the bryophyte flora of cacao plantations is similar to that of the rainforest and that agroforests are a suitable surrogate habitat for the understory bryophyte flora of natural forests.

Microclimate effects on species richness and composition

From natural forest to cacao agroforests, microclimate differed significantly in minimum relative humidity (lowest values in cacao agroforests) and maximum temperature and vapour pressure deficit (highest values in cacao agroforests). These results indicate the occurrence of a daily 'bottleneck' of drier and warmer microclimatic conditions, generally between 1230 hours and 1530 hours (Fig. 4), in cacao agroforests as compared with the rainforest. Such microclimatic changes due to habitat change have been reported previously from South American rainforests (e.g. Walsh 1996; Leigh 1999; Acebey *et al.* 2003; Nöske 2005).

Several authors (Sillett *et al.* 1995; da Costa 1999; Acebey *et al.* 2003) have predicted major epiphytic bryophyte species losses in response to microclimatic changes resulting from forest management intensification such as canopy thinning as a result of the sensitivity of these organisms to the microclimate (e.g. Barkman 1958; Gignac 2001). Surprisingly, the results of the present study revealed that neither overall means nor mean daily minimum and maximum values of the microclimatic factors were related to levels of species richness. In contrast, it is shown that bryophyte species compositions and microclimatic similarities

Table 4. Results of Spearman Rank analysis between the microclimatic factors and observed and estimated bryophytes species richness, and the dimension values of the multidimensional scaling Bryo, overall bryophytes; est., first-order Jackknife estimated species richness; Liv, liverworts; max, maximum values; MDS1, the values of the first dimension of the multidimensional scaling; MDS2, the values of the second dimension of the multidimensional scaling; min, minimum values; Moss, mosses; obs., observed species richness; RH, relative humidity; T, temperature; VPD, vapour pressure deficit. Asterisks indicate significance at the **P* < 0.05, ***P* < 0.01 and ****P* < 0.001 level

| | T | | RH | | VPD | | Moss | | Liv | | Bryo | | Moss | | Liv | | Bryo | | Moss | | Liv | | Moss | |
|------------|-------|-------|--------|--------|---------|-----------|-----------|----------|-----------|-----------|----------|------------|------------|-----------|------------|-----------|------------|------------|-----------|------------|-----------|------------|------|--|
| | T min | T max | RH min | RH max | VPD max | Bryo obs. | Moss obs. | Liv obs. | Bryo est. | Moss est. | Liv est. | Bryo MDS 1 | Moss MDS 1 | Liv MDS 1 | Moss MDS 2 | Liv MDS 2 | Bryo MDS 2 | Moss MDS 2 | Liv MDS 2 | Moss MDS 2 | Liv MDS 2 | Moss MDS 2 | | |
| T | 1.00 | 0.51 | 0.69* | -0.11 | 0.49 | 0.06 | -0.19 | 0.06 | -0.12 | -0.36 | 0.16 | 0.52 | 0.25 | -0.45 | 0.25 | -0.14 | 0.24 | 0.21 | | | | | | |
| T min | | 1.00 | 0.07 | 0.68* | -0.39 | 0.28 | -0.10 | 0.28 | 0.24 | -0.17 | 0.28 | 0.24 | -0.07 | -0.20 | 0.15 | -0.25 | 0.16 | | | | | | | |
| T max | | | 1.00 | -0.41 | 0.75** | -0.33 | -0.30 | -0.31 | -0.39 | -0.30 | -0.28 | 0.77** | -0.77** | 0.56 | -0.35 | 0.44 | 0.15 | | | | | | | |
| RH | | | | 1.00 | -0.83** | 0.42 | 0.39 | 0.16 | 0.56 | 0.37 | 0.15 | -0.49 | 0.26 | -0.49 | 0.13 | -0.35 | -0.11 | | | | | | | |
| RH min | | | | | 1.00 | 0.21 | -0.93** | 0.19 | 0.02 | 0.20 | 0.22 | -0.51 | 0.59 | -0.58 | 0.26 | -0.31 | 0.07 | | | | | | | |
| RH max | | | | | | 1.00 | -0.29 | 0.18 | 0.22 | -0.11 | 0.25 | -0.04 | -0.13 | -0.16 | -0.21 | -0.03 | -0.10 | | | | | | | |
| VPD | | | | | | | 1.00 | 0.85** | -0.20 | -0.22 | -0.02 | 0.60 | 0.65* | 0.65* | 0.58 | -0.10 | | | | | | | | |
| VPD max | | | | | | | | 1.00 | -0.21 | -0.05 | -0.29 | -0.25 | -0.66* | 0.58 | -0.35 | 0.41 | | | | | | | | |
| Bryo obs. | | | | | | | | | 1.00 | 0.75** | 0.95** | 0.49 | 0.71* | 0.37 | 0.37 | -0.68* | -0.46 | | | | | | | |
| Moss obs. | | | | | | | | | | 1.00 | 0.81** | 0.89** | 0.16 | -0.72* | 0.34 | -0.12 | -0.25 | -0.47 | | | | | | |
| Liv obs. | | | | | | | | | | | 1.00 | 0.65* | -0.12 | 0.95** | 0.14 | 0.83* | -0.9** | -0.29 | | | | | | |
| Bryo est. | | | | | | | | | | | | 1.00 | 0.61* | 0.25 | -0.28 | 0.40 | -0.7* | -0.49 | | | | | | |
| Moss est. | | | | | | | | | | | | | 1.00 | 0.44 | -0.55 | -0.33 | -0.03 | -0.34 | | | | | | |
| Liv est. | | | | | | | | | | | | | | 1.00 | 0.24 | 0.81* | -0.77** | -0.43 | | | | | | |
| Bryo MDS 1 | | | | | | | | | | | | | | | 1.00 | 0.11 | 0.09 | 0.24 | 0.11 | 0.23 | 0.36 | | | |
| Liv MDS 1 | | | | | | | | | | | | | | | | 1.00 | -0.79** | 0.82** | -0.05 | -0.04 | -0.31 | | | |
| Moss MDS 1 | | | | | | | | | | | | | | | | | 1.00 | 0.43 | 0.43 | -0.12 | -0.12 | | | |
| Bryo MDS 2 | | | | | | | | | | | | | | | | | | 1.00 | 1.00 | 1.00 | -0.85** | -0.18 | | |
| Liv MDS 2 | | | | | | | | | | | | | | | | | | | 1.00 | 1.00 | 1.00 | 0.21 | | |
| Moss MDS 2 | | | | | | | | | | | | | | | | | | | | 1.00 | 1.00 | 0.21 | | |

Table 5. The results of the Mantel tests for associations between differences in species composition and species richness, and differences in microclimate values in four forest sites and seven cacao (*Theobroma cacao*) agroforests in Central Sulawesi, Indonesia

max, maximum values; min, minimum values; RH, relative humidity; T, temperature. Asterisks indicate significance at the **P* < 0.05, ***P* < 0.01 and ****P* < 0.001 level

| Composition | T | | RH | | T max | | RH min | | RH max | | VPD | | VPD max | |
|------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|------------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|--------|-----|---------|---------|---------|
| | T min | T max | T min | T max | T min | T max | RH min | RH max | RH min | RH max | VPD | VPD max | VPD | VPD max |
| Bryophytes | r = 0.08, <i>t</i> = 0.39 | r = 0.42, <i>t</i> = 2.86** | r = 0.01, <i>t</i> = 0.05 | r = 0.23, <i>t</i> = 1.16 | r = 0.61, <i>t</i> = 3.50*** | r = -0.26, <i>t</i> = -1.17 | r = -0.26, <i>t</i> = -1.17 | r = 0.60, <i>t</i> = 3.01** | r = 0.62, <i>t</i> = 3.30** | | | | | |
| Liverworts | r = 0.10, <i>t</i> = 0.46 | r = 0.41, <i>t</i> = 2.72** | r = -0.01, <i>t</i> = -0.05 | r = 0.24, <i>t</i> = 1.15 | r = -0.24, <i>t</i> = -1.03 | r = -0.24, <i>t</i> = -1.03 | r = -0.24, <i>t</i> = -1.03 | r = 0.59, <i>t</i> = 2.83** | r = 0.59, <i>t</i> = 3.05** | | | | | |
| Mosses | r = 0.08, <i>t</i> = 0.48 | r = 0.38, <i>t</i> = 2.72** | r = 0.12, <i>t</i> = 0.73 | r = 0.16, <i>t</i> = 1.05 | r = 0.54, <i>t</i> = 3.69*** | r = -0.21, <i>t</i> = -1.26 | r = -0.21, <i>t</i> = -1.26 | r = 0.47, <i>t</i> = 2.98** | r = 0.49, <i>t</i> = 3.24** | | | | | |
| Richness | | | | | | | | | | | | | | |
| <i>Observed</i> | | | | | | | | | | | | | | |
| Bryophytes | r = 0.09, <i>t</i> = 0.47 | r = -0.03, <i>t</i> = -0.18 | r = 0.13, <i>t</i> = 0.67 | r = -0.07, <i>t</i> = -0.39 | r = 0.00, <i>t</i> = 0.00 | r = -0.14, <i>t</i> = -0.67 | r = -0.14, <i>t</i> = -0.67 | r = 0.02, <i>t</i> = 0.10 | r = 0.02, <i>t</i> = 0.14 | | | | | |
| Mosses | r = 0.02, <i>t</i> = 0.10 | r = -0.03, <i>t</i> = -0.19 | r = 0.06, <i>t</i> = 0.26 | r = -0.08, <i>t</i> = -0.39 | r = 0.08, <i>t</i> = 0.45 | r = -0.19, <i>t</i> = -0.78 | r = -0.19, <i>t</i> = -0.78 | r = 0.09, <i>t</i> = 0.42 | r = 0.09, <i>t</i> = 0.45 | | | | | |
| Liverworts | r = -0.01, <i>t</i> = -0.05 | r = -0.15, <i>t</i> = -0.96 | r = -0.07, <i>t</i> = -0.29 | r = -0.1, <i>t</i> = -0.43 | r = -0.18, <i>t</i> = -0.93 | r = -0.01, <i>t</i> = -0.03 | r = -0.01, <i>t</i> = -0.03 | r = -0.17, <i>t</i> = -0.71 | r = -0.18, <i>t</i> = -0.84 | | | | | |
| <i>Estimated</i> | | | | | | | | | | | | | | |
| Bryophytes | r = 0.13, <i>t</i> = 0.62 | r = 0.08, <i>t</i> = 0.51 | r = 0.18, <i>t</i> = 0.94 | r = 0.11, <i>t</i> = 0.58 | r = 0.12, <i>t</i> = 0.72 | r = -0.06, <i>t</i> = -0.3 | r = -0.06, <i>t</i> = -0.3 | r = 0.15, <i>t</i> = 0.78 | r = 0.17, <i>t</i> = 0.94 | | | | | |
| Mosses | r = 0.14, <i>t</i> = 0.62 | r = 0.04, <i>t</i> = 0.27 | r = 0.15, <i>t</i> = 0.74 | r = -0.02, <i>t</i> = -0.10 | r = 0.13, <i>t</i> = 0.76 | r = -0.22, <i>t</i> = -0.94 | r = -0.22, <i>t</i> = -0.94 | r = 0.18, <i>t</i> = 0.88 | r = 0.15, <i>t</i> = 0.77 | | | | | |
| Liverworts | r = -0.08, <i>t</i> = -0.29 | r = -0.16, <i>t</i> = -1.04 | r = -0.13, <i>t</i> = -0.53 | r = -0.05, <i>t</i> = -0.20 | r = -0.17, <i>t</i> = -0.83 | r = 0.04, <i>t</i> = 0.15 | r = 0.04, <i>t</i> = 0.15 | r = -0.14, <i>t</i> = -0.59 | r = -0.17, <i>t</i> = -0.76 | | | | | |

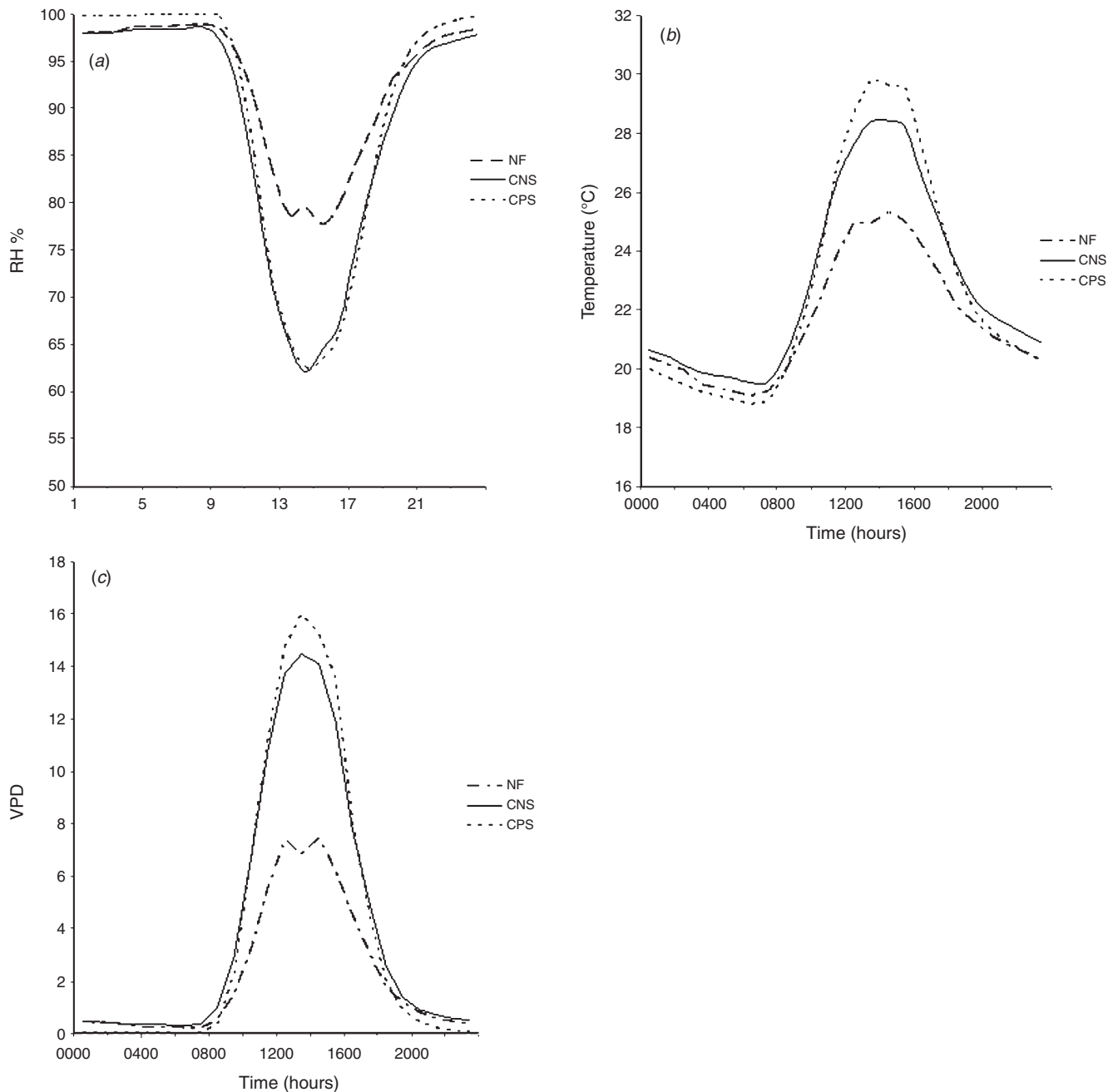


Fig. 4. Daily course of (a) relative air humidity (RH %), (b) temperature (Temp °C) and (c) vapour pressure deficit (VPD) in natural forests (dashed line), cacao agroforests under natural shade (solid line) and cacao forests under planted shade (dotted line) at the Lore Lindu national park, Sulawesi, Indonesia.

were strongly related, this indicates that differences between bryophyte communities increased with increasing microclimatic differences. This strong relation between species composition and a microclimatic 'bottleneck' of maximum temperature and drought is also supported by a study in montane forests of Ecuador (Nöske 2005). Epiphytic bryophytes are known to have narrow microclimatic ranges at which optimal photosynthesis takes place (Léon-Vargas *et al.* 2006), which may explain the strong correlation between similarities in bryophytes species composition and microclimatic similarities.

Bryophyte species that are specialists of shaded and moist microhabitats ('shade epiphytes') have limited tolerance to microclimatic changes and are the first to be threatened along a disturbance gradient (Gradstein 1992; Acebey *et al.* 2003; Andersson and Gradstein 2005). Contrastingly, ecological generalists and 'sun-epiphyte' species occurring in forest canopies, forest edges and in gaps, may invade the understory of more open disturbed forests (Gradstein 1992; Rice and Greenberg 2000; Acebey *et al.* 2003; Andersson and Gradstein 2005). This mechanism most likely underlies the high turnover in bryophyte

composition from understory in natural forest sites to that in cacao agroforests. Whether the species found on cacao trees in the agroforests do indeed originate from the forest canopy cannot be answered yet and requires analysis of the canopy bryophyte flora.

Differences between mosses and liverworts

Composition on cacao trees did not differ between the two types of cacao agroforests for all bryophytes or liverworts, but differed clearly for mosses. This agrees with Acebey *et al.* (2003) who found that bryophyte species richness on trees in natural forests and fallows only differed for mosses and not for liverworts.

Nevertheless, species richness of neither liverworts nor mosses was related to microclimatic factors. However, the observed daily bottleneck in microclimate (maximum VPD and temperature values) did drive changes in species composition of liverworts and only weakly of mosses. This may have represented a shift from a liverwort species composition in natural forests dominated by shade epiphytes, to a composition with more 'sun-epiphytes' in the agroforests. Mosses seemed to be less sensitive and more generalistic in terms of microclimate changes. Hence, these results suggest that other factors than the investigated microclimate factors may drive changes in species composition of mosses, a group that is otherwise suggested to be particularly sensitive to microclimate changes (Barkman 1958; Frahm 2003). Such factors may be continuous or annual microclimate dynamics and light conditions, which were not included in the present study. Furthermore, differences in previous land-use, time since conversion, age of the trees, or differences in pruning techniques used in the plantations may have also influenced the distribution of mosses. For example, Wolf (1994) stated that changes in bryophyte communities in Columbian upper montane forests were driven by tree height and age, which may have been true for epiphytic mosses in the present study as well. Tree age (which differed between the two types of cacao agroforests) is also suggested to affect bryophyte species composition by the slow re-establishment of epiphytic bryophytes in disturbed habitats (Nadkarni 2000; Acebey *et al.* 2003). Indeed, liverwort taxa such as Lejeuneaceae are described as being pioneers, appearing in fallows within 4 years after rainforest clearance, whereas mosses did not re-establish until 10 years after clearance (Acebey *et al.* 2003).

Conclusion

The present study shows that conversion of natural forest to cacao agroforests may not lead to decreases in the species richness of epiphytic bryophytes on understory trees, but may result in considerable changes in species composition. This high turnover from natural to cultivated forest types is most likely driven by the microclimatic 'bottleneck' of low humidity and high temperatures occurring during the early afternoon in the agroforests. To corroborate these results and investigate underlying mechanisms, experimental approaches under standardised conditions, such as transplant experiments between different habitat types, are recommended. It is concluded that microclimate factors can be a strong predictor for changes in species composition in relation to habitat change in tropical rainforest areas where levels of species richness often remain unaffected by disturbance. Therefore, it

is strongly recommended that microclimate measurements are included in studies on epiphytic bryophyte assemblages in tropical forest landscapes. Conversely, the present study shows that species counts alone may be misleading as a basis for evaluating the impact of land use intensification in tropical habitats, and that species identities must be taken into account.

Acknowledgements

This study was carried in the framework of the German–Indonesian research program 'Stability of Rainforest Margins in Indonesia' (STORMA) funded by the German Research Foundation (DFG-SFB 552, grant to SRG). Additional financial support was received from the 'SYNTHESYS' project of the European Community. We thank two anonymous reviewers for their valuable comments on a previous version of the manuscript. We gratefully acknowledge the help from our counterpart Ibu Sri Tjitrosoedirdjo from the Herbarium in Bogor (BIOTROP), STORMA's partner university in Palu (Universitas Tadulako), Sulawesi, the Ministry of Education in Jakarta (DIKTI), the authorities of Lore Lindu National Park, the cacao farmers in Toro village, and STORMA's coordinating teams in Germany and Indonesia. Furthermore, we thank Mina, Hardianto and Grischa Brokamp for field assistance, and Nunik Ariyanti, Michael Burghardt, Jörn Hentschel and Bastian Steudel for help with collection sorting and identification.

References

- Acebey C, Gradstein SR, Krömer T (2003) Species richness and habitat diversification of bryophytes in submontane rain forest and fallows in Bolivia. *Journal of Tropical Ecology* **18**, 1–16.
- Achard F, Eva HD, Stibig HJ, Mayaux P, Gallego J, Richards T, Malingreau JP (2002) Determination of deforestation rate of the world's humid tropical rain forest. *Science* **297**, 999–1002. doi: 10.1126/science.1070656
- Andersson MS, Gradstein SR (2005) Impact of management intensity on non-vascular epiphyte diversity in cacao plantations in Western Ecuador. *Biodiversity and Conservation* **14**, 1101–1120. doi: 10.1007/s10531-004-7840-5
- Ariyanti NS, Bos MM, Kartawinata K, Tjitrosoedirdjo SS, Guhardja E, Gradstein SR (2008) Bryophytes on tree trunks in natural forests, selectively logged forests and cacao agroforests in Central Sulawesi, Indonesia. *Biological Conservation* **141**, 2516–2527. doi: 10.1016/j.biocon.2008.07.012
- Ariyanti NS, Gradstein SR, Sporn SG, Angelika R, Tan BC (2009) Catalogue of the bryophytes of Sulawesi. Supplement 1: new species records. *Blumea*, in press.
- Ataroff M, Rada F (2000) Deforestation impact on water dynamics in a Venezuelan Andean cloud forest. *Ambio* **29**, 440–444. doi: 10.1639/0044-7447(2000)029[0440:DIOWDI]2.0.CO;2
- Barkman JJ (1958) 'Phytosociology and ecology of cryptogamic epiphytes.' (Van Gorcum: Assen).
- Barlow J, Gardner TA, Araujo IS, Avila-Pires TC, Bonaldo AB, *et al.* (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 18555–18560. doi: 10.1073/pnas.0703333104
- Bos MM, Steffan-Dewenter I, Tschamtkte T (2007) The contribution of cacao agroforests to the conservation of lower canopy ant and beetle diversity in Indonesia. *Biodiversity and Conservation* **16**, 2429–2444. doi: 10.1007/s10531-007-9196-0
- Bos MM, Tylianakis JM, Steffan-Dewenter I, Tschamtkte T (2008) The invasive Yellow Crazy Ant in Indonesian cacao agroforests and the decline of forest ant diversity. *Biological Invasions* **8**, 1399–1409. doi: 10.1007/s10530-008-9215-4
- Brockerhoff EG, Jactel H, Parrota JA, Quine P, Sayer J (2008) Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation* **17**, 925–951. doi: 10.1007/s10531-008-9380-x

- Cannon CH, Summers M, Harting JR, Kessler JA (2007) Developing conservation priorities based on forest type, condition, and threats in a poorly known ecoregion: Sulawesi, Indonesia. *Biotropica* **39**, 747–759. doi: 10.1111/j.1744-7429.2007.00323.x
- Colwell RK (2004) 'EstimateS. Statistical estimation of species richness and shared species from samples. Version 7.0.' (University of Connecticut: Connecticut).
- da Costa DP (1999) Epiphytic bryophyte diversity in primary and secondary lowland rainforests in southeastern Brazil. *The Bryologist* **102**, 320–326. doi: 10.2307/3244372
- Dietz J, Hölscher D, Leuschner C, Hendrayanto (2006) Rainfall partitioning in relation to forest structure in differently managed montane forest stand in Central Sulawesi, Indonesia. *Forest Ecology and Management* **237**, 170–178. doi: 10.1016/j.foreco.2006.09.044
- Frahm J-P (2003) Manual of tropical bryology. *Tropical Bryology* **23**, 1–196.
- Gignac D (2001) Bryophytes as indicators of climate change. *The Bryologist* **104**, 410–420. doi: 10.1639/0007-2745(2001)104[0410:BAIOCC]2.0.CO;2
- Gradstein SR (1992) Threatened bryophytes of the neotropical rain forest: a status report. *Tropical Bryology* **6**, 83–94.
- Gradstein SR (2008) Epiphytes of tropical montane forests – impact of deforestation and climate change. *Göttingen Centre for Biodiversity and Ecology. Biodiversity and Ecology Series* **2**, 51–65.
- Gradstein SR, Tan BC, Zhu RL, King C, Drubert C, Pitopang R (2005) Catalogue of the bryophytes of Sulawesi, Indonesia. *Journal of the Hattori Botanical Laboratory* **98**, 213–257.
- Gravenhorst G, Ibroms A, Rauf A, June T (2005) 'Climatological parameters in the research area – supporting measurements and regionalization. STORMA research report.' (University of Göttingen: Göttingen).
- Greenberg R (1998) 'Biodiversity in the cacao agroecosystem: shade management and landscape considerations.' (Manuscript of the 'First Sustainable Workshop on Sustainable Cacao Growing', Panama City, Panama) 30.03–02.04.1998 (on-line). Available from <http://national.zoo.si.edu/conservationandscience/migratorybirds/research/cacao/greenberg.cfm> [Accessed 3 June 2008].
- Harvey CA, González Villalobos JA (2007) Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. *Biodiversity and Conservation* **16**, 2257–2292. doi: 10.1007/s10531-007-9194-2
- Hietz P (2005) Conservation of vascular epiphyte diversity in Mexican coffee plantations. *Conservation Biology* **19**, 391–399. doi: 10.1111/j.1523-1739.2005.00145.x
- ICCO (2008) 'Annual report for 2006/2007. The International Cocoa Organization (ICCO).' (ICCO, London).
- Lamb D (1998) Large-scale ecological restoration of degraded tropical forest lands: the potential role of timber plantations. *Restoration Ecology* **6**, 271–279. doi: 10.1046/j.1526-100X.1998.00632.x
- Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* **16**, 605–618. doi: 10.1046/j.1523-1739.2002.01025.x
- Leigh EG, Jr (1999) 'Tropical forest ecology. A view from Barro Colorado Island.' (Oxford University Press: New York)
- Léon-Vargas Y, Engwald S, Proctor MCF (2006) Microclimate, light adaptations and desiccation tolerance of epiphytic bryophytes in two Venezuelan cloud forests. *Journal of Biogeography* **33**, 901–913. doi: 10.1111/j.1365-2699.2006.01468.x
- McCune B, Mefford MJ (1999) 'PC-ORD. Multivariate analysis of ecological data, Version 4.0.' (MjM Software Design, Gleneden Beach: Oregon)
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858. doi: 10.1038/35002501
- Nadkarni NM (2000) Colonization of stripped branch surfaces by epiphytes in a lower montane cloud forest Monteverde Costa Rica. *Biotropica* **32**, 358–363.
- Nöske N (2005) 'Effekte anthropogener Störung auf die Diversität kryptogamischer Epiphyten (Flechten, Moose) in einem Bergregenwald in Südecuador.' (Dissertation, University of Göttingen: Göttingen) Available from <http://webdoc.sub.gwdg.de/diss/2005/noeske/noeske.pdf>
- Perfecto I, Vandermeer J, Hanson P, Cartin V (1997) Arthropod biodiversity loss and the transformation of a tropical agro-ecosystem. *Biodiversity and Conservation* **6**, 935–945. doi: 10.1023/A:1018359429106
- Rice RA, Greenberg R (2000) Cacao cultivation and the conservation of biological diversity. *Ambio* **29**, 167–173. doi: 10.1639/0044-7447(2000)029[0167:CCATCO]2.0.CO;2
- Roos MC, Kessler PJA, Gradstein SR, Baas P (2004) Species diversity and endemism of five major Malesian islands: diversity-area relationships. *Journal of Biogeography* **31**, 1893–1908. doi: 10.1111/j.1365-2699.2004.01154.x
- Schulze CH, Waltert M, Kessler PJA, Pitopang R, Veddeler D, Mühlberg M, Gradstein SR, Leuschner C, Steffan-Dewenter I, Tscharntke T (2004) Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications* **14**, 1321–1333. doi: 10.1890/02-5409
- Sillett S, Gradstein SR, Griffin D (1995) Bryophyte diversity of Ficus tree crowns from cloud forest and pasture in Costa Rica. *The Bryologist* **98**, 251–260. doi: 10.2307/3243312
- Sodhi NS, Koh LP, Brook BW, Ng PKL (2004) Southeast Asian biodiversity: an impending disaster. *Trends in Ecology & Evolution* **19**, 654–660. doi: 10.1016/j.tree.2004.09.006
- StatSoft Inc (2001) STATISTICA (data analysis software system), Version 7. Available from www.statsoft.com.
- Steffan-Dewenter I, Kessler M, Barkman J, Bos MM, Buchori D, et al. (2007) Socioeconomic context and ecological consequences of rainforest conversion and agroforestry intensification. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 4973–4978. doi: 10.1073/pnas.0608409104
- Walsh RPD (1996) Microclimate and hydrology. In 'The Tropical Rain Forest an Ecological Study' (Ed. PW Richards) pp. 206–36. (Cambridge University Press: Cambridge)
- Wolf JHD (1994) Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio* **112**, 15–28. doi: 10.1007/BF00045096

Manuscript received 13 July 2008, accepted 18 November 2008