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Simone Goda Sporn

Epiphytic bryophytes in natural forests and cacao agroforests of Central Sulawesi, Indonesia

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Für meine Familie

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Chapter

1

General Introduction

Introduction

Tropical landscapes, forest conversion and biodiversity

Along the equator, tropical rainforests embrace the earth's surface, representing ecosystems with immense yet poorly understood biological diversity of species and processes. The diurnal and stabile climate allowed here to develop heterogenic, multistratous forests which harbour a unique biodiversity (Richards 1996; Whitmore 1998). Of the about 1.7 million described plant and animal species, more than half that number occur in the tropics, especially in rainforests, the most species rich ecosystems of the world (Heywood & Watson 1995; Myers et al. 2000; Lamoreux et al. 2006). Tropical rainforests provide valuable products and processes that constitute crucial parts of the earth's water, carbon and nutrient cycles (Bawa 2004), and form the economic base of millions of households worldwide.

Alarmingly, ever rising local and global demands for timber and agricultural products still lead to unprecedented levels of deforestation and habitat degradation into agricultural land. In the past 50 years, almost a third of the world's tropical rainforests have been destroyed and a further loss of 10-15% is predicted until 2050 (Millenium Ecosystem Assessment 2005). The destruction of the fragile tropical rainforests causes immediate losses of flora and fauna (Whitmore & Sayer 1992; Turner et al 1997; Brook et al. 2003; Laurance 2007), with irrecoverable effects on ecosystem services, increasing threats such as erosion, depletion of soil nutrients, and invasive species introduced as crops, putting extra pressure on human health and welfare in the developing world (Tilman et al. 1994; Chazdon 2003; Hobbs et al. 2006; Laurance 2007).

The ongoing loss of tropical forests has led to a growing interest in the study of primary forests and biological processes therein, to increase our understanding, and to build upon conservation strategies that as yet fail to preserve rainforests on global scale.

Agroforests as opportunities

Some of the most important tropical cash crops are grown as perennial tree crops, such as coffee (*Coffea* spp.), cacao (*Theobroma cacao*), rubber (*Ficus elastica*), and oil palm (*Elaeis* spp.). Because such plantations more and more represent the only remaining tree cover and because of their superficial resemblance with tropical forests, conservation biologists have studied the ecological function of such “agroforests” for biodiversity and ecosystem services.

Increasingly, agroforests with low management intensity in particular are recognized to be able to shelter high levels of natural forest species and at the same time provide sustainable production and income to farmers (Rice & Greenberg 2000; Schroth et al. 2004; Barlow et al. 2007; Brockerhoff et al. 2008). Typically, agroforests with low management intensity represent the first step in the conversion of natural forests to permanent agriculatural land.

Commonly, agroforestry crops such as coffee and cacao are planted under remaining forest trees or intercropped with shading tree species, along with a variety of other crop plants that diversify farmer’s income sources (Rice & Greenberg 2000; Schroth et al. 2004; Steffan-Dewenter et al. 2007). Such multilayered agroforestry systems with various emergent shading trees, a dense understorey, and herb layer may offer a high variety of habitats that are even suitable for forest species with specific habitat requirements. For various groups, species richness in shaded agroforests even equals that of undisturbed rainforests (Perfecto et al. 1997; Siebert 2002; Andersson & Gradstein 2005; Schulze et al. 2004; Steffan-Deventer et al. 2007; Brockerhoff et al. 2008).

However, when agroforests undergo agricultural intensification, practices are introduced that are believed to increase the productivity of the crop. With agroforestry intensification, traditional management that is characterized by low intensity and multicropping is transformed to zero-shade monocultures. Shade trees that remain from the previous natural forest cover are replaced by monocultures of fast-growing, nitrogen-fixing shade trees (*Gliricidia sepium, Erythrina spp.*), or shade trees are even completely removed. Such management intensifications can result in major declines of species richness to be found in these cultivated forests, thus undermining the potential of agroforests as substitute habitats for natural rainforests (Perfecto et al. 1997; Rice & Greenberg 2000; Siebert 2002).

Impact of forest conversion on microclimate conditions

Envrionmental parameters that change most drastically in response to forest degradation and conversion are climatic factors. Comparative studies on the climatic conditions in pristine and secondary forests revealed sharp increases in temperatures and decreases in relative humidity, particularly as a result of drastic anthropogenic disturbance (Walsh 1996; Siebert 2002; Acebey et al. 2003). After logging events, lower strata become exposed to direct insolation, fall-through of precipitation, and increased air circulation, leading to higher evaporation and soil degradation (Green et al. 1995; Thomas et al. 1999; Dietz et al. 2006).

Bryophytes in tropical forests

One biological group particularly sensitive to forest degradation and conversion due to the related climatic changes are bryophytes. Opening up the canopy of tropical rainforests, either after natural treefall or after anthropogenic logging and deforestation, causes a major threat to bryophytes, particularly those that prefer cool and humid habitats that characterize lower layers of primary, undisturbed rainforests (Frahm 2003; Acebey et al. 2003; Gradstein et al. 2008a, b).

Without cuticle that protects vascular plants against climatic changes in the environment, bryophytes need to compensate daily fluctuations in temperature and humidity by morphological adaptations to store water (e.g., water sacs, a dense rhizoid, folded or filamentous leaves) and by their ability to survive short periods of drought by becoming dormant, but a fast adsorption of water and immediate resumption of the photosynthetic activity as soon as moisture becomes available again (“poikilohydry”; Barkman 1958; Richards 1984; Kürschner & Frey 1999; Gignac 2001; Leon-Vargas et al. 2006).

Long periods of severe drought, however, can not be compensated and lead to definite desiccation (Proctor 2000). This sensitivity to changes in climatic conditions makes bryophytes a valuable indicator of forest integrity and even of global climate changes (Richards 1984; Vanderpoorten & Engels 2002; Frego 2007; Gradstein 2008a).

The need to develop strategies to cope with extreme microclimates and to compete successfully for substrate to settle resulted in various morphological adaptations within the Bryophyta. This is since the Devonian the reason for the high species richness of this ancient plant group (Qiu et al. 2006) and is today reflected in about 15,000 species worldwide (Frahm 2001). About half of these species occur in tropical regions, with highest species richness of about 4000 in the Neotropics, followed by tropical Asia with about 3000, and tropical Africa with about 2000 species (Gradstein et al. 2001; Frahm et al. 2003).

Epiphytic bryophytes

Due to the high relative humidity throughout the year, tropical rainforests form excellent habitats for an epiphytic lifestyle of a wide range of bryophyte species. Although suitable environmental and substrate conditions are even more crucial for this group than for terrestrial species (Frahm 1990; Frahm et al. 2003), they were able to reach high abundance in submontane and montane rainforests throughout the tropics (e.g. Wolf 1993; Holz et al. 2002, Acebey et al. 2003; Gradstein 2008b).

The massive, often overhanging mats and cushions of epiphytic bryophytes cover forest trees, provide valuable sources as growing substrate and nutrition pool to entire communities of vascular epiphytes such as ferns and orchids, and serve as breeding and nesting space for wide ranges of animals such as birds, amphibians and insects (Richards 1984; Nadkarni & Longino 1990; Pharo et al. 1999). Furthermore, epiphytic bryophytes have the ability to store high amounts of precipitation water, causing a “delayed release” and to dissolve nutrients with capillary structures (Pócs 1976; Longton 1984; Clark et al. 2005; Köhler et al. 2007), thereby contributing to the stability of the forest ecosystem (Frego 2007).

Aims, outline and contents of this dissertation

Using the previously mentioned indicative value of epiphytic bryophytes, the present study aims to assess the impact of anthropogenic disturbance on forest ecosystems. By investigating the richness, composition, ecology and distribution of this valuable plant group, pristine tropical forests are compared with cacao agroforests. For the enhanced determination of underlying factors that relate to a disturbance of forest integrity and ongoing degradation, detailed microclimate measurements were included and aligned with the epiphytic bryophyte communities.

To develop fitting recommendations for biodiversity conservation, an international and multidisciplinary research project on the sustainability of rainforest margins ("STORMA"; grant DFG-SFB 552) was set up with three main research goals:

"Analysis of key factors and processes that lead to destabilisation and forest degradation in the forest margin zone of Central Sulawesi"

"Identification and assessment of social, economic, political and ecological conditions that are imperative for stability in the forest margin zone"

"Development of Rapid Appraisal Systems that may serve to evaluate the socio-economic and ecological status of tropical forest margin regions. which aims to achive broad insight into a further step to develop"

This dissertation was part of this project focussing on the biodiversity and socio-economic impacts of epiphytic bryophytes in natural forests and cacao agroforests.

Study region

The study was carried out on the island of Sulawesi, one of the 17 508 islands of Indonesia (Fig. 1), the largest country of SE Asia. Alfred Russel Wallace (1869) described the Indonesian islands as habitat for an unequalled number of species that science did not find anywhere else, a finding that almost 250 years later was, in a more refined form, used by Myers et al. (2000) in the designation of the world's biodiversity hotspots.

The explanation of the extraordinarily high biodiversity in the Southeast Asian region lays in the geological history of the region in general, but of Sulawesi in particular. While other areas underwent major climatic changes in the Pleistocene, the climate in SE Asia was remarkably stabile and largely free from glaciations (Whitmore 1991; McLoughlin, 2001; Whitten et al 2002). Moreover, at times of low sea levels, the Eurasian side of Southeast Asia (e.g., Java, Sumatra, Borneo, and some western parts of Sulawesi) formed continuous land masses, separated by a deep sea from the Australasian side of Southeast Asia (e.g., New Guinea, Australia, and some eastern parts of Sulawesi). This resulted in largely independent floral and faunal speciations followed by a long-term isolation from the Eurasian mainland. This sharp distinction in flora and fauna between Eurasia and Australasia is now called Wallace's Line (e.g. van Oosterzee 1997; Myers et al. 2000) which runs through the Island of Sulawesi, explaining the fact that it is the centre of one of the richest areas in terms of biodiversity (Whitmore 1991; Whitten et al 1996; Myers et al. 2000; Sodhi et al. 2004; Cannon et al. 2007).

Figure 1. Map of Indonesia, study area indicated by and asterisk

Since the the introduction of western agriculture in the 14th century, Indonesian rainforests face ever rising deforestation rates, which still continue with 1.9 million hectare every year (Achard et al. 2002; Wright 2005; FAO 2007). Fourty percent of Indonesia's forests has been lost in the past 50 years, most at the benefit of agricultural land. This large scale conversion from pristine forests to secondary systems requires the formulation and evaluation of implementations for sustainable land-use management and to address those to governmental institutions as well as local stakeholders.

Study sites

The studies in this dissertation were conducted in and around Toro Village (Fig. 2, 1°30'24"S, 120°2'11"E, 800-900 m a.s.l.), situated in the Kulawi Valley at the western border of 231,000 ha largely unfragmented submontane rainforest of Lore Lindu National Park, Central Sulawesi, which generally had a "buffer zone" of 300m between forest sites and agricultural land where selective logging was allowed. The village is surrounded by a mosaic pattern of rice fields, pastures, homegardens and cacao agoforests. In the valley, the overall annual temperature is 23.4°C, relative humidity is 85%, and annual precipitation is 2000 to 3000 mm, without clear seasonal fluctuations (Gravenhorst et al. 2005).

To incorporate a gradient of anthropogenic disturbance in the study set-up, three different land-use types with increasing human impact were defined (Fig.2-4, Appendix).

I) Natural forests (NF):

This habitat type was represented by submontane primary rainforests of Lore Lindu National Park. These natural forests underwent only minor anthropogenic disturbance (e.g., minor rattan extraction, collection of medicinal plants, extensive hunting) and had therefore a high canopy closure approaching 100%, and an intact, dense understorey. The mature canopy trees reached 30 to 50 m in height.

Figure 2. Three different land-use types investigated in this study. On top: Cacao agroforests under planted shade trees (CPS); bottom left: natural forest (NF); bottom right: Cacao agroforests under natural shade (CNS)

2. *Cacao agroforests under natural shade* (CNS):

This habitat type is comprised of cacao agroforests with remaining natural forest trees to provide shade after removal of the majority of the previous forest cover (described as “rustic cacao” by Rice and Greenberg (2000)). Forest conversion took place 10 to 40 years ago, which was started as coffee agroforests and subsequently converted to cacao agroforests. The cacao trees, aged 2 to 15 years, were between 3 and 6.5 m high and shaded by mature trees with up to 35 m height.

3. *Cacao agroforests under planted shade trees* (CPS)

The third habitat type was represented by cacao-dominated agroforests that were shaded by a variety of planted fruit trees such as Langsat (*Lansium domesticum*), Rambutan (*Nephelium lappaceum*) and clove (*Syzygium aromaticum*), timber trees like Bishop wood (*Bischofia javanica*) and the Candlenut tree (*Aleurites moluccana*), as well as the non-indigenous legume trees Gliricidia (*Gliricidia sepium*) and the December tree (*Erythrina subumbrans*). Cacao trees were between four and 10 years old, between 3 and 5 m high, and shaded by trees 15 to 25 m high.

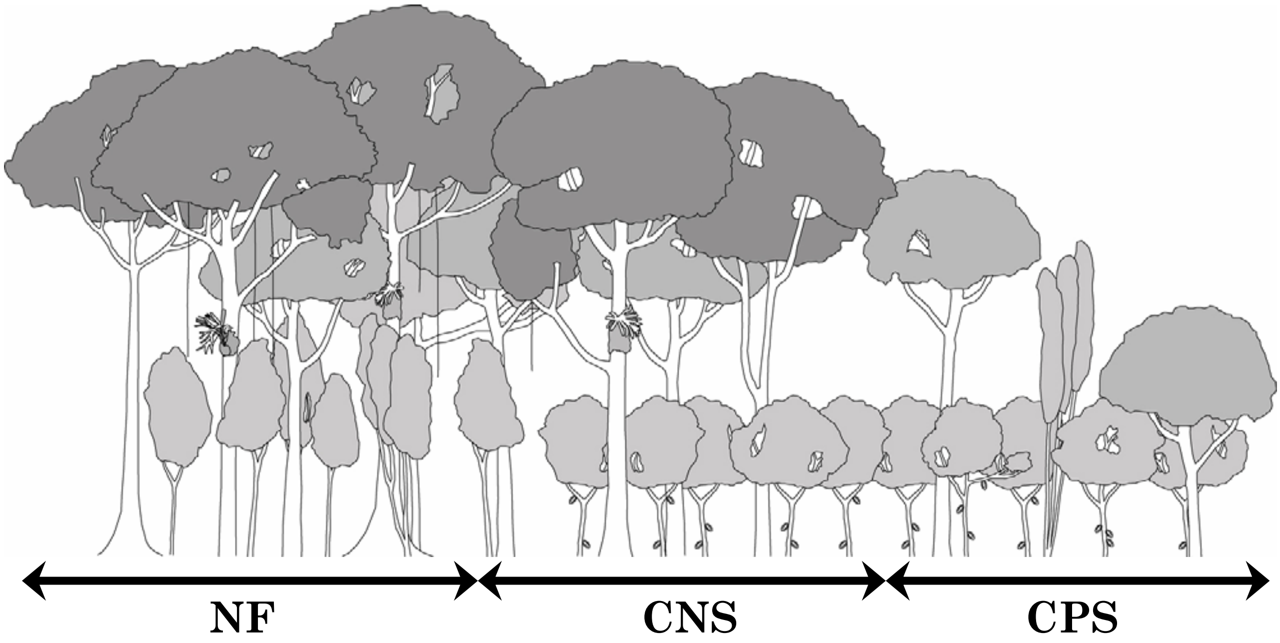

Figure 3. Three different land-use type – a schematic presentation (by MM Bos) CPS: Cacao under planted shade trees; CNS: Cacao under natural shade; NF: Natural forest

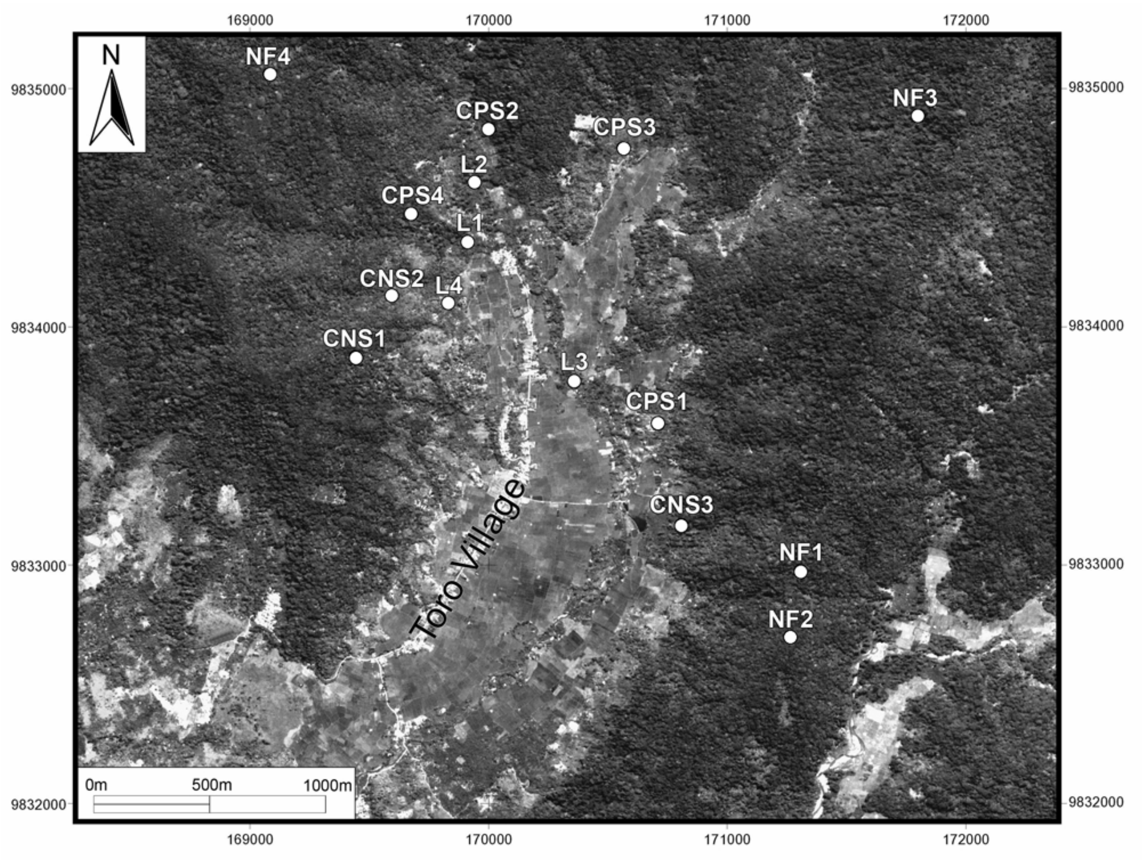

Figure 4. Study sites situated in the Kulawi valley in and around Toro village and surrounded by natural forest of Lore Lindu National Park, Central Sulawesi. CPS1-4: Cacao under planted shade trees; CNS1-3: Cacao under natural shade; NF1-4: Natural forest; L: Sites of epiphyte removal experiment (Chapter 5).

Chapter outline

The diversity of bryophytes on the Island of Sulawesi is still poorly known. In **Chapter 2** an introduction is given to what kind of epiphytic bryophyte communities can be found in pristine natural forest sites. Species richness and species composition was studied along a vertical gradient in the canopy to investigate the sensitivity of bryophyte assemblages to changes in climatic conditions,. For the first time, bryophytes were included from upper canopy trees as well as from understorey trees. This allowed to test the hypothesis that bryophytes respond to climatic differences such as those between understorey and upper canopy in dense, primary rainforests.

To investigate the extent to which the bryophyte flora characterizing forest understoreys can also occur on cacao trees in agroforests, microclimate conditions, species richness, and species compositions are compared between natural forests and cacao agroforests in **Chapter 3**.

Whereas the climatic change from forest understorey to the understorey of cacao agroforests is drastic (see Chapter 3), changes from upper rainforest canopy to the understorey of cacao agroforests are expected to be less sharp. Accordingly, species turnover may be lower from cacao trees to upper canopies than from cacao trees to forest understorey trees, which would suggest that cacao trees are a potential refuge for sun-adapted upper canopy bryophytes. In **Chapter 4**, bryophyte communities in upper forest canopy trees are included in the comparison, along with microclimate measurements from upper forest canopies.

The high species richness of epiphytic bryophytes on cacao trees is threatened by the active removal of epiphytes by farmers, a practice that is known from South America accordingly, and undermines the high biodiversity of cacao agroforests in general and the already low value of cacao agroforests as refuge for native epiphytic bryophytes in particular. Because epiphyte removal is based on the general assumptions that epiphytes impede crop productivity, in **Chapter 5** the impact of epiphyte removal is investigated for potential effects on flower pollination, fruit development, and harvest from 80 cacao trees in four agroforests.

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Chapter

2

Epiphytic bryophyte diversity on understorey and canopy trees in rainforest sites in Central Sulawesi, Indonesia

Abstract

The impact of the climatic change from understorey to upper canopy trees on species richness, composition, and ecology ("life-forms") of epiphytic bryophytes was studied in four natural forest sites in Central Sulawesi, Indonesia. Bryophytes were collected from six height zones of canopy trees and from three vertical zones on understorey trees. Microclimate measurements were carried out at 2 m height and at the base of tree crowns. Hence, this study was the first to include understorey trees in the characterization of epiphytic bryophytes. Overall, the richness of epiphytic bryophytes in the studied forests was high when compared with similar studies in tropical forests elsewhere, and was highest in inner crowns of upper canopy trees. Species composition changed significantly between understorey trees and canopy tree trunks on the one hand, and canopy tree crowns on the other. Dendroid and fan-like species were mostly found in the understorey habitats, whereas tufts were most species rich in the tree crowns. This indicates that in the understorey and on canopy tree trunks, bryophyte communities are characterized by species adapted to more humid conditions, whereas those in tree crowns cope best with sunny and exposed circumstances, which is reflected in climatic patterns that were more humid and cool in the forest understorey and warmer and drier in the canopy tree crowns. Importantly, whereas the exclusion of understorey trees from this study would not have lead to an underestimation of species richness, it would have lead to an underestimation or even negligence of species with dendroid and fan-like life-forms, adapted to the unique humid and cool habitats of the understorey in dense, undisturbed rainforests.

Introduction

Tropical rainforests constitute the most species rich terrestrial ecosystems in the world (e.g., Whitmore 1991; Richards et al. 1996; Myers et al. 2000). Much of this richness is the result of the heterogeneity in habitats and geological history, driving levels of species turnover that are second to none (e.g., Huston 1994; Richards et al. 1996). Such high species turnover can explain over half of regional species richness and may reflect differences in habitat preference, seasonality or geological history (Huston 1994; Myers et al. 2000; Tylianakis et al. 2005; Bos et al. 2007).

Within tropical rainforests, habitat differences primarily result from climatic differences that relate to elevation above sea level (colder towards higher altitudes), soil conditions, vegetation structure (warmer and drier towards higher positions in the canopy), or to anthropogenic disturbances that involve thinning or complete removal of the canopy (Parker 1995; Walsh 1996; Leigh 1999; Acebey et al. 2003; Tuomisto et al. 2003; Dietz et al. 2006). One of the most characteristic groups to be found in tropical forests are epiphytes, but these are also among the organisms most sensitive to habitat differences because they are generally restricted to narrow niches determined by specific substrate, and light and climate conditions (Benzing 1990). Hence, epiphyte species commonly are among the most species rich botanical groups (Gentry & Dodson 1987; Gradstein 2008).

This study focuses on epiphytic bryophytes, which are particularly sensitive indicators for climatic conditions due to the lack of a protective cuticle (Gignac 2001; Frahm 2003; Frego 2007). Although most species can cope with minor environmental changes, exposure to drastic increases in insulation or fluctuations in humidity can easily result in desiccation (Barkman 1958; Frahm 2003; Léon-Vargas et al. 2006), leading to vertical shifts of bryophyte communities on host trees (Gradstein 1992a,b; Acebey et al. 2003).

An additional factor that affects the distribution of epiphytic bryophyte species is the substrate they growth on. Important substrate characteristics are structure, hardness, pH-value and water holding capacity of the bark, as well as chemical properties of exudates from the host tree (Barkman 1958; Rhoades 1995; Richards et al. 1996; Holz 2003). In comparison to microclimate and substrate structure as the main driving factors for bryophyte distributions, chemical factors are considered to play only a minor role in host preference (Frahm 1990) and also host specificity is rare among tropical bryophytes (Pócs 1982; Richards 1984; Kürschner 1990).

Although epiphytic bryophytes are highly sensitive to habitat parameters and are thus unlikely to be found homogeneously from forest understorey to canopy, only few studies have investigated vertical bryophyte distributions in tropical rainforest canopies. For South American forests, species assemblages have been separated into 4 to 6 vegetational zones within the host tree, characterized by species with similar life forms and life history strategies (Pócs 1982; Richards 1984; Cornelissen & ter Steege 1989; Montfoort & Ek 1990; Gradstein et al. 2001; Holz et al 2002; Acebey et al. 2003). Most studies were carried out using (or slightly modifying) the vertical zones described by Johansson (1974) based on differing ecological conditions and species composition of epiphytes on the trunk base (zone 1), the trunk (zone 2), the inner canopy including the main ramification (zone 3), the middle third of the canopy (zone 4), and the outer third of the canopy (zone 5).

Vertical differences in epiphytic bryophyte communities can be related to microclimatic preferences of the individual bryophyte species. Many species possess specific morphological or physiological adaptations to their preferred microclimatic conditions, for example thickened cell walls, pigmentation, water sacs, filamentous leaves, etc. More generally, the ecological adaptation is reflected in the basic architecture or "life-form" of the plant (Mägdefrau 1982). Accordingly, epiphytic bryophytes can be divided in two main groups. Firstly, "specialist" species are those that have a narrow distribution and are often perennial ("perennials" after During 1979). These species can be adapted either to shaded, cooler and more humid habitats or to exposed, sunny and drier habitats. Specialist species in shaded habitats can often be recognized by an exposed life-form (e.g., tufts, pendants, or carpets), and by morphological adaptations such as large leaves, large leave cells, and thin cell walls ("shade epiphytes"; Richards 1996; Gradstein 1992b). Specialist species that are adapted to more exposed, less-shaded habitats can be recognized by compact, mostly creeping life-forms, small and imbricated leaves that spread immediately after remoisturing, and small and thick-walled cells ("sun epiphytes": Richards 1996; Gradstein 1992b; Gradstein 2003).

Secondly, "generalist" species (mostly short-living pioneer species; "shuttle species" after During 1979) have a broader vertical distribution and are morphologically less adapted to specific microclimate conditions. Generalist species can occur in dynamic and young habitats (outer tree crowns, disturbed forests) as well as in older and stabile habitats (inner tree crowns, understorey, undisturbed forests).

In this study, we investigate patterns of epiphytic bryophyte distribution in primary rainforest of Sulawesi, Indonesia. In Southeast Asia, studies on epiphytic bryophytes have to date been restricted to tree trunk bases (Frahm 1990; Kürschner 1990; Ariyanti et al. 2008); this is the first study that includes sampling of bryophytes on whole trees. The purpose of this paper is to analyse patterns of species richness and species composition along the vertical gradient on whole forest trees and treelets, and to explore the correlations between these species diversity patterns and bryophyte life-forms.

Material 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 area has an annual precipitation of 2000-3000 mm, without clear seasonal fluctuations (Gravenhorst et al. 2005).

Within an altitudinal range of 950–1100 m four study sites were selected in primary submontane forests within the park. Sites were sloping at an inclination of 20 to 30 degrees, canopy cover in each site was over 95% with single large trees reaching a height of around 45 m, and anthropogenic disturbance were minor (e.g., minor rattan extraction, collection of medicinal plants, extensive hunting). The fairly dense understorey was dominated by rattan.

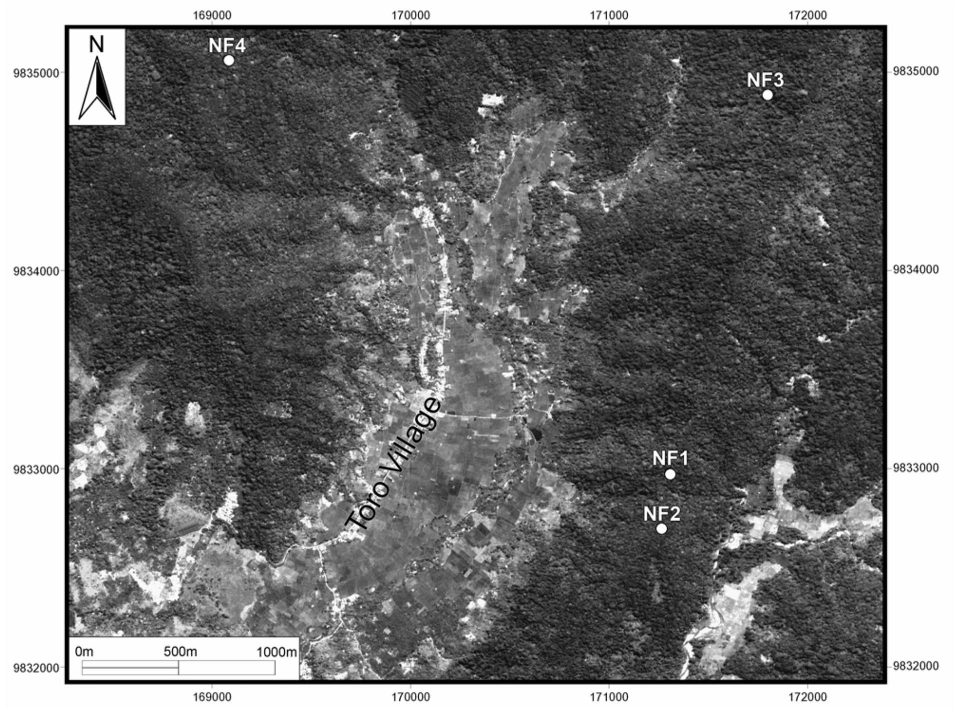

Figure 1. Four study sites situated in the Kulawi valley in and around Toro village and surrounded by natural forest of Lore Lindu National Park.

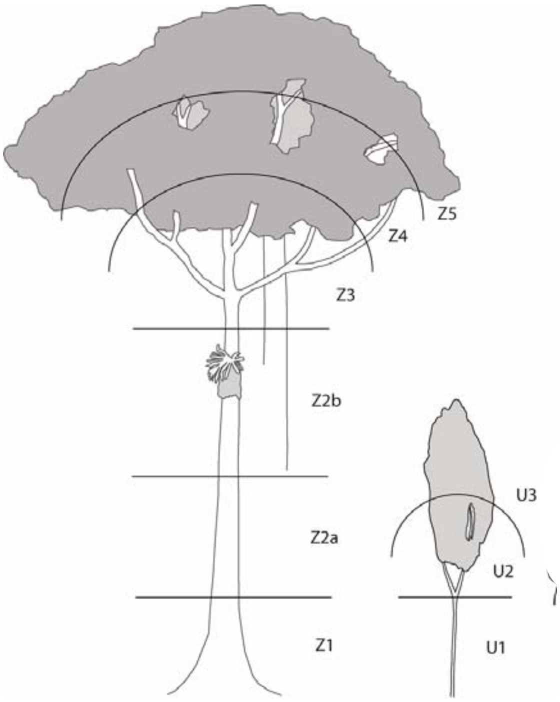

Figure 2. Distribution of sampled zones on canopy and understorey trees (by MM Bos)

Recording microclimate data

In each study site, air temperature (°C) and relative humidity (%RH) were measured at 2 m height and at the ramification that marked the beginning of the tree crown. With data-loggers (HOBO RH/Temp, ©SYNOTECH) measurements were taken with 15 minute intervals during one week in each site in July 2005.

Collecting epiphytic bryophytes

In each study site (Fig. 1), two understorey and two canopy trees minimally 15 m apart were selected. Understorey trees were 3-6.5 m in height with a dbh varying of 20-60 cm. Upper canopy trees were 30-45 m in height and had dbh values varying of 2-6.5 m. To minimize variance in substrate conditions, the bark of all selected trees was of a smooth texture.

Epiphytic bryophytes were collected from plots of 200 cm^2 positioned at each cardinal direction in six height zones on mature canopy trees (zones Z1, Z2a, Z2b, Z3, Z4 and Z5 according to Johansson 1974, Fig. 2) and in three zones on understorey trees (U1 = trunk from base to first ramification, U2= inner crown, U3= outer crown. To reach higher zones, canopy trees were climbed using the single rope technique (e.g. Ter Steege & Cornelissen 1988). Due to inaccessible or brittle tree structures, samples in height zones 4 and 5 were mainly taken from sewn branches. Total bryophyte cover (%) was estimated for each plot. In total, 24 plots (4800 cm^2) per upper canopy and 12 plots (2400 cm^2) per understorey tree were sampled. The height of each sampled zone is given in Appendix 2.

Bryophyte species were assigned to the following life forms: dendroid, fan, mat, pendant, tail, short turf, tall turf and weft (Mägdefrau 1982). Bryophytes were identified using taxonomic literature and reference collections from GOET and L or sorted to morphospecies. Vouchers were deposited in BO, CEB, GOET and L.

Statistical analysis

To assess overall sampling completeness and sampling completeness per tree type and zone, we used the Chao2 species richness estimator (as recommended by Walther & Moore, 2005). To test whether there were differences in species richness between sites, trees and zones (U1 to U3 and Z1 to Z5), we used general linear models (GLMs) with Type I hierarchical variance decomposition. “Site” was entered first, followed by “tree” and “zone”. All were entered as random variables.

To quantify differences in species composition between sites and zones, we calculated Sørensen’s similarity index for each pairwise comparison of zones per site. Using non-metric multidimensional scaling (MDS), we reduced the similarity matrix to a dimensional scaling. The number of dimensions that reduced the majority of the “raw D-star stress” was chosen for the final scaling. Stress values below 0.20 were considered to indicate a good fit of the scaling to the matrix. With analyses of similarity (ANOSIM), differences in species composition between sites and zones were tested.

All analyses were carried out for overall bryophytes and separately for mosses (Bryophyta s.str.) andliverworts (Marchantiophyta). Chao2 richness estimates were calculated using Estimate*S* (Colwell 2004), GLMs and MDS with Statistica 7.0 (Statsoft Inc. 1984-2004), and Sørensen’s similarity index and ANOSIM with Primer 5.0 (PRIMER-E Ltd 2002).

Results

Microclimate

The daily fluctuations in microclimate measured in Z1 and at the base of Z3 showed steepest changes between 7:00 AM and 7:00 PM (Fig. 3). In the forest canopy, air temperature was on average 1.6°C higher and relative air humidity 4.9% lower than at trunk bases (Table 1).

Table 1. The mean temperature and relative humidity from 7:00AM to 7:00PM in the understorey (Z1, 2 m height) and at the lower base of the canopy (Z3) of the four forest sites (N1 to N4) in the study area. Means are given ± 1 standard error.

	Relative humidity (%)		**Temperature (^oC)**	
	Understorey	***Canopy***	***Understorey***	***Canopy***
N1	76.6 ± 1.87	73.6 ± 2.20	24.0 ± 0.35	27.1 ± 0.43
N2	74.5 ± 2.09	70.6 ± 2.35	23.8 ± 0.44	24.1 ± 0.50
N3	87.1 ± 1.05	89.3 ± 1.50	25.5 ± 0.28	23.3 ± 0.35
N4	99.0 ± 0.48	90.4 ± 1.31	20.5 ± 0.13	21.5 ± 0.29

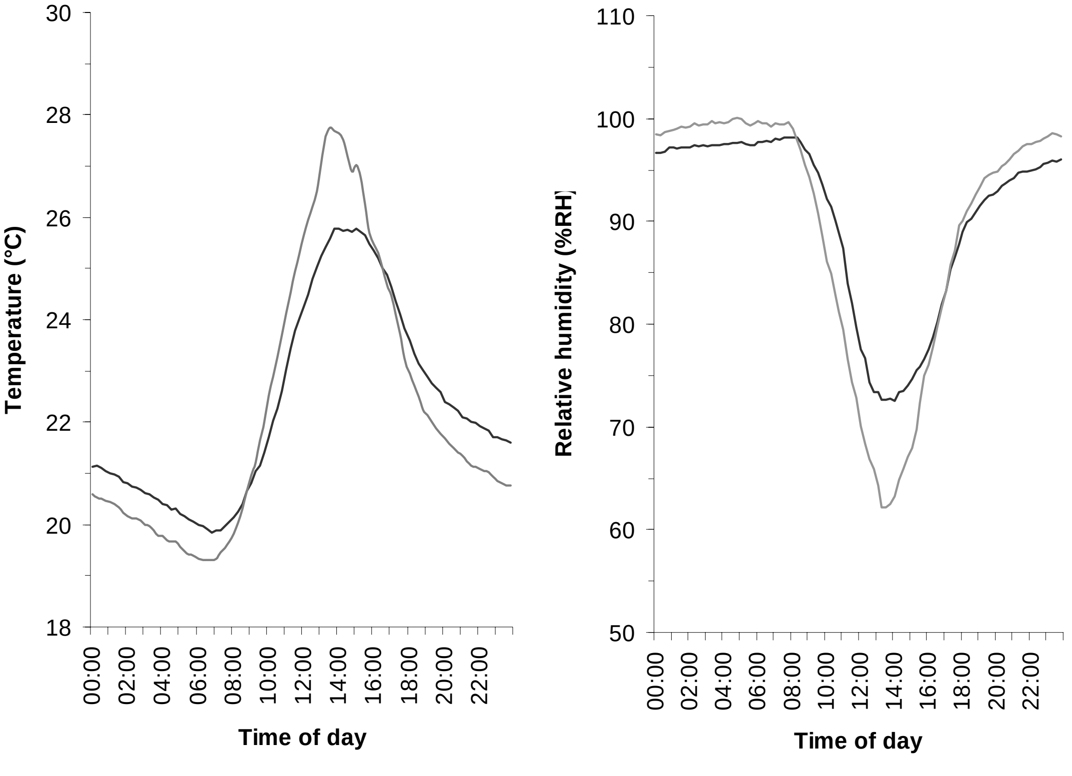

Figure 3. Temperature (^oC, left) and relative humidity (%RH, right) in understorey (Z1, black lines) and lower canopy (Z3, grey lines) during 24 hours. The values are averages for the four forest sites in the study area.

Species richness

In total, 175 bryophyte species were collected (Appendix 3) including 98 liverwort and 77 moss species (Table 2). Forty-nine species (= common spp.) occurred in more than 10% of all samples and 38 species were found in only one tree zone (Appendix 3).

Eighty-five species or 73% of estimated total species richness (Table 2) were recorded from understorey trees (Fig. 4) and 155 species or 86% of estimated total richness from canopy trees (Fig. 4, Table 2). Overall bryophyte richness and liverwort richness differed significantly between trees and zones (Table 3) with highest values in Z3 and lowest values in Z1 (Figs. 5a, 5b, Table 3). Species richness of mosses, however, differed significantly between zones but not between trees (Fig. 3b, Table 3). No significant differences in species richness between sites were found (Table 3).

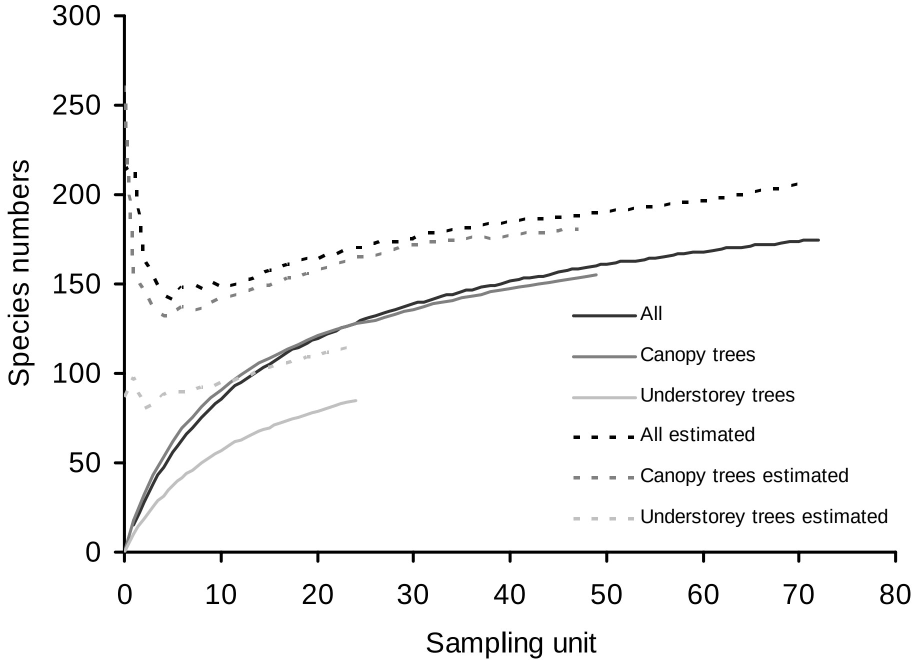

Figure 4. Accumulation curves of observed and estimated (Chao2) species richness of epiphytic bryophytes, in the investigated canopy trees and understorey trees in the study area.

Table 2. Observed (Bryo obs) and estimated (Bryo est) species richness and percent sampling completeness per tree type and zone in the study area.

	Bryo obs	**Bryo est**	**Sampling completeness (%)**
Tree type			
Understorey	85	115	74
Canopy	155	181	86
Zone			
U1	46	76	61
U2	52	72	73
U3	51	81	64
Z1	36	58	62
Z2a	81	126	64
Z2b	69	86	80
Z3	116	161	72
Z4	92	123	75
Z5	74	122	61

Table 3. The results of general linear models that tested for the effects of site, tree, and zone differences on overall richness of epiphytic bryophytes, richness of liverworts, and richness of true mosses in the study area.

Effect	**S**	**D.f**	***F***	***p***
Site	165.29	3	1.27	0.32
Tree	410.15	3	4.07	0.01
Zone	299.77	8	3.51	0.00
Error	85.40	56		
Liverworts				
Site	158.97	3	2.36	0.12
Tree	226.19	3	4.87	0.00
Zone	109.73	8	2.64	0.02
Error	41.58	56		
Mosses				
Site	17.46	3	1.07	0.38
Tree	33.50	3	2.05	0.12
Zone	48.64	8	3.51	0.00
Error	13.86	56		

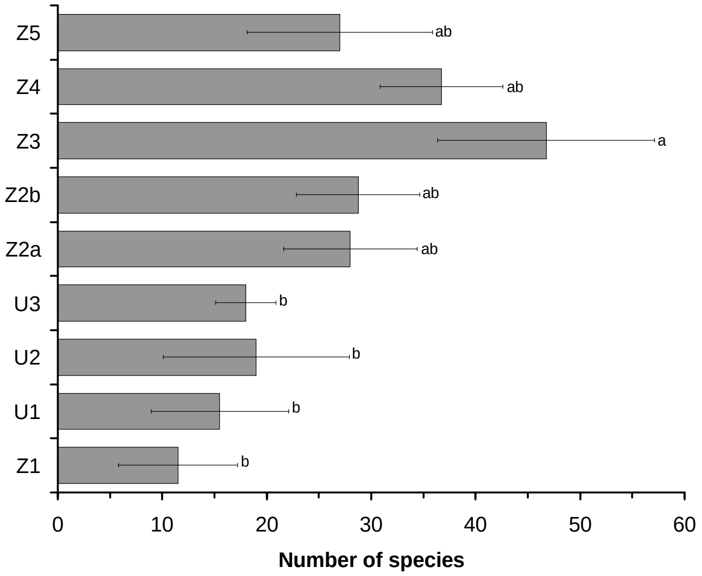

Figure 5a. The mean overall richness of epiphytic bryophyte species per zone in the investigated canopy trees (zones Z1 to Z5) and understorey trees (zones U1 to U3). Different letters indicate significant differences based on Tukey HSD post-tests and horizontal bars indicate standard errors.

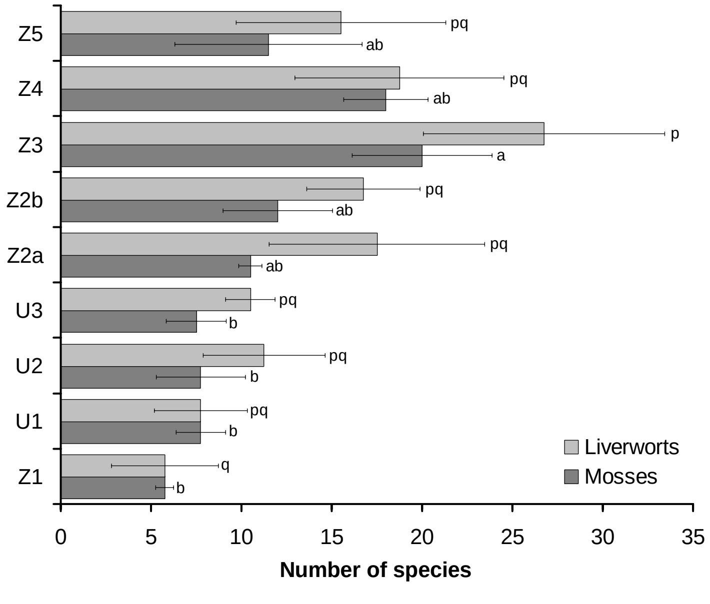

Figure 5b. The mean species richness of epiphytic liverworts (light grey) and mosses (dark grey) per zone in the investigated canopy trees (zones Z1 to Z5) and understorey trees (zones U1 to U3). For further explanation see Fig. 5a.

Species composition

The liverwort family of Lejeuneaceae was the most species rich, representing 37% of all bryophyte species recorded, followed by Plagiochilaceae (9%, also liverworts) and Neckeraceae (6%, mosses). The liverwort family of Frullaniaceae and the moss families Hookeriaceae and Meteoriaceae were represented by 5% of all species, other families by less than 5%.

Fifty-one percent of all collected species were found only on canopy trees. Here, four percent of all species were restricted to trunks (with no species being exclusive to zone Z1) and 23% to tree crowns. Eleven percent of all collected species were exclusively found on understorey trees.

The first two dimensions of the multidimensional scaling of the Sørensen's similarity index reduced more than 77% of the raw stress with stress values below 0.20. Within understorey trees, species composition did not differ between zones, which was confirmed by ANOSIM results (Table 4). Species assemblages on understorey trees were similar to those on zones 1 and 2 of canopy trees (Table 4).

Table 4. The R values of the results of analysis of similarity (ANOSIM) after a multidimensional scaling of Sørensen's index calculated for pairwise comparisons of epiphytic bryophytes in different tree zones in the investigated understorey trees (zones U1 to U3) and canopy trees (zones Z1 to Z5). Bold values and black cells indicate significant differences, grey cells non-significant ones.

	U1	**U2**	**U3**	**Z1**	**Z2a**	**Z2b**	**Z3**	**Z4**	**Z5**
U1	╳	▒	▒	▒	▒	▒	■	■	■
U2	0.08	╳	▒	▒	▒	■	■	■	■
U3	0.05	0.14	╳	▒	▒	▒	■	■	▒
Z1	0.09	0.06	0.05	╳	▒	▒	■	■	■
Z2a	0.40	0.01	0.07	0.21	╳	▒	▒	▒	▒
Z2b	0.43	**0.33**	0.26	0.33	0.35	╳	▒	▒	▒
Z3	**0.58**	**0.46**	**0.31**	**0.57**	0.08	0.14	╳	▒	▒
Z4	**0.79**	**0.62**	**0.41**	**0.55**	0.27	0.17	0.05	╳	▒
Z5	**0.57**	**0.56**	0.20	**0.46**	0.09	0.25	0.16	0.04	╳

Within the canopy trees, the ANOSIM results only showed significant composition dissimilarity between Z1 on the one hand and Z3, Z4 and Z5 on the other (Table 4). Thus, bryophyte assemblages in the different tree types and zones can be divided in two groups, those on understorey trees and zone 1 of canopy trees, and those in crowns of canopy trees (Z3, Z4, Z5). Zones 2a and 2b form a transition zone between understorey and tree crown.

Life forms

Seventy-four percent of all collected bryophytes species had mat- or weft-like life forms (each 37%); species belonging to these categories occurred on all sampled canopy and understorey trees. Other life forms included less than 10% of all species (Figure 6).

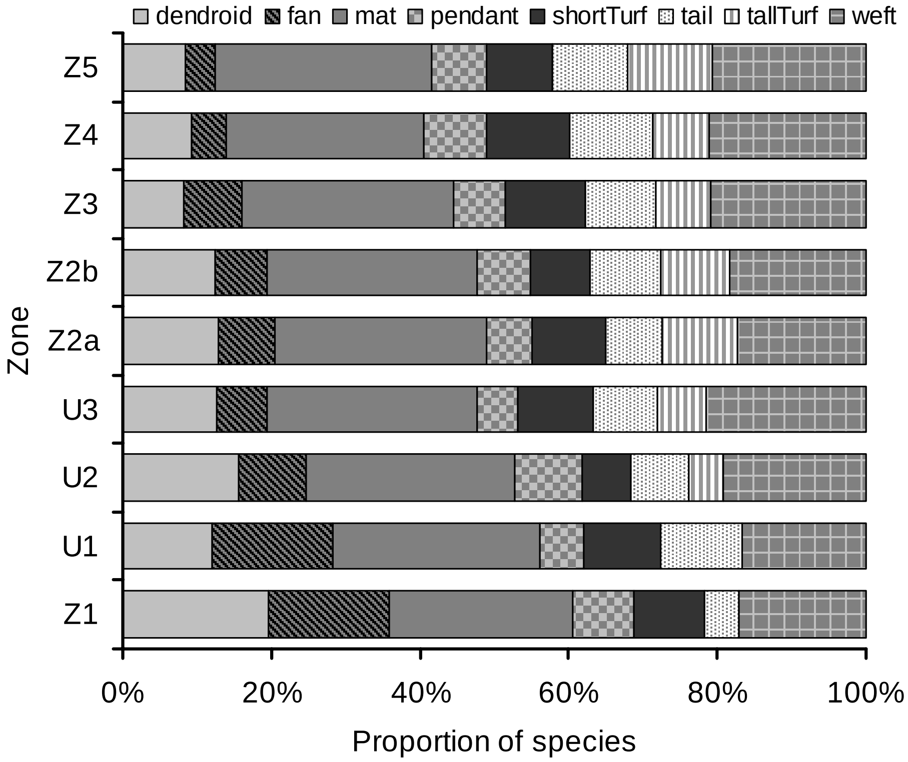

Figure 6. The proportion of species with eight different life-forms per zone in the investigated canopy trees (zones Z1 to Z5) and understorey trees (zones U1 to U3).

Table 5. The results of general linear models that tested for the effects of site and zone differences on relative life-form of epiphytic bryophytes in the study area.

Effect	MS	D.f.	*F*	*p*
Dendroid				
Site	10.14	3	2.31	0.09
Tree	7.55	1	1.72	0.20
Zone	3.29	5	0.75	0.59
Error	4.38	37		
Fan-like				
Site	4.59	3	4.13	0.01
Tree	4.91	1	4.41	0.04
Zone	2.82	5	2.53	0.04
Error	1.11	37		
Mat-like				
Site	874.58	3	8.83	0.00
Tree	100.16	1	1.01	0.32
Zone	216.26	5	2.19	0.08
Error	98.95	37		
Pendant				
Site	8.07	3	13.14	0.00
Tree	5.15	1	8.40	0.01
Zone	1.79	5	2.93	0.03
Error	0.61	37		
Short turf-like				
Site	10.72	3	3.55	0.02
Tree	2.06	1	0.68	0.41
Zone	8.43	5	2.80	0.03
Error	3.02	37		
Tail				
Site	10.21	3	2.97	0.04
Tree	1.04	1	0.30	0.58
Zone	7.97	5	2.32	0.06
Error	3.43	37		
Tall turf-like				
Site	15.69	3	4.72	0.01
Tree	6.23	1	1.87	0.18
Zone	2.59	5	0.78	0.57
Error	3.33	37		
Weft-like				
Site	119.39	3	2.85	0.05
Tree	146.54	1	3.50	0.07
Zone	94.33	5	2.25	0.07
Error	41.86	37		

Except for tuft-like species, life forms were unequally distributed among sites (Table 5). Moreover, richness of pendant, mat-, short turf-, tail- and weft-like taxa did not differ between zones. However, dendroid and fan-like species were significantly most numerous in the understorey and on the lower trunk of canopy trees, whereas tall turf-like taxa occurred only in the crowns of canopy trees.

Discussion

Species richness

The recorded number of 175 epiphytic bryophyte species on eight understorey and eight canopy trees (estimated sampling completeness: over 90% for canopy trees, < 70% for understorey trees) is among the highest values ever recorded in tropical forests (e.g., Cornelissen & ter Steege 1989; Montfoort & Ek 1990; Wolf 1993; Acebey et al. 2003). Overall richness is only exceeded by that in a Costa Rican montane cloud rainforest (Gradstein et al. 2001), where growth conditions for epiphytic bryophytes are presumably better due to higher humidity. The latter study, however, included 4 hectare of forest, which underscores the high species richness of the studied rainforest of Sulawesi. The higher richness of liverworts compared to mosses in our study area is in line with findings in South America (e.g., Florschütz-de Waard & Bekker 1987; Gradstein et al. 2001) and does not fit the assumed higher relative richness of mosses in palaeotropical forests (Gradstein & Pócs 1989).

Comparable high levels of species richness have also been recorded for trees and ferns (Kessler et al. 2005; Gradstein et al. 2007) in the study area and underline the importance of the Malesian region as a global biodiversity hotspot (Myers et al. 2000; Sodhi et al. 2004). However, within and between trees, bryophyte species richness and composition differed strongly. The causes for these differences remain unclear and may be due to a variety of historical and ecological factors (Barkman 1958; Richards 1996; Frahm 1990, 2003; Cardelús & Chazdon 2005). As expected, the greatest differences were between assemblages of understorey and canopy trees. Moreover, species richness differed greatly between zones, with lowest values in the three zones of understorey trees and on canopy tree bases, and highest values in the lower portion of the crowns of canopy trees (zone Z3), generally at 14 - 25 m height. Although a direct comparison with other studies is difficult because of differences in forest type (lowland, submontane, montane), sampling method and sample size, roughly similar patterns were reported from Guyanan lowland forest (Cornelissen & ter Steege 1989; Cornelissen & Gradstein 1990; Montfoort & Ek 1990), submontane forest of Bolivia (Acebey et al. 2003), and Costa Rican montane cloudforests (Gradstein et al. 2001). Among these studies, our study is the only one which included understorey trees.

The increase of air temperature of ca. 2°C and ca. 5 % decrease of air humidity from the forest understorey (2 m height) towards the base of the canopy (14-19 m height) are in general agreement with microclimate readings of other rainforest studies (e.g., Richards et al. 1996; Walsh 1996; Leigh 1999; Acebey et al. 2003; Kluge et al. 2006). The species richness peak in inner tree crowns suggests optimal conditions for bryophyte growth in this zone. Lower down, bryophyte establishment may have been limited by insufficient light and higher up by excessive exposure to sunlight and wind. Beside microclimate conditions, bark and branch structure, affecting nutrient and water flows on the tree (Barkman 1958; Smith 1982; Rhoades 1995; Cordelús & Chazdon 2005) may have been important factors determining species richness. Although we selected tree species with comparable bark texture, unstudied bark factors such as pH, hardness, water holding capacity, or chemical differences in solutions excreted by the host tree (Richards et al. 1996; Barkman 1958; Smith 1982; Holz 2003), may have influenced bryophyte occurrence and richness in this study.

Species composition

The majority of species found in our study (37%) belonged to Lejeuneaceae, Plagiochilaceae, Neckeraceae, Frullaniaceae, Hookeriaceae and Meteoriaceae; all of these are core bryophyte families in tropical rainforest (Gradstein & Pócs 1989). The common presence of species such as *Radula javanica* Gott., *Phychanthus striatus* (Lehm. & Lindenb.) Nees, *Thysananthus spathulistipus* (Reinw. et al.) Lindenb., *Cheilolejeunea trifaria* (Reinw. et al.) Mizutani, *Lopholejeunea subfusca* (Nees) Schiffn., *Mastigolejeunea auriculata* (Wils.) Schiffn., *Frullania riojaneirensis* (Raddi) Angstr. and *Metalejeunea cucullata* (Reinw., Blume & Nees) Grolle fits well to the general description of the characteristic bryophyte communities of lowland and submontane tropical forests ("Coeno-Ptychanthetalia"; Kürschner & Parolly 1999).

At a smaller scale, species composition changed clearly with increasing height in the trees, and species assemblages in the crowns of canopy trees were significantly different from those on trunks of canopy trees and on understorey trees. In neotropical montane forest, bryophyte assemblages of tree bases have been reported to be more similar to terrestrial communities than to those elsewhere on trees (Holz et al. 2002). In the studied forest, however, a terrestrial bryophyte layer was almost lacking.

While all species and liverwort composition were markedly different on canopy and understorey trees, moss species composition of the outer crowns of canopy (Z5) and understorey (U3) trees showed some overlap. This overlap may be due to pioneer"ramicolous" bryophyte species occurring on twigs in canopy as well as the forest understorey (Cornelissen & Ter Steege 1989) Moreover, random dispersal of epiphytic bryophytes may have occurred, for example by small plant parts fallen from higher strata into lower vegetation layers. In the wind-exposed outer crown habitats, bryophytes may easily be ripped off by wind and thus fall onto the understorey trees.

Because the level of adaptation of bryophyte species to their optimal microclimatic environment is reflected in their life form, we included the vertical distribution of eight commonly distinguished bryophyte life forms in our study (Mägdefrau 1982). Exposed dendroid and fan-like species were most numerous on tree trunks and understorey trees, while compact and tall, turf-like forms only occurred above the first ramification of the understorey trees and were most numerous in the crowns of canopy trees. These results support the idea that species with exposed life forms are more successful in understorey where they are well-protected against sunlight and desiccation, whereas species with compact life forms can better cope with warmer and drier circumstances such as those found in higher canopy strata (León-Vargas et al. 2006).

Lastly, branch structure, such as diameter and inclination of twigs and branches, is an important factor determining the composition of epiphytic bryophyte species that settle in the canopy (Yamada 1975-1977; Holz 2003; N. Mandl *pers. comm*). The high number of species with tall turf-like life forms in the tree crowns may be due to the presence of horizontal braches and crutches, which allows exposed growth. On the vertical structures of lower zones, tall turfs may not find enough suitable substrate for secure establishment. Other exposed and oustanding life forms such as dendroid, and tail- and fan-like are attached only at few points of their surface on the substrate and may therefore be less dependent on horizontal substrate as anchoring place.

Conclusion

The vertical distribution of habitat parameters in tropical forests such as microclimate and tree structure is clearly reflected in epiphytic bryophyte diversity, both in terms of species richness as well as in species composition. Thus, we found greatest differences in diversity between tree trunks and understorey trees versus tree crowns.

Our study was the first to include understorey trees in studying the vertical distribution of epiphytic bryophytes in standardized sampling methods. Although only 11 percent of all species were restricted to the understorey trees, particularly the species groups with dendroid and fan-like life forms were richest in the lowest parts of the rainforest (on tree trunks and on understorey trees), and would thus have been underestimated or even neglected if understorey trees would have been excluded. Thus, conservation strategies aiming at preserving the variety of tropical habitats and recognition of suitable indicator species should include the small understorey trees in addition to mature canopy trees. The importance of .understorey trees as a habitat for vascular epiphytes has recently been emphasized by Krömer et al. (2007).

This study once more reveals the importance of undisturbed rainforests with a dense, closed canopy and well-shaded, cool and moist understorey for the preservation of high levels of biodiversity. Disruption of the forest canopy would inevitably risk levelling these habitat differences posing an immediate threat to the unique bryophyte flora in the understorey. Pristine rainforests thus provide optimal conditions for the development of the specialized bryophyte assemblages detected in this study,, including on the one hand those of understorey trees and lower tree trunks, and on the other hand those of the exposed and little studied upper parts of the tree crowns.

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Chapter

3

Microclimate determines community composition but not richness of epiphytic understorey 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 understorey trees in natural forest and cacao trees in two types of cacao agroforests (natural shade trees and planted shade trees) in Central Sulawesi, Indonesia. The microclimate in the agroforests was characterized 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.

Introduction

The ongoing deforestation and habitat degradation in the tropics continue to cause losses of highly diverse flora and fauna (Myers et al. 2000; Laurance et al. 2002; Achard 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, e.g., removal of shade trees and cleaning of the understorey, however, may again lead to depletion of biodiversity (Acebey et al. 2003; Steffan-Dewenter et al. 2007; Bos et al. 2008; Ariyanti 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 and decreasing air humidity, while throughfall of rainwater increases (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 understorey (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 cacao agroforests on the island of Sulawesi, Indonesia. The flora of the Southeast Asian region is characterized by high diversity and levels of endemism (Roos 2004; Sodhi et al. 2004; Gradstein et al. 2005; Ariyanti et al. in press) making it one of the world's hotspots in terms of biodiversity (Myers et al. 2000). However, the region is also characterized 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 agroforestry activities 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 understorey of rainforests and differently managed cacao agroforests in Sulawesi.

Material 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 about 800 m a.s.l., 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 to 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 10-15 years old, shading canopy trees 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. & Perry, timber trees like *Bischofia javanica* Blume and *Aleurites mollucana* Willd., as well as the non-indigenous legume trees *Gliricidia sepium* (Jacq.) Walp. and *Erythrina subumbrans* Hassk. Cacao trees were between four and 10 years old, shading canopy trees 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 minute intervals during February-March 2005, using data-loggers (type HOBO RH/Temp, © SYNOTECH). 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 $E = 6107 \text{ x } 10^{(17,27 \text{x} T/237,3 + T)}$[hPa] and e = E x 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 (dbh 20-60 cm) and at a minimum distance of 15 m from each other were selected for collecting epiphytic bryophytes. All sampled trees in the agroforests were cacao trees (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 cm^2 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 cm^2) per tree were sampled.

The collected epiphytic bryophytes were identified using taxonomic literature and reference collections from GOET and L or were sorted to morphospecies. Vouchers were deposited in BO, CEB, 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. Jacknife estimates were calculated using EstimateS (Colwell 2004), one-way ANOVA's, Spearman Rank correlations and GLMs with Statistica 7.0 (Statsoft Inc. 1984-2004), 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

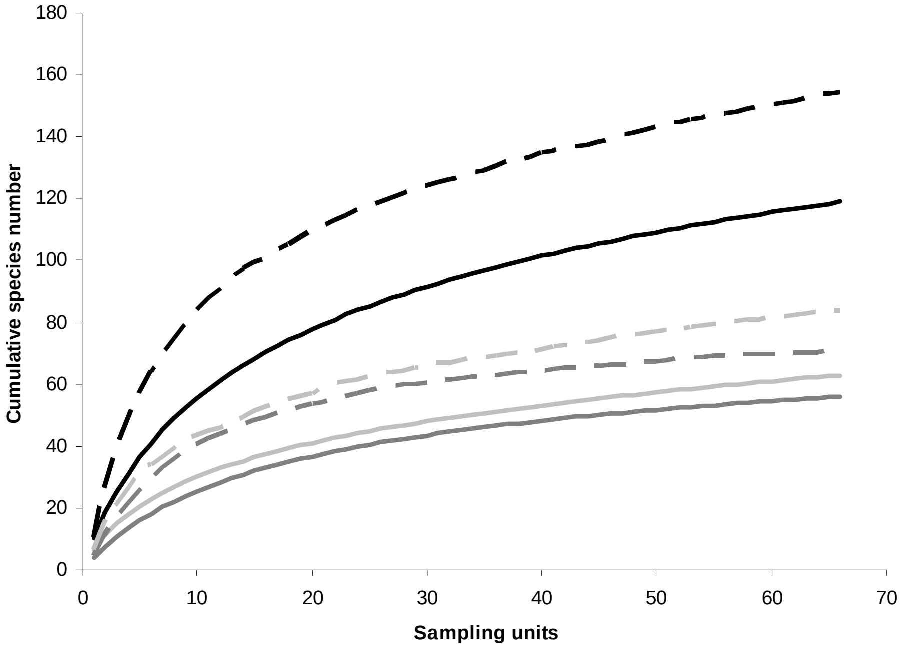


Figure 1. Species accumulation curves for overall bryophytes (black lines), mosses (dark shaded lines) and liverworts (light shaded lines) on understorey trees in 11 study sites in Central Sulawesi, Indonesia. Continuous lines are for observed species richness and dotted lines are for estimated species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

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 (73% of estimate), and in CPS 58 (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).

Table 1. The results of the ANOVA and GLM 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 agroforests in Central Sulawesi, Indonesia. NF = natural forest, CNS = cacao plantation under natural shade, CPS = cacao plantation under planted shade, obs = observed species richness, est = first-order jackknife estimated 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

Species composition

In terms of species composition, 48 species (40%) were exclusively found in natural forest sites, 14 (12%) in CPS and seven (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.

Figure 2a-b. Mean numbers of observed (bars) and estimated (dots) species richness of (a) bryophytes and (b) mosses (dark shaded) and liverworts (light shaded) on understorey 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.

Figure 2a

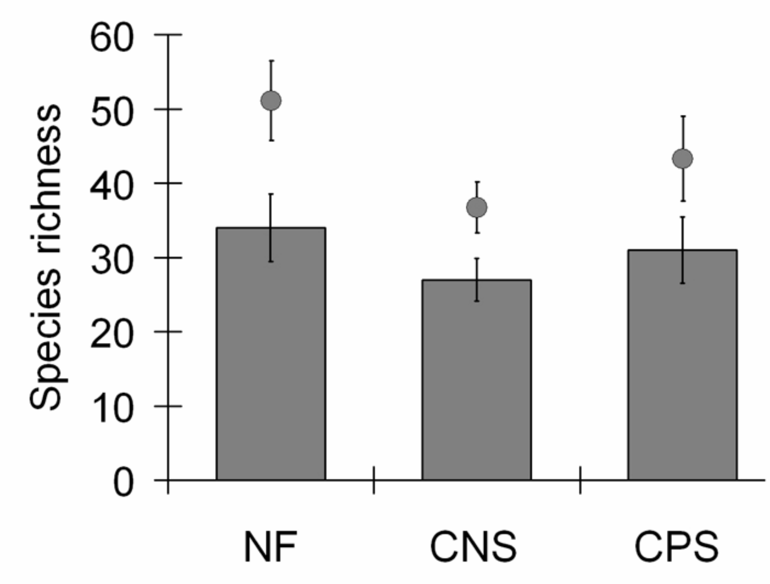
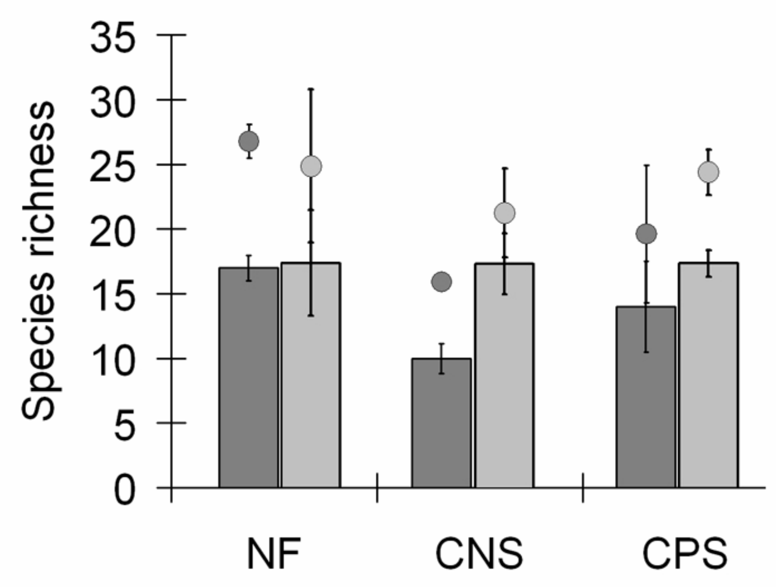


Figure 2b



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 natural forest 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 4).

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

Figure 3a.

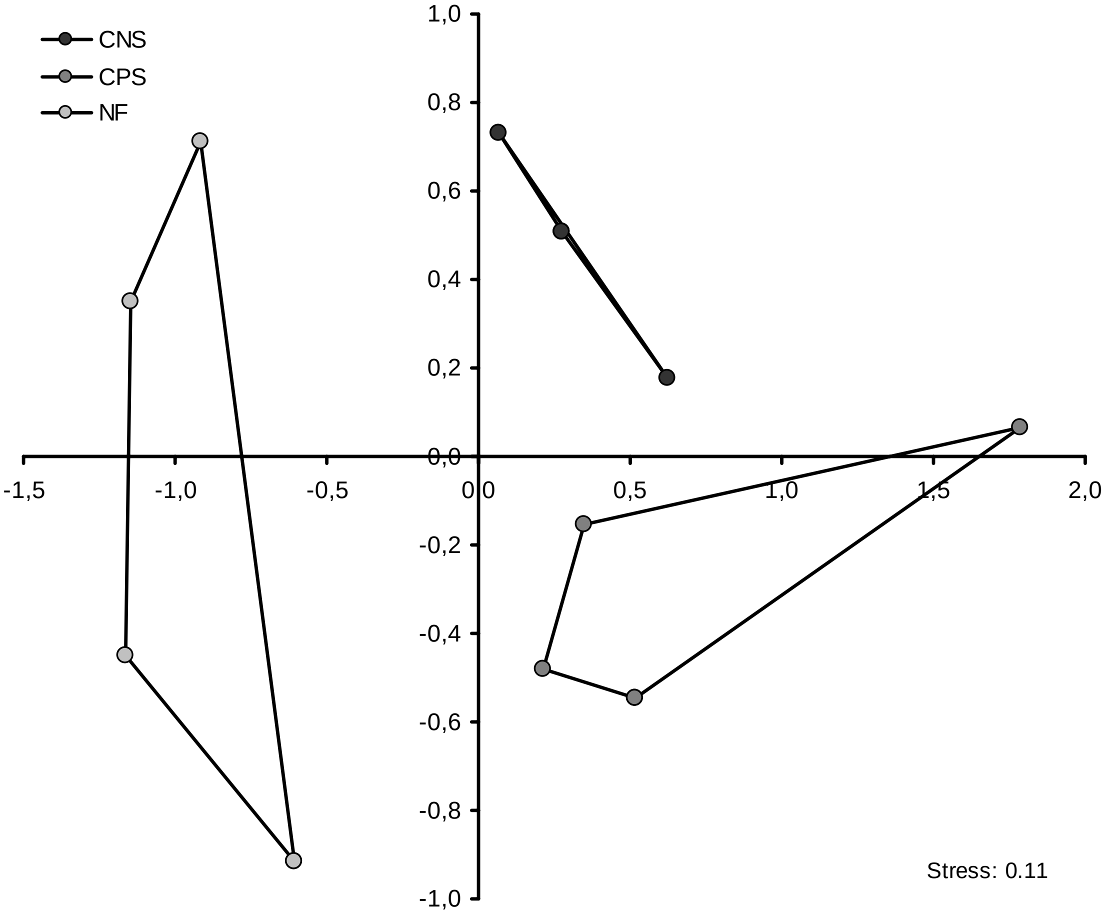
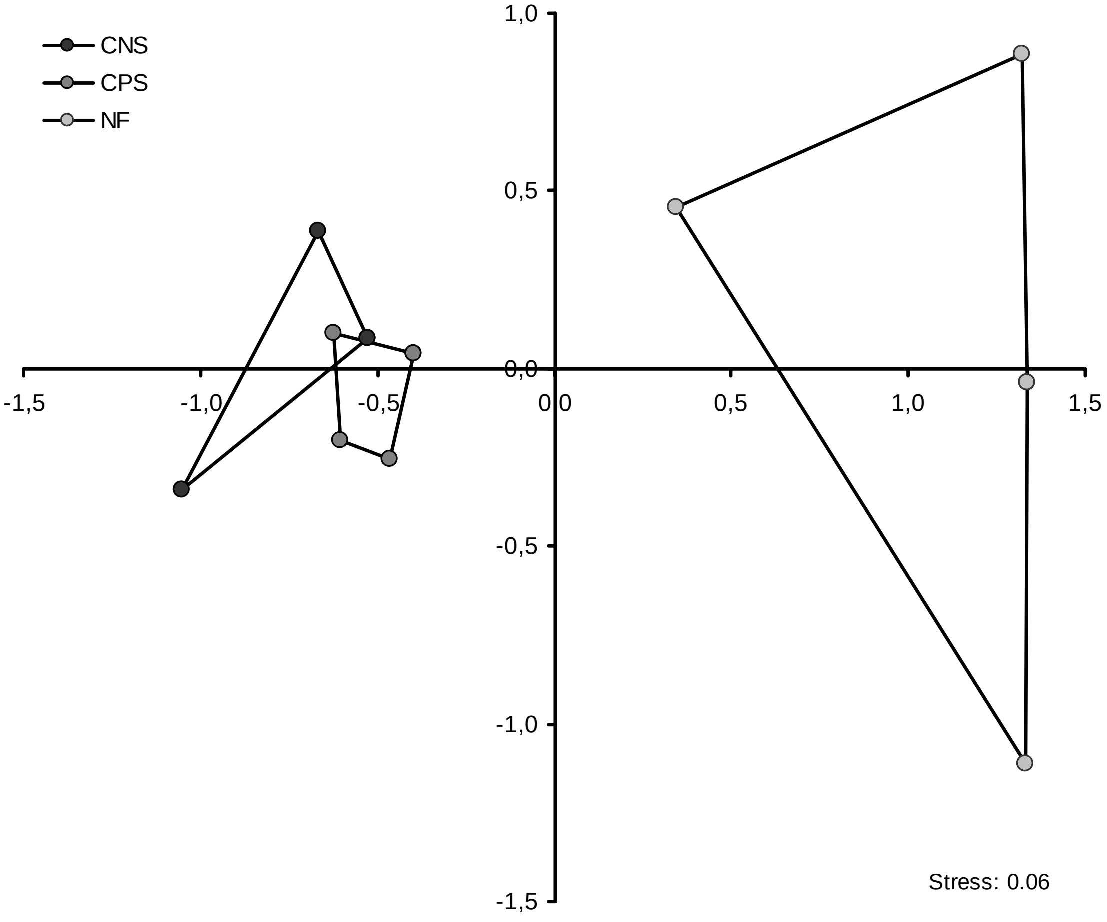


Figure 3b.



Microclimate and species richness

While overall air temperature and relative air humidity did not differ between habitat types, maximum temperature and the minimum relative humidity differed significantly with highest resp. lowest values being measured in CPS (Table 2). Both overall and maximum values of VPD differed significantly between habitat types with highest values also in CPS (Table 2).

None of the species richness values per site (neither observed nor estimated) were significantly correlated with any of the microclimate variables (Table 3).

Table 2. The mean values of the microclimatic factors per habitat type in Central Sulawesi, Indonesia. NF = natural forest, CNS = cacao plantation under natural shade, CPS = cacao plantation under planted shade. Statistical significance between habitat types are indicated by superscript letters based on Tukey HSD post hoc tests after the ANOVA.

	NF	**CNS**	**CPS**	**ANOVA results**
T	21.8 ± 0.37	22.84 ± 1.29	22.61 ± 0.11	F(2, 8)=0.75, p=0.50
T min	19.36 ± 0.51	19.41 ± 1.14	18.58 ± 0.18	F(2, 8)=0.58, p=0.58
T max	26.17 ± 0.55 ^{a}	29.43 ± 1.47 ^{ab}	30.64 ± 0.60 ^{b}	F(2, 8)=8.11, p=0.01
RH	93.23 ± 1.35	89.15 ± 2.04	89.51 ± 0.53	F(2, 8)=3.07, p=0.10
RH min	74.6 ± 4.03 ^{a}	59.92 ± 2.36 ^{b}	55.56 ± 1.28 ^{b}	F(2, 8)=12.65, p=0.003
RH max	99.68 ± 0.18	98.66 ± 1.17	99.41 ± 0.34	F(2, 8)=0.75, p=0.50
VPD	2.1 ± 0.44 ^{a}	3.64 ± 0.30 ^{b}	4.31 ± 0.12 ^{b}	F(2, 8)=13.25, p=0.003
VPD max	8.88 ± 1.68 ^{a}	16.52 ± 1.16 ^{b}	20.54 ± 1.21 ^{b}	F(2, 8)=18.79, p=0.001

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 max. temperature and max. VPD, in that bryophyte are positively and liverworts negatively correlated for both values (Table 3). 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 min. relative humidity and max. temperature, and to overall and max. VPD (Tables 3, 5). In contrast, none of the species richness similarity matrices correlated with microclimatic similarity (Table 5).

Table 3. Results of Spearman Rank analysis between the microclimatic factors and observed and estimated bryophytes species richness, the dimension values of the multidimensional scalings. B = overall bryophytes, L = Liverworts, M = Mosses, obs = observed species richness, est = first-order jackknife estimated species richness, MDS1 = the values of the first dimension of the multidimensional scaling, MDS2 = the values of the second dimension of the multidimensional scaling. Asterisks indicate significance at the * = p<0.05, ** = p<0.01, and *** = p<0.001 level.

	T	**T min**	**T max**	**RH**	**RH min**	**RH max**	**VPD**	**VPD max**	**B obs**	**M obs**	**L obs**	**B est**	**M est**	**L est**	**B MDS 1**	**L MDS 1**	**M MDS 1**	**B MDS 2**	**L MDS 2**	**M MDS 2**
T	1,00	0,51	0.69*	-0,11	-0,27	0,25	0,49	0,49	0,06	-0,19	0,06	-0,12	-0,36	0,16	0,52	-0,45	0,25	-0,14	0,24	0,21
T min		1,00	0,07	0.68*	0,53	0.68*	-0,39	-0,25	0,28	-0,10	0,28	0,24	-0,17	0,28	0,03	-0,07	-0,20	0,15	-0,25	0,16
T max			1,00	-0,41	-0.75**	0,26	0.75**	0.92***	-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	0.74**	0.71*	-0.83**	-0,55	0,42	0,39	0,16	0,56	0,37	0,15	-0,49	0,26	-0,53	0,13	-0,35	-0,11
RH min					1,00	0,21	-0.88***	-0.93***	0,19	0,02	0,20	0,23	0,05	0,22	-0,51	0,59	-0,58	0,26	-0,31	0,07
RH max						1,00	-0,29	0,10	0,18	0,22	-0,11	0,25	0,27	-0,14	-0,04	-0,13	-0,16	-0,21	-0,03	-0,10
VPD							1,00	0.85**	-0,20	-0,22	-0,08	-0,37	-0,32	-0,02	0,60	-0,47	0.65*	-0,19	0,35	-0,10
VPD max								1,00	-0,21	-0,05	-0,29	-0,25	-0,06	-0,26	0.61*	-0.66*	0,58	-0,35	0,41	-0,08
B obs									1,00	0.75**	0.75**	0.95***	0,49	0.71*	-0,57	0,28	-0,26	0,37	-0.68*	-0,46
M obs										1,00	0,19	0.81**	0.89***	0,16	-0.72*	0,34	-0,46	-0,12	-0,25	-0,47
L obs											1,00	0.65*	-0,12	0.95***	-0,14	0,03	0,20	0.83*	-0.9***	-0,29
B est												1,00	0,60	0.61*	0.61*	0,25	-0,28	0,40	-0.7*	-0,49
M est													1,00	-0,18	-0.74**	0,44	-0,55	-0,33	-0,03	-0,34
L est														1,00	-0,11	0,09	0,24	0.81*	-0.77**	-0,43
B MDS 1															1,00	-0.79**	0.82**	0,11	0,23	0,36
L MDS 1																1,00	-0.65*	-0,05	-0,04	-0,31
M MDS 1																	1,00	0,43	-0,12	-0,12
B MDS 2																		1,00	-0.85**	-0,18
L MDS 2																			1,00	0,21
M MDS 2																				1,00

Table 4. 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. NF = natural forest, CNS = cacao plantation under natural shade, CPS = cacao plantation under planted shade. Asterisks indicate significance.

	NF vs. CNS		**NF vs. CPS**		**CNS vs. CPS**	
	R	**p**	**R**	**p**	**R**	**p**
Bryophyte	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

Figure 4a-c. Daily course of (a) relative air humidity (RH %) (b) temperature (Temp °C) and (c) vapour pressure deficit (VPD) in 4 natural forests sites (light shaded lines), 3 cacao agroforest sites under natural shade (black lines) and 4 cacao forest sites under planted shade (dark shaded lines) at the Lore Lindu national park, Sulawesi.

Figure 4a)

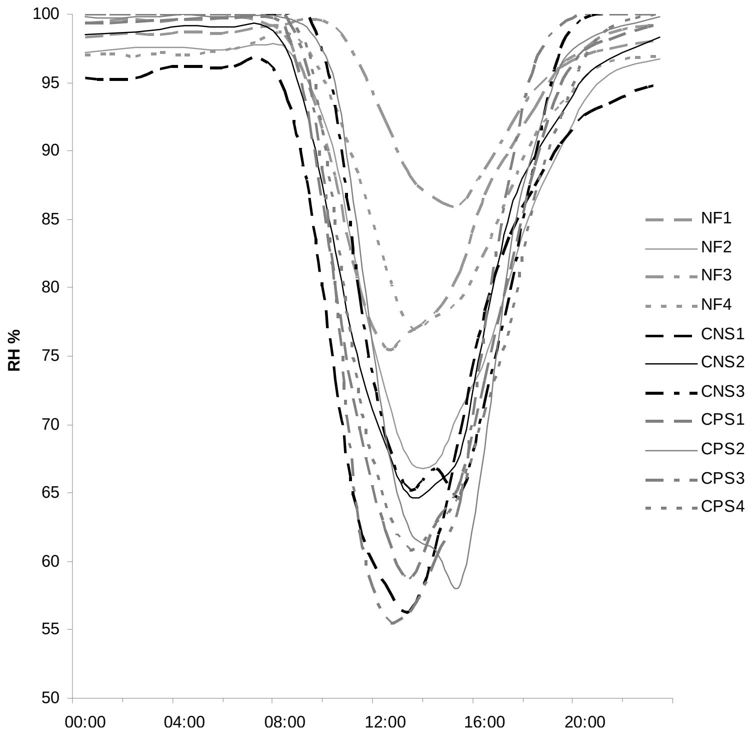


Figure 4b)

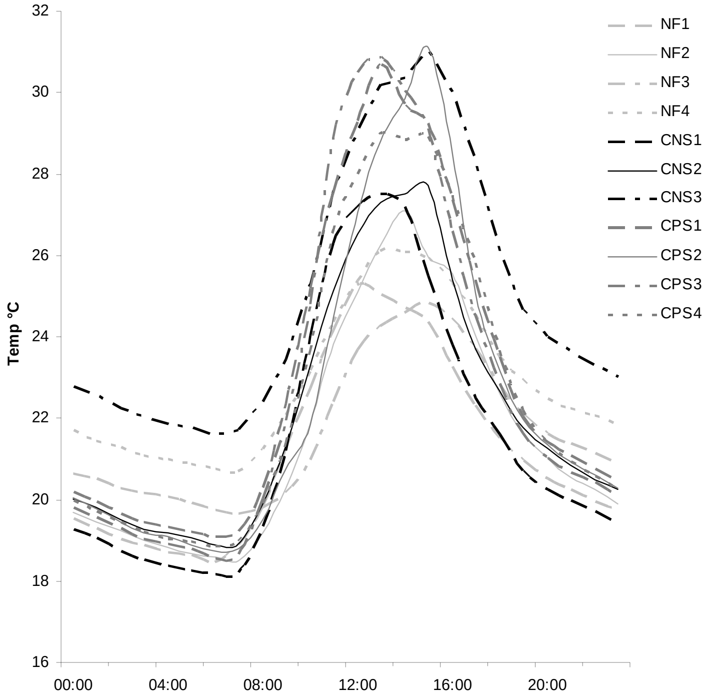


Figure 4c)

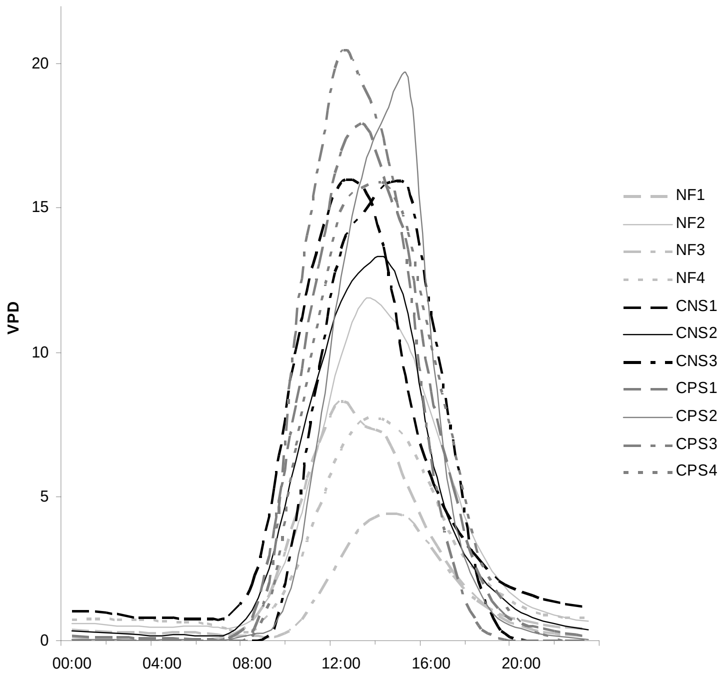


Table 5. The results of the Mantel tests for associations between differences in species composition and species richness, and differences in microclimate values in four forest sites and seven cacao agroforests in Central Sulawesi, Indonesia. Asterisks indicate significance at the * =p< 0.05, ** = p<0.01, and *** = p<0.001 level.

	T	**T min**	**T max**	**RH**	**RH min**	**RH max**	**VPD**	**VPD max**
Composition								
Bryophytes	r = 0.08, t = 0.39	r = 0.01, t = 0.05	r = 0.42, t = 2.86**	r = 0.23, t = 1.16	r = 0.61, t = 3.50***	r = -0.26, t = -1.17	r = 0.60, t = 3.01**	r = 0.62, t = 3.30**
Liverworts	r = 0.10, t = 0.46	r = -0.01, t = -0.05	r = 0.41, t = 2.72**	r = 0.24, t = 1.15	r = 0.57, t = 3.19**	r = -0.24, t = -1.03	r = 0.59, t = 2.83**	r = 0.59, t = 3.05**
Mosses	r = 0.08, t = 0.48	r = 0.12, t = 0.73	r = 0.38, t = 2.72**	r = 0.16, t = 1.05	r = 0.54, t = 3.69***	r = -0.21, t = -1.26	r = 0.47, t = 2.98**	r = 0.49, t = 3.24**
Richness								
Observed								
Bryophytes	r = 0.09, t = 0.47	r = 0.13, t = 0.67	r = -0.03, t = -0.18	r = -0.07, t = -0.39	r = 0,00, t = 0.00	r = -0.14, t = -0.67	r = 0.02, t = 0.10	r = 0.02, t = 0.14
Mosses	r = 0.02, t = 0.10	r = 0.06, t = 0.26	r = -0.03, t = -0.19	r = -0.08, t = -0.39	r = 0.08, t = 0.45	r = -0.19, t = -0.78	r = 0.09, t = 0.42	r = 0.09, t = 0.45
Liverworts	r = -0.01, t = -0.05	r = -0.07, t = -0.29	r = -0.15, t = -0.96	r = -0.1, t = -0.43	r = -0.18, t = -0.93	r = -0.01, t = -0.03	r = -0.17, t = -0.71	r = -0.18, t = -0.84
Estimated								
Bryophytes	r = 0.13, t = 0.62	r = 0.18, t = 0.94	r = 0.08, t = 0.51	r = 0.11, t = 0.58	r = 0.12, t = 0.72	r = -0.06, t = -0.3	r = 0.15, t = 0.78	r = 0.17, t = 0.94
Mosses	r = 0.14, t = 0.62	r = 0.15, t = 0.74	r = 0.04, t = 0.27	r = -0.02, t = -0.10	r = 0.13, t = 0.76	r = -0.22, t = -0.94	r = 0.18, t = 0.88	r = 0.15, t = 0.77
Liverworts	r = -0.08, t = -0.29	r = -0.13, t = -0.53	r = -0.16, t = -1.04	r = -0.05, t = -0.20	r = -0.17, t = -0.83	r = 0.04, t = 0.15	r = -0.14, t = -0.59	r = -0.17, t = -0.76

Discussion

Species richness

Our results show that levels of bryophyte species richness on cacao trees in agroforests can be comparable to those found in the understorey 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 (Costa 1999; Acebey et al. 2003; Nöske 2005; Harvey and Gonzáles Villalobos 2007) and Southeast 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 understorey of natural forests in Central Sulawesi with 84 species on eight understorey 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 understorey trees in the study area is also reflected in that of adjacent cacao agroforests where we recorded 71 species 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 yrs) than those in Indonesia (4-15 yrs). Moreover, the bryophyte flora of Ecuador with almost 1500 reported species (Léon et al. 2006) is richer than that of Sulawesi (597 species recorded; Ariyanti et al. in press).

Species composition

In terms of species composition, our study revealed a significant turnover from the natural forest sites to the cacao agroforests. Only 30% of the species recorded on understorey 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 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 rain forest and that agroforests are a suitable surrogate habitat for the understorey 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 12:30h and 15:30h (Fig. 4), in cacao agroforests as compared to 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 (Sillet et al. 1995; 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, our results 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, our study showed that bryophyte species compositions and microclimatic similarities were strongly related, which 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 understorey 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 understorey 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 between the two types of cacao agroforests did not differ 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.

Surprisingly, although liverwort families such as Lejeuneaceae are known to be more resistant to desiccation than mosses because of morphological adaptations like water sacs and strongly attached growth forms (Kürschner and Frey 1999; Frahm 2003), species richness of neither liverworts nor mosses was related to microclimatic factors. Moreover, the observed daily bottleneck in microclimate (maximum VPD and temperature values) did drive changes in species composition of liverworts and not of mosses. These results suggest that other 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 can be differences in previous land-use, time since conversion, age of the trees, or differences in pruning techniques used in the plantations. 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 our 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

Our study shows that conversion of natural forest to cacao agroforests may not lead to decreases in the species richness of epiphytic bryophytes on understorey 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. We conclude 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. We therefore strongly recommend inclusion of microclimate measurements in studies on epiphytic bryophyte assemblages in tropical forest landscapes. Conversely, our 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.

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Chapter

4

On the origin of the bryophyte flora on trees of cacao agroforests of Sulawesi, Indonesia

Abstract

Cacao is one of the world's most important cash crops grown throughout the tropics. Because of their superficial resemblance with forests, cacao plantations ("agroforests") can harbor high levels of biodiversity and can therefore function as important tool in biodiversity conservation in tropical landscapes dominated by ongoing forest conversion. We studied the epiphytic bryophyte flora of cacao agroforests and nearby natural rainforest sites in Central Sulawesi, Indonesia. By comparing the bryophyte flora on cacao trees with that in the canopy and on understorey trees of the nearly undisturbed rainforest, we investigate the possible origin of the rich bryophyte flora on cacao, a tree that is exotic to the study area. Epiphytic bryophytes were collected from four habitat types ("cacao trees", "understorey trees", "canopy tree trunks" and "canopy tree crowns"). Cacao and understorey trees were comparable in terms of species richness. However, forest canopy trees had nearly three times higher levels of species richness. Species compositions differed significantly between cacao trees, forest understorey trees and canopy tree crowns. High numbers of "indicator species" are found for cacao trees (10 spp.) and canopy tree crowns (25 spp.). No less than 84% of bryophyte species found on cacao trees originated from the nearby natural forest sites and the majority seemed to originate from canopy trees crowns, which may relate to comparable microclimate conditions measured in these habitat types. Conversely, only 30% of the species in the forest sites also occurred in cacao agroforests, which indicates that after forest conversion, agroforests may only poorly serve as refuge for epiphytic forest bryophytes.

Introduction

Deforestation and habitat fragmentation in the tropics take place at an alarming pace (FAO 2001; Achard et al. 2002; Wright 2005). To assess their impact on biodiversity, conservation biologists have used biodiversity inventories before and after habitat disturbance, revealing unprecedented rates of local and regional species extinctions (Brook et al. 2003). Other studies have identified semi-natural and cultivated forests as potential tools in turning the tide of tropical species extinctions (Rice & Greenberg 2000; Barlow et al. 2007a; Steffan-Dewenter et al. 2007). Agroforests are plantations of perennial tree crops such as rubber and coffee and because of their structural resemblance to natural forests, shaded agroforests in particular have been related to high levels of alpha diversity, even resembling those of undisturbed rainforests (Perfecto et al 1997; Bos et al. 2007; Fujisaka et al. 1998; Andersson & Gradstein 2005; Brockerhoff et al. 2008).

More recently, an increasing focus on species turnover (beta diversity) between natural and cultivated habitats has revealed a major species turnover from natural to cultivated forests (e.g., Tylianakis et al; Barlow et al. 2007b Kessler et al. *in prep.*). Thus, for local and endemic flora and fauna, which should have highest conservation priority, cultivated forests appear to have a limited contribution to their protection. Reasons for this can be diverse and depend strongly on the group studied. In the case of epiphytic bryophytes, the most important driving factors for species turnover are likely to be related to changes in microclimate (e.g., Gradstein 2008; Chapters 2 and 3 in this dissertation). Bryophytes are particularly sensitive to climatic changes because of their lack of a protective cuticle and the therefore higher threat of desiccation (Barkman 1958; Richards 1984; Proctor 1990).

Species richness of epiphytic bryophytes on cacao trees in agroforests is comparable to that in forest understorey and can be highly heterogeneous (Andersson & Gradstein 2005; Chapter 2 and 3). However, species turnover between cacao trees in agroforests and understorey trees in nearby natural forests is high (Chapter 3), leading to the question from where the bryophytes on cacao trees originate.

A possible natural habitat of cacao bryophytes might be canopy of nearby natural forests from were they may switch to cacao tree after the conversion of rainforest to cacao agroforest. Alternatively, bryophytes may have originated from forests elsewhere in the same region or even from forests on other islands. Both settings imply shifts in microclimate scenarios in which anthropogenic disturbances trigger climatic homogenization of upper crowns of natural rainforest canopies and lower vegetation strata of secondary forests and agroforests (Walsh 1996; Acebey et al. 2003; Figure 1, Table 1) or of different forest types (e.g. submontane and lowland forests; Richards et al. 1996; Whitten et al. 2002). Hence, the bryophyte flora would represent biotic homogenization in which non-native species become regionally or globally widespread at the expense of local and endemic species (McKinney & Lockwood 1999; Fine 2002).

In this study we investigate the epiphytic bryophyte flora of cacao agroforest and rainforest in Central Sulawesi, Indonesia, an area where the cacao tree is non-native. The island of Sulawesi lies just east of Wallace's line, in a region characterized by high levels of endemism among flora and fauna and forming the centre of one of the world's largest biodiversity hotspots (Whitten et al 1996; Myers et al. 2000; Sodhi et al. 2004). Specifically, we aim at determining the origin of the cacao bryophyte flora by comparing this flora with that in the canopy and the understorey of the nearly undisturbed rainforest.

Table 1. The mean temperature and relative humidity from 7:00 AM to 7:00 PM in the upper canopy and in the understorey (2 m height) of four forest sites and in the understorey (2 m) of four cacao agroforest sites in Central Sulawesi, Indonesia. Means are given ± standard error.

	Temperature °C	RH %
Forest understorey	23.44 ± 0.31	84.78 ± 1.39
Forest canopy	23.99 ± 0.40	80.97 ± 1.86
Agroforest understorey	25.55 ± 0.42	81.06 ± 1.86

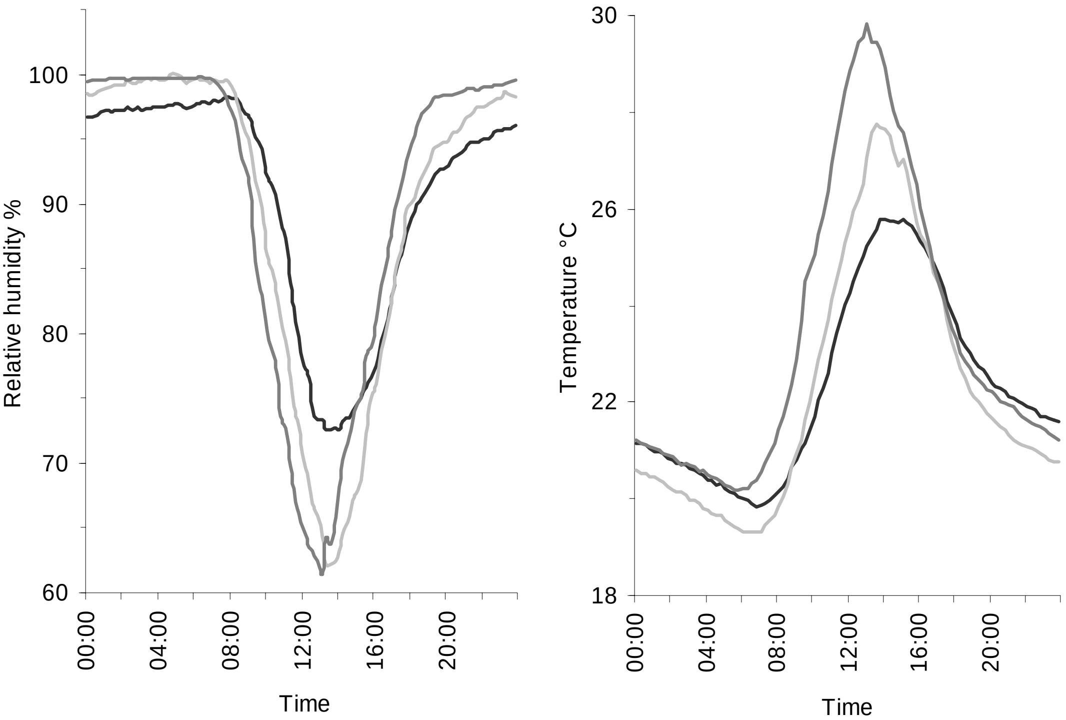

Figure 1. Temperature (°C, left) and relative humidity (%RH, right) in agroforest understorey (grey lines), forest understorey (black lines) and forest upper canopy (light grey lines) during 24 hours. The values are averages for the four agroforests and four forest sites in the study area.

Material and Methods

Study sites

The study took place in and around Toro Village at the western border of 231,000 ha Lore Lindu National Park, Central Sulawesi, Indonesia. Within an altitudinal range of 850–1100 m, four study sites were selected in the primary submontane forests of the national park and four in the cacao plantations that formed a continuous band of agroforests in the border of the national park (Fig. 2). The forest sites were characterized by only minor anthropogenic disturbance (e.g., minor rattan extraction, collection of medicinal plants, extensive hunting). Cacao agroforests had a diverse stand of

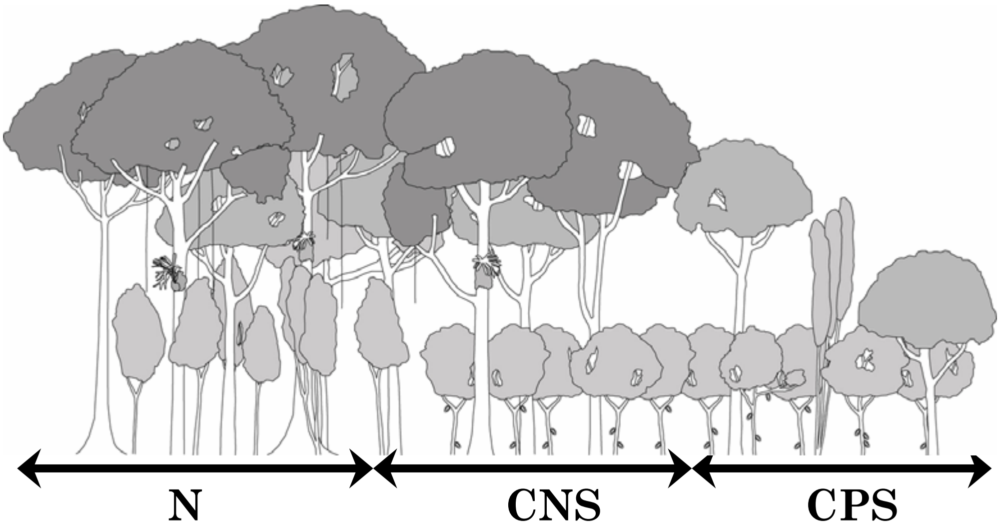

Figure 2. The three different land-use type – a schematic presentation (by MM Bos) CPS: Cacao under planted shade trees; CNS: Cacao under natural shade; NF: Natural forest

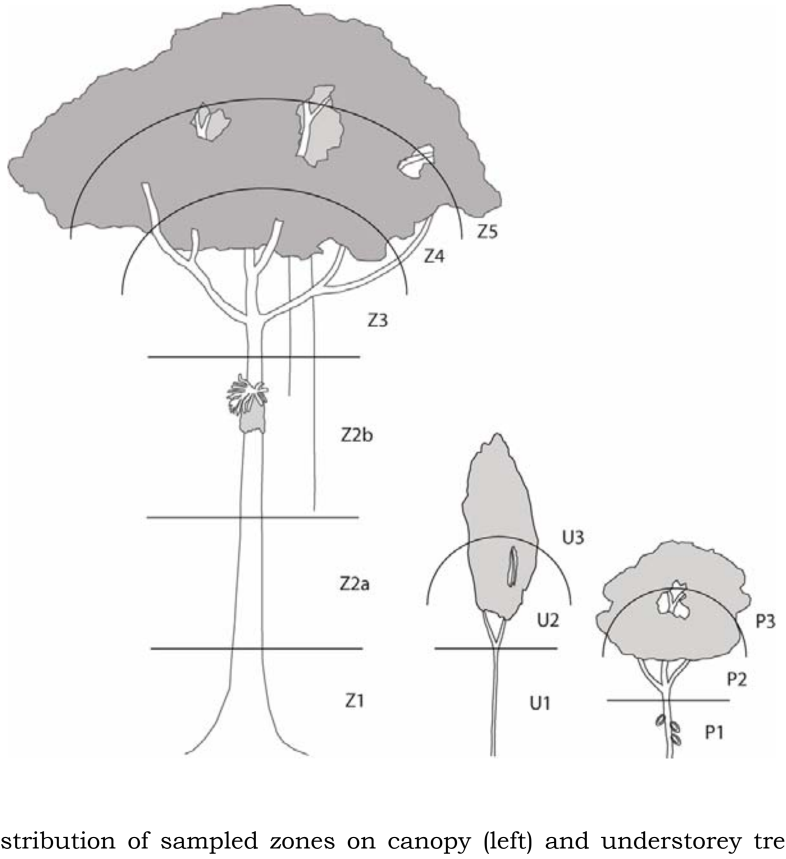

Figure 3. Distribution of sampled zones on canopy (left) and understorey trees (middle) in natural forest, and on cacao trees (right) in agroforests – a schematic presentation (by MM Bos)

shade trees that consisted of trees that remained from previous forest cover, various planted timber and fruit trees, and planted leguminous trees. See Appendix for more details.

The area had mean annual temperatures of 23.4°C, relative humidities of 85%, and an annual precipitation of 2000-3000 mm, without clear seasonal fluctuations (Gravenhorst et al. 2005). In the forests, microclimate measurements at 2 m and at the height of the first ramification (14-19 m) showed highest relative humidity in the forest understorey, and highest temperatures in forest canopy and agroforest understorey (Table 1, Fig. 1, Chapter 3).

Bryophyte sampling

In each forest site, two understorey and two canopy trees with a minimum distance of 15 m between them were selected. Understorey trees were between 3 and 6.5 m in height with a dbh varying from 20 to 60 cm. Upper canopy trees were between 30 and 45 m in height and had dbh values varying from 2 to 6.5 m. To minimize variance in substrate conditions, the bark of all selected trees was of a smooth texture. In each cacao agroforest, two cacao trees were selected. These were between 3 and 5.5 meters in height and had a dbh that varied between 20 and 45 cm.

Epiphytic bryophytes were collected from quadratic plots of 200 cm^2 positioned at each cardinal direction in six height zones on upper canopy trees (zones Z1, Z2a, Z2b, Z3, Z4, and Z5 according to Johansson 1974, Fig. 3) and in three zones on understorey (U1 = trunk from base to first ramification, U2= inner crown, and U3= outer crown) and cacao trees (P1= trunk from base to first ramification, P2= inner crown, and P3= outer crown). To reach higher zones, canopy trees were climbed using a single rope technique. Due to inaccessible or brittle tree structures, samples in height zones 4 and 5 were mainly taken from sewn branches. In total, 48 plots (9600 cm^2) per upper canopy and 24 plots (4800 cm^2) per understorey and cacao tree were sampled.

For the analyses, the zones were grouped into four “habitat types”. Zones Z1, Z2a and Z2b on the upper canopy tree in the natural forests were grouped as “Forest tree trunk” and zones Z3, Z4 and Z5 as “Forest tree crown”. The zones on understorey trees in the natural forest sites were grouped (zones U1, U2, U3) as “Forest understorey” and the zones on cacao trees in agroforest sites (zones P1, P2, P3) as “Cacao tree”. Bryophyte species were assigned to five life-forms: dendroid (including “fan” and “pendant”), mat (including “weft”), tail, turf (including “short” and “tall turf”). Bryophytes were identified using taxonomic literature and reference collections from GOET and L or sorted to morphospecies. Vouchers were deposited in BO, CEB, GOET and L.

Statistical analysis

To assess overall sampling completeness and sampling completeness per habitat type (“forest tree trunk”, “forest tree crown”, “understorey tree”, and “cacao tree”), we used the Chao2 species richness estimator (as recommended by Walter & Moore, 2005).

To quantify differences in species composition between sites and zones, we calculated Sørensen’s similarity index for each pairwise comparison of zones per site. Using non-metric multidimensional scaling (MDS), we reduced the similarity matrix to a graphic representation with the number of dimensions that reduced the majority of the “raw D-star stress”. Stress values below 0.20 were considered to indicate a good fit of the scaling to the matrix. With analyses of similarity (ANOSIM), differences in species composition between sites and zones were tested.

To assess habitat specificity of the collected species for the different habitat types, we calculated the indicator value (IV) of each of the species (Dufrene & Legendre, 1997). Indicator values of zero express no indication for a habitat group and values of 100 represent perfect indication of the species for the habitat type. To test for homogeneous distribution of life-forms within the habitat types, G-values were calculated.

Where relevant, analyses were carried out separately for overall bryophytes, for mosses (Bryophyta s.str.), and for liverworts (Marchantiophyta). The Chao2 richness estimates were calculated using Estimate*S* (Colwell 2004), indicator values using PC-ORD, MDS with Statistica 7.0 (Statsoft Inc. 1984-2004), and Sørensen’s similarity index and ANOSIM with Primer 5.0 (PRIMER-E Ltd 2002).

Results

Species richness

In total, 185 epiphytic bryophyte species (103 liverworts, 82 mosses) were collected in the four natural forest and four agroforest sites. Fifty-eight species occurred in agroforest (82 % sampling completeness) and 155 (86% sampling completeness) in natural forest. Of forest species, 84 were found on understorey trees (72% sampling completeness), 99 on tree trunks of canopy trees (91% sampling completeness) and 142 in crowns of canopy trees (82% sampling completeness) (Table 2, Fig. 4).

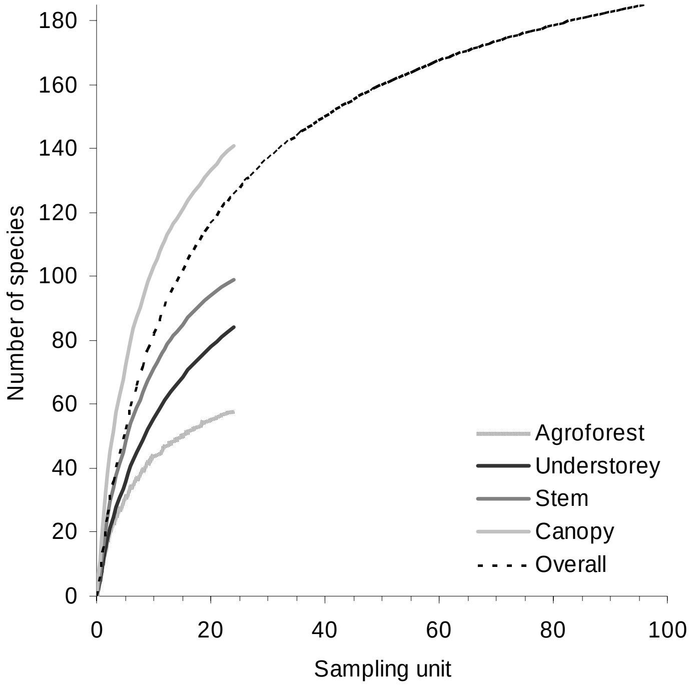

Figure 4. Accumulation curves of species richness of epiphytic bryophytes in the study area. For sampling details see text.

Species composition

Fifty-one species (i.e., 28% of all collected species, 84% (9 species) of species collected from cacao trees, 30% of the species collected in the forest) occurred in agroforests as well as in natural forest sites. Of all species collected from cacao trees, 50% (29 species) were also found on forest understorey trees, 57% (33 species) on forest tree trunks, and 76% (44 species) in forest tree crowns.

Table 2. Observed (obs) and estimated (est) species richness per tree type and zone and mean species richness averaged per zone in the study area. Bryo= Bryophytes; Hep= liverworts; Moss= mosses; Habitat: FC= Forest upper canopy tree crown, FCS= Forest total, FS= Forest upper canopy tree trunk, FU= Forest understorey tree, P= Cacao trees in agroforests.

	Bryo obs	Bryo est	Hep obs	Hep est	Moss obs	Moss est	Bryo average	Hep average	Moss average
Habitat									
P	58	71	28	41	25	28	10 ± 2.0	6 ± 1.2	4 ± 0.8
FU	84	116	47	62	37	48	10 ± 2.0	6 ± 1.2	4 ± 0.8
FS	99	108	60	70	37	38	14 ± 1.9	9 ± 1.5	6 ± 0.7
FC	142	173	80	97	59	68	22 ± 3.2	14 ± 2.0	8 ± 1.2
FCS	155	181	88	112	66	76	18 ± 1.8	10 ± 1.3	8 ± 0.7
Forest total	173	206							

Seventy-one percent of the species were exclusively found in the natural forest sites, whereas only 5% of all sampled species in this study were restricted to agroforest sites. The 5 % were made up by 9 species (*Aequatoriella sp., Cololejeunea planissima, Cololejeunea sp., Diplasiolejeunea sp., Erythrodontium julaceum, Frullania ericoides, Leptolejeunea balansae, Palamocladium leskeoides, Papillaria* sp.).

In the natural forest, 66 species (36% of all species in the forest) occurred on understorey trees as well as upper canopy trees. Nine percent of all species were only collected from understorey trees and 41% were exclusively found to upper canopy trees, with 3% (5 species) only collected from the stem and 18% (34 species) from the canopy zones.

Table 3. Shared species (%) in cacao agroforests and natural forest sites in Central Sulawesi, Indonesia. FC= Forest upper canopy tree crown, FS= Forest upper canopy tree trunk, FU= Forest understorey tree, P= Cacao trees in agroforests.

	P	**U**	**FS**	**FC**
% in P	100	35	33	31
% in FU	50	100	51	42
% in FS	57	60	100	61
% in FC	76	71	87	100

Table 4: The R and p values of the results of analysis of similarity (ANOSIM) of Sørensen's index calculated for pairwise comparisons of epiphytic bryophytes on different tree types and tree levels in the study area. Bold values indicate significant differences.

	Bryophytes		**Liverworts**		**Mosses**	
	R	*p*	*R*	*p*	*R*	*p*
Cacao tree vs. Understorey tree	**0.67**	**0.001**	**0.67**	**0.001**	**0.38**	**0.001**
Cacao tree vs. Canopy tree trunk	**0.69**	**0.001**	**0.65**	**0.001**	**0.42**	**0.001**
Cacao tree vs. Canopy tree crown	**0.73**	**0.001**	**0.59**	**0.001**	**0.52**	**0.001**
Understorey tree vs. Canopy tree trunk	0.13	0.016	0.15	0.013	0.15	0.013
Understorey tree vs. Canopy tree crown	**0.46**	**0.001**	**0.38**	**0.001**	0.13	0.028
Canopy tree trunk vs. Canopy tree crown	**0.19**	**0.003**	0.13	0.017	0.06	0.914

Only five species were exclusive to trunks of upper canopy trees and 34 species were restricted to upper canopy tree crowns.

Species composition differed clearly between the agroforest and forest sites, which was confirmed by ANOSIM results and did not differ between mosses and liverworts (Tables 3 & 4). Within forest sites, no significant difference between species composition of understorey trees and canopy tree trunks was found but turnover from understorey trees to forest tree crowns was significant for overall bryophytes and for liverworts, yet not significant for mosses (Table 3). Differences in species composition between trunk and crown of canopy trees were just significant for overall bryophyte composition, but insignificant for mosses and liverworts when analysed separately (Table 3).

Indicator values, life-forms and geographical distribution

Forty species had significant indicator values for one of the habitat types “forest tree trunk”, “forest tree crown”, “forest understorey tree” or “cacao tree” (Table 5). Overall, 17.2% of the species on cacao trees were specific for that habitat, 3.5% of the species on understorey trees, 4% of the species on forest tree trunks and 16% of the species on forest tree crowns.

Only epiphytic bryophytes belonging to the life-form group mat (including “wefts”) were evenly distributed among the habitat types (Table 6). Tails, turfs and dedroids showed a significant association to a habitat type (Fig. 5, Table 6). The composition of life-forms differed significantly between cacao trees and forest tree crowns as well as between cacao trees and forest understorey trees and canopy tree trunks (Fig. 5, 6). Among cacao trees and forest tree trunks, the frequency of mats (including wefts) and tails was homogeneous distributed, whereas dendroids dominated on forest tree trunks, and tufts showed significant preference for cacao trees (Figs. 5 & 6, Table 6). On cacao trees, most of the common species have a pantropic/Asian distribution, whereas most of the common species in the forest habitat types are restricted to the Paleotropics (Table 5).

Table 5. Significant indicator species, their indicator values for and abundance in four habitat types in Central Sulawesi, Indonesia. FC= Forest upper canopy tree crown, FCS= Forest total, FS= Forest upper canopy tree trunk, FU= Forest understorey tree, P= Cacao trees in agroforests. A= Asiatic, P= Pantropic, Pal= Paleotropic, n.a.= not assigned.

	IV	**p**	**P**	**U**	**FC**	**FS**	**Total**	**% of all zones**	**Geo-graphical Distribution**
Cacao tree									
Frullania riojaneirensis	93.3	0.0002	42	0	3	0	45	22	P
Mastigolejeunea auriculata	58.3	0.0002	66	4	24	10	104	44	P
Lejeunea exilis	56.8	0.0004	28	0	5	4	37	16	A
Garovaglia sp.	56.6	0.0002	46	4	5	6	61	29	A
Frullania ericoides	50	0.0006	10	0	0	0	10	8	P
Leptolejeunea sp.	41.7	0.0018	5	0	0	0	5	5	n.a.
Meteoriaceae sp. 3	41.7	0.0012	10	0	0	0	10	6	n.a.
Lejeunea cf. *obscura*	34	0.0192	17	4	2	2	25	16	A
Palamocladium leskeoides	33.3	0.0102	8	0	0	0	8	4	A
Cololejeunea lanciloba	30.3	0.0192	10	0	0	1	11	6	A
Forest understorey tree									
Pinatella mucronata	40.3	0.0088	0	36	18	13	67	30	A
Archilejeunea planiuscula	39.4	0.0220	1	35	16	22	74	40	A
Metzgeria spp.	30.7	0.0218	0	10	7	2	19	14	n.a.

Table 5, continue

	IV	p	P	U	FC	FS	Total	% of all zones	Geo-graphical Distribution
Forest upper canopy tree									
Forest tree trunk									
Lejeunea flava	36.6	0.0104	0	0	14	17	31	19	P
Himantocladium sp. 1	30.8	0.0440	0	9	8	19	36	22	n.a.
Aerobryopsis sp.	27.8	0.0358	0	0	1	5	6	5	n.a.
Cheilolejeunea vittata	25.9	0.0324	0	0	2	7	9	5	A
Forest tree crown									
Meteoriopsis squarrosa	58.8	0.0002	0	0	15	2	17	10	A
Plagiomnium sp.	58.3	0.0004	0	0	13	0	13	9	n.a.
Plagiochila bantamensis	47.4	0.0012	0	2	13	1	16	9	A
Lopholejeunea wiltensii	45.5	0.0026	0	0	10	1	11	7	A
Neckeropsis lepineana	43.1	0.0058	2	11	30	15	58	34	Pal
Meteoriaceae sp. 2	42.3	0.0024	0	0	11	2	13	7	n.a.
Lejeunea discreta	41.7	0.0020	0	0	10	0	10	7	n.a.
Chaetomitrium sp.	40.8	0.0044	0	1	14	5	20	16	n.a
Schiffneriolejeunea tumida	40.5	0.0036	0	0	17	4	21	10	A
Meteorium miquelianum	40	0.0044	12	2	21	0	35	21	A
Chaetomitrium sp. 5	36.7	0.0100	0	3	11	1	15	10	n.a.
Syrrhopodon sp. 3	33.9	0.0112	0	0	13	3	16	7	n.a.
Floribundaria floribunda	33.1	0.0400	6	11	19	7	43	27	Pal
Lejeunea punctiformis	32.7	0.0262	0	7	23	11	41	22	A
Lejeunea sp.	31.5	0.0452	6	1	20	10	37	20	n.a.
Pterobryopsis sp.	31.2	0.0230	0	0	6	2	8	7	n.a.
Sematophyllaceae sp.	27.8	0.0362	1	0	5	0	6	5	n.a.
Lejeunea sordida	27.3	0.0470	1	0	12	9	22	14	A
Cheilolejeunea trapezia	27.2	0.0466	0	0	15	8	23	13	A
Aerobryopsis sp. 2	27	0.0366	0	0	11	6	17	9	n.a.
Macromitrium sp. 3	26.8	0.0360	0	0	9	5	14	9	n.a.
Aerobryum speciosum	22.2	0.0468	0	0	4	2	6	5	A
Cheilolejeunea sp. 2	22.2	0.0450	0	0	6	3	9	7	n.a

Table 6: G-values (G_{adj}) based on G-test on one-way frequency classification of life-forms in the four habitat groups in the study area. For explanation see text.

G_{adj}	de	m	T	ta	df
All habitat types	128.33***	5.28	19.46*	13.9*	9
Cacao tree vs crown	56.82***	464.02***	29.21***	36.86***	4
Cacao tree vs forest understorey	89.31***	1076.63***	135.40***	153.13***	4
Cacao tree vs trunk	91.50***	2.92	10.88*	1.24	4

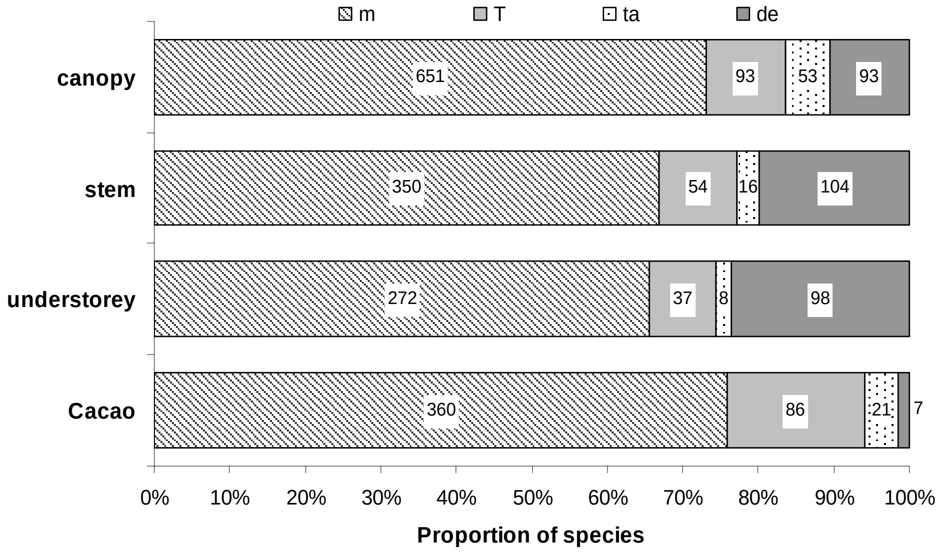

Figure 5. Proportion of bryophytes life forms in different habitats in the study area. de=dendroid, m= mat, T= turf, ta= tail.

Discussion

The species richness of epiphytic bryophytes was similarly high on cacao trees in agroforests and on understorey trees in natural forest (see also Chapter 2), which is in accordance with similar studies based on other floral or faunal groups (e.g. Schulze et al. 2004; Steffen-Deventer et al. 2007; Ariyanti et al. in press). However, the pattern changed drastically when canopy habitats were taken into consideration: Species richness was nearly three times higher in the rainforest canopy than in the understorey and on cacao trees. This indicates little suitability of agroforests for preserving levels of species richness that resemble that of the rainforest canopy.

The high turnover we found in species composition from natural forests to cacao agroforests (no less than 70% of forest species was not found on cacao trees), suggests that cacao agroforests only poorly contribute to preserving the local forest bryophyte flora. These turnover rates between natural forests and cultivated land are high compared to those reported for other areas. For example, in South American natural forests, Hietz (2005) found a turnover of 40% of vascular epiphytes from forest to nearby coffee plantations, and Acebey et al. (2003) described a 55% turnover of epiphytic bryophytes from forest to fallows of Bolivia.

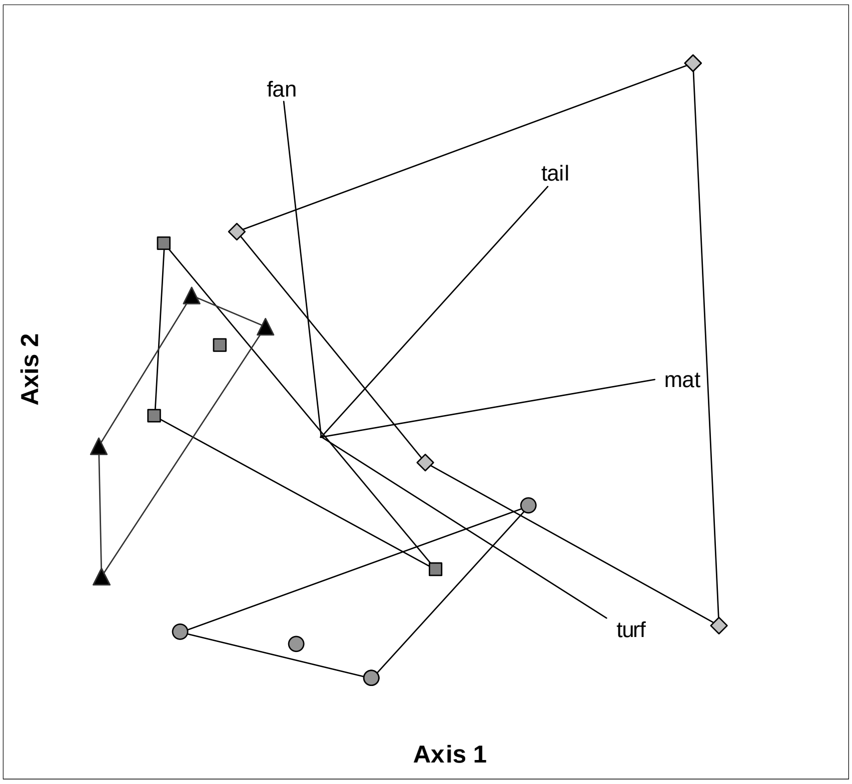

Figure 6. Principal component analysis based on Sørensen's indices for similarity of the compositions of different life-forms on cacao trees (grey dots), understorey trees (black triangles), upper canopy tree trunks (grey square) and upper canopy tree crowns (light grey rhomb) in the study area.

In our study, species turnover from forest to cacao trees did not differ when comparing the understorey trees, upper canopy tree trunks, or upper canopy tree crowns: For all comparisons, species compositions on cacao trees were significantly different from those in the three forest canopy habitats. Overall, no less than 76% (44 species) of the observed species on cacao trees also occurred in upper canopy tree crowns in the forest sites, whereas only 57% (33 species) was also found on tree trunks of upper canopy trees and only 50% (29 species) on understorey trees in the forest sites. After forest disturbance, it has been recorded that epiphytic bryophyte species change in habitat from upper canopy to lower canopy layers (Gradstein 1992; Acebey et al. 2003; Andersson & Gradstein 2005), which may as well explain the large proportion of bryophyte species on cacao trees that can also be found in upper forest canopy.

The high turnover from forest understorey to cacao trees can be explained by related drastic changes in microclimate conditions (Walsh 1996; Acebey et al 2003: see also Chapter 3), which can drive composition change in that species adapted to shaded habitats disappear at the benefit of drought tolerant “sun-epiphytes” (Gradstein 1992; Acebey et al. 2003; Holz 2003). This is also reflected by significant differences in the life-form spectrum of both habitat types. Here, the pronounced presence of dendroid species which are characteristic for moister and colder habitats (Mägdefrau 1982) of the understorey in particular divides these habitats from the exposed ones on cacao trees were dendroid species barely occur.

In contrast, microclimate hardly changed from forest upper canopies to agroforest understorey. Nevertheless, similarity in species compositions between agroforests and forest crowns was not significantly higher compared to the forest understorey. Also the composition of life-forms differed significantly, but manly due to a more balanced distribution of life-forms within the crown of upper canopy forest trees. Both habitat types harbored a composition of bryophytes which is more adapted on dryer and sunnier habitats with mats and turfs as prominent life-forms. The remaining high amount of the dendroid-group, including fans, dendroids and pendants, in the canopy may reflect the presence of shaded and more humid habitats in the protected inner canopy (see also Chapter 2).

The significant dissimilarity between bryophyte compositions on cacao trees and in the forest sites was clearly due to the 9 species (16% of the cacao bryophytes) that were not observed in the forest sites. Cacao trees in the agroforests and crowns of upper forest canopy trees had clearly distinct compositions of epiphytic bryophyte species. Over 15% of the species occurring in cacao tree and upper forest canopy tree crowns had significant indicator values for each habitat, whereas only few species (less than 5%) had significant indicator values for forest understorey trees and forest tree trunks. Of the 10 bryophyte species that had significant indicator values for cacao trees as habitat, six were also found in at least one habitat type in the natural forest sites. Thus, before cultivated habitats were introduced in the area, some of the characteristic “cacao bryophytes” may have occurred in low densities in the previous landcover by natural forests.

Four of the characteristic “cacao bryophytes”, which also occurred in the natural forest sites, are pantropical and well known from tropical America (i.e., *Frullania riojaneirensis, Frullania ericoides, Lejeunea flava, Mastigolejeunea auriculata*) with a preference for secondary, disturbed or fast changing habitats, including cacao agroforests (Acebey et al. 2003; Andersson & Gradstein 2005). Such species are examples of pantropical pioneer species adapted to young, dynamic habitats, and apparently existed in the local species pool of our study area as well.

The question remains where the remaining bryophyte species typical to cacao plantations come from. It is possible that some of these species did occur in the natural forest, but remained undetected within the sampling scheme used in this study. This is a very likely effect, considering the sampling incompleteness of 14% for the forest and the low density in which “cacao bryophytes” occurred in the forest habitats. However, it is as well possible that among these species there are non-native species that did not occur in the study area before the submontane forests were converted to cultivated land. They may have originated from lowland forests in the region, which resemble the microclimatic conditions of the cacao agroforests (Richards et al. 1996; Whitten et al. 2002). In this case, cacao agroforestry may have paved the way for invasive species (McKinney & Lockwood 1999; Fine 2002), which is an example of biotic homogenization. This will, however, be difficult to investigate because most of the lowland forests in Southeast Asia are severely disturbed or already converted to agricultural systems (Cannon et al. 2007).

Conclusion

In conclusion, agroforests provided suitable habitats for only a minority of the local epiphytic bryophyte flora on trees in natural forests. However, of the species that did occur on cacao trees, the majority seemed to be native to upper canopy tree crowns in nearby natural forests, possibly due to a less steep microclimatic gradient. Most of the characteristic bryophyte species in the agroforests have a pantropical distribution and are known from cacao plantations in South America as well. Despite the suggestion that cacao agroforests can contribute to tropical biodiversity conservation, bryophyte species that are exclusive to cacao trees possibly reflect biotic homogenization and clearly have low conservation priority as compared to those species that characterize tree crowns in natural forests.

Acknowledgements

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Chapter 5

Is productivity of cacao impeded by epiphytes? An experimental approach

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Abstract

The impact of epiphytes on cacao productivity was investigated in agroforests in Central Sulawesi, Indonesia. Effects of epiphyte removal on fruit-set success and eventual yields were studied on 80 trees in an experiment with a balanced full factorial design. The removal treatment had no significant effect on the eventual harvest of the cacao trees. Pollinator availability had the greatest impact on fruit-set success, whereas yields were mainly determined by site-specific factors that mediate fruit-abortion and occurrence of fungal diseases. The results illustrate that epiphytic flora dominated by non-vascular species may have no effects on cacao tree functioning and removal of non-vascular epiphytes is unnecessary for improving the productivity of cacao. Hence, farmers' labour can be reduced and conservation of the rich biodiversity outside natural forests supported.

Introduction

Tropical rainforests harbour a wide range of epiphytic plants (Schimper 1888; Richards 1996; Nieder et al. 2001). Among these, non-vascular epiphytes such as bryophytes and lichens, are the most diverse and abundant groups, yet they are also one of the least studied (Pócs 1982; Gradstein et al. 2005). Epiphytic bryophytes play an important role in the stabilization of the abiotic environment in trees (Stuntz et al. 2002) and provide a suitable habitat for various groups of arthropods (Nadkarni & Longino 1990).

Recent work on non-vascular epiphyte diversity on cacao (*Theobroma cacao* L.) in tropical agroforestry systems has shown that epiphyte assemblages on cacao trees can resemble those of natural tropical rainforest trees (Andersson & Gradstein 2005). Hence, these agricultural systems may serve as a tool in the conservation of the highly diverse and functionally important, native non-vascular epiphyte flora. In the case of cacao, however, it is believed that epiphytic layers may constrain the development of the cauliflorous flowers of the host plants, causing decreases in fruit growth and, eventually, losses in harvest. The latter assumption has led to the common management practice of epiphyte removal in cacao plantations (Kautz & Gradstein 2001; Andersson & Gradstein 2005; David 2005). Although dense epiphytic layers can cause damage through breakage of branches (Strong 1977) and some vascular epiphyte species may have virulent effects on host trees via their symbiotic mycorrhiza ("epiphytosis"; Ruinen 1953), a negative effect of epiphytes on cacao trees remains essentially unproven.

The present study is an experimental approach into the impact of epiphytes on cacao productivity in Indonesian cacao systems. Indonesia, the third most important cacao producing country in the world (International Cacao Organization 2005), is a hotspot in terms of both biodiversity (Myers et al. 2000) and deforestation (Achard et al. 2002). We tested two hypotheses on the effects of epiphytic layers on cacao production: (1) epiphytic layers have direct effects on cacao productivity in that flowering and fruit development is inhibited, and (2) epiphytic layers have indirect effects by promoting pests that depend on the availability of moist habitats provided by the layers density. The cacao pest Black Pod Disease (*Phytophthora* sp., BPD) was common in the study region (Bos et al., 2007) and is known to depend on moist habitats (Thorold 1952; David 2005).

Materials and Methods

The study took place in cacao-dominated agroforestry systems around Toro Village in the Kulawi Valley, Central Sulawesi, Indonesia. The village is situated at ca. 800 m a.s.l. along the western border of the 231 000 ha. Lore Lindu National Park. Four agroforestry systems owned by farmers who did not practice removal of epiphytic layers were selected. The sites had similar shade tree stands, consisting of diverse species such as *Durio zibethinus* Murr., *Nephelium lappaceum* L., *Syzygium aromaticum* (L.) Merr. & Perry, *Erythrina subumbrans* Hassk., *Aleurites mollucana* Wild., *Calamus zollingerii* Becc., *Lansium domesticum* Corr., *Persea americana* Mill. and *Myristica fragrans* Houtt.

To study the direct and indirect effects of epiphytic layers on cacao productivity, a balanced full factorial design repeated in four blocks was used. In each of the four agroforestry systems (blocks) 20 cacao trees (i.e., a total of 80 trees) were selected randomly. The epiphytic layers were removed from half of these trees before the start of the experiment. Per site, trees were divided into four treatment groups: (1) 5 trees with removed epiphytic layers and with emerging flowers being manually cross-pollinated until development of a minimum of 16 fruits, (2) 5 trees with emerging flowers being manually cross-pollinated, but with epiphytic layers left intact, (3) 5 trees with removed epiphytic layers and emerging flowers left for natural pollination, and (4) 5 control trees (epiphytic layers intact, emerging flowers left for natural pollination). Epiphyte removal was done very carefully, avoiding damage to the flowers and bark.

Cacao flowers are generally self incompatible and under natural circumstances mainly pollinated by midges of the family Ceratopogonidae (e.g., Entwistle 1972; Young 1994). Manual standardization of cross pollination was achieved by transferring pollen from flowers of three other trees to the stigma of the target flower.

The experiment started in December 2004. Fruits were monitored and measured regularly until growth was terminated due to harvest or other causes (see also Bos et al. 2007). The number of wilted fruits was noted as well, serving as an indicator of physiological constraints on fruit development (Valle et al. 1990). All measurements were carried out on the tree's main stem, where most flowering and fruiting takes place (Entwistle 1972). The experiment ended with the harvest of the last fruits in June 2005.

The effects of the treatments were statistically tested in general linear models (GLMs) with study site as random factor and treatments (pollination and removal of epiphytic layers) as fixed factors, using Type III decomposition of variance. Interaction effects were included in the model to identify treatment- and site-specific effects of both treatments on the tested variables. Effects were tested on fruit-set success, amount of fruit-wilt, amount of fruits infected with BPD and numbers of fruits harvested. All variables were calculated as percentages of initial amounts of flowers per tree.

Initial fruit-set, subsequent fruit wilt and incidence of BPD, and harvested fruit data, were proportional and therefore arcsine square-root transformed before analyses. Additionally, data were square-root transformed where necessary to achieve normal distribution of model residuals. All analyses were conducted using Statistica 7.0 (Statsoft Inc. 1984-2004).

Results

In total, 3077 flowers on 80 trees were studied. About half of the flowers (1534) were successfully pollinated. Of these, a total of 182 resulted in mature fruits.

Removal of the epiphytic layers had no significant effect on fruit-set (Table 1a.). Instead, a non-significant, positive effect ($p=0.07$) of the presence of epiphytic layers on fruit-set was found (Table 1a, Fig. 1a).

The pollination treatment had the strongest impact on fruit-set success (Table 1a, Fig. 1a), with hand-pollination resulting in a much more successful fruit-set (75±3%) than natural pollination (43±5%). Natural pollination differed significantly between sites; in one site natural fruit-set success even equalled that resulting from hand-pollination.

Incidence of the BPD was not affected by the treatments, although the effect of moss removal differed between sites (Table 1c, Fig. 1b). The proportion of wilted fruits was significantly higher after hand pollination than after natural pollination (Table 1b).

Table 1. Impact of site, pollination, and epiphyte removal on fruit-set success, fruit wilt, occurrence of Black Pod Disease (BPD) and cacao harvest, using general linear models (GLMs) with type III decomposition of variance. Site entered as random factor (values 1-4), epiphyte removal and pollination type as fixed variables (1, 0). MS=Means of Squares, D.f.=Degrees of freedom * analyses after square root transformation of the data to reach normal distribution of model residuals

a. FRUIT-SET	**MS**	**D.f.**	**F**	**p**
Site	0.33	3, 1.9	2.09	0.345
Pollination	**4.07**	**1, 3**	**20.73**	**0.020**
Epiphyte removal	0.13	1, 3	7.27	0.074
*Pollination*Epiphyte removal*	0.02	1, 67	0.41	0.525
*Site*Pollination*	**0.20**	**3, 67**	**3.48**	**0.021**
*Site*Epiphyte removal*	0.02	3, 67	0.33	0.806
Error	0.06			
b. WILT				
Site	0.08	3, 1.3	1.70	0.457
Pollination	**0.91**	**1, 3**	**13.49**	**0.035**
Epiphyte removal	0.05	1, 3	4.57	0.122
*Pollination*Epiphyte removal*	0.00	1, 67	0.02	0.899
*Site*Pollination*	0.07	3, 67	1.99	0.124
*Site*Epiphyte removal*	0.01	3, 67	0.35	0.791
Error	0.03			
c. BPD*				
Site	0.05	3, 2.3	0.25	0.854
Pollination	0.06	1, 3	3.05	0.179
Epiphyte removal	0.01	1, 3	0.03	0.881
*Pollination*Epiphyte removal*	0.00	1, 67	0.03	0.854
*Site*Pollination*	0.02	3, 67	0.43	0.734
*Site*Epiphyte removal*	**0.23**	**3, 67**	**4.74**	**0.005**
Error	0.05			
d. HARVEST*				
Site	0.26	3, 1.4	3.38	0.301
Pollination	0.05	1, 3	0.71	0.461
Epiphyte removal	0.00	1, 3	0.03	0.884
*Pollination*Epiphyte removal*	0.18	1, 67	2.27	0.136
*Site*Pollination*	0.07	3, 67	0.94	0.425
*Site*Epiphyte removal*	0.08	3, 67	1.03	0.385
Error	0.08			

Finally, the percentage of flowers that resulted in mature fruits (overall average 7±1%) did not seem to depend on either epiphyte removal or on the pollination treatment (Table 1d, Fig. 1c).

Figure 1: a. The significant effect of hand-pollination on fruit-set and the insignificant effect of epiphyte removal on cacao's fruit-set success (%). b. The significant effect of hand-pollination on subsequent fruit-wilt and the insignificant effect of epiphyte removal. c. The insignificant effects of hand-pollination and epiphyte removal on eventual harvest. Bars indicate the standard error. Values indicated with a and b are significantly different based on Tukey's HSD post-hoc tests.

Figure 1a.

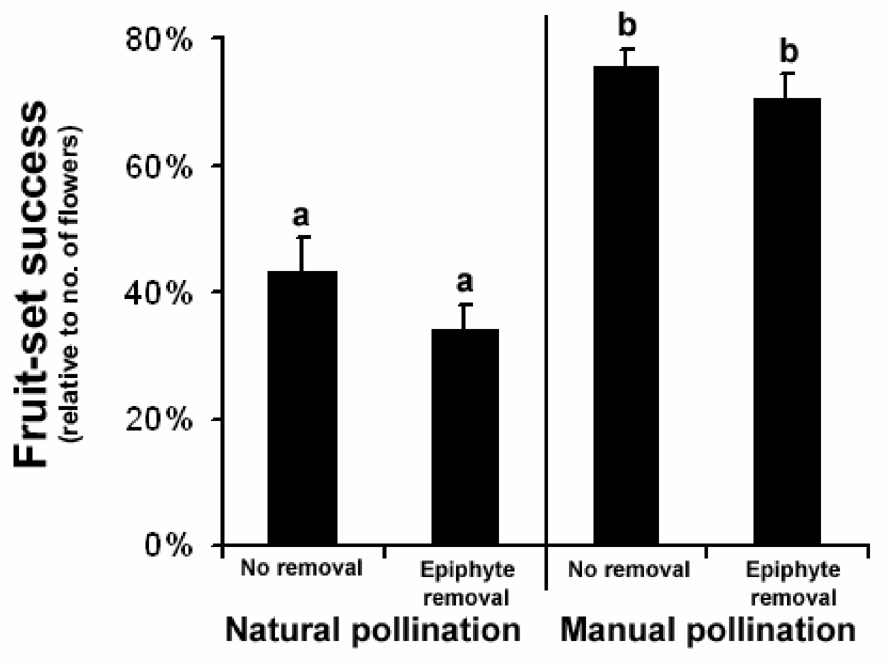


Figure 1b.

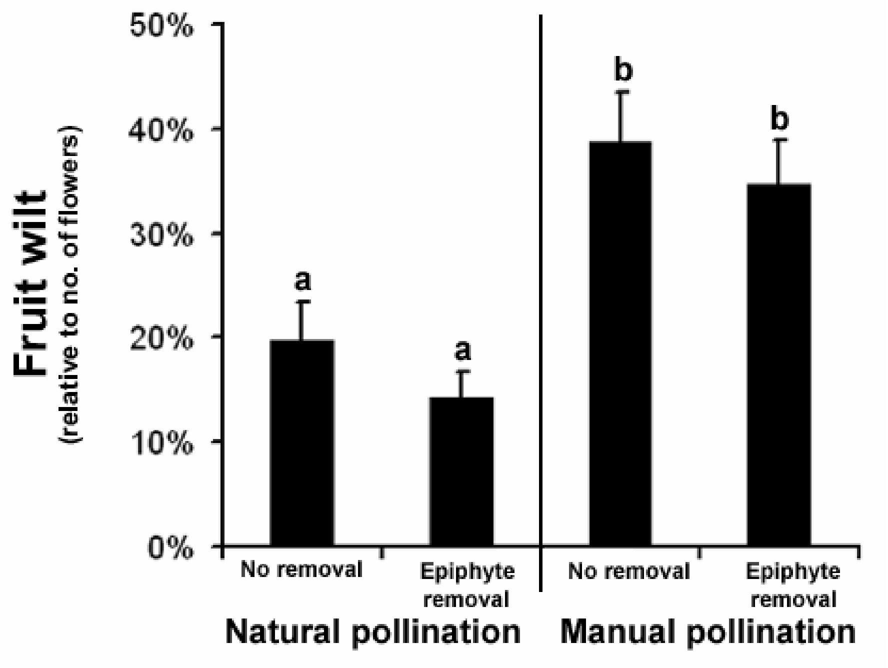
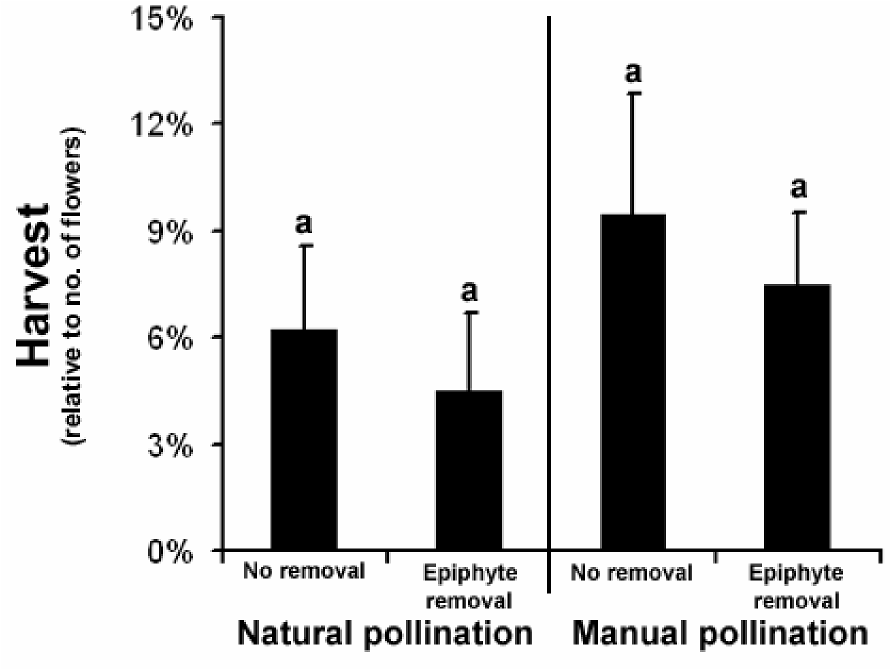


Figure 1c



Discussion

The results of this study show that epiphyte removal had no significant effect on the productivity of the cacao trees. Neither initial proportions of fruit-set success, subsequent levels of fruit-wilt and BPD-infections, nor final proportions of fruits harvested were significantly altered by the removal of the epiphytic layers. In fact, natural fruit-set was even slightly lower ($p=0.07$) on trees with epiphyte layers removed.

Epiphytic bryophyte layers are an indicator of abiotic environmental variables, especially of humidity (van Reenen & Gradstein 1983; Frahm & Gradstein 1991). It has been shown that moist environments also promote fungal cacao diseases such as BPD (Thorold 1952). However, these results indicate that the association between non-vascular epiphytes and fungal cacao diseases might be merely correlative instead of causal. No impact of epiphytic layers on BPD infection rates could be found. These results imply that removal of epiphytic layers eliminates the indicators, not the underlying causes of increased chances of BPD-infections in the research area.

Importantly, epiphytic assemblages on cacao in the study area consisted almost exclusively of lichen and bryophyte species while vascular epiphytes were rare (SG Sporn, unpublished data). Future studies in other regions should take into account the possible impact vascular epiphytes may have on cacao production. Moreover, epiphytic layers may have long-term deteriorative effects on their hosts (Ruinen 1953), which were not studied in this experiment.

A strikingly low percentage of flowers produced mature fruits, which for cacao is not unusual (Valle et al. 1990) and may be explained by the relatively unspecialized natural pollination system of the cacao trees (Young 1994). Fruit-set success significantly increased with hand pollination, indicating a significant pollination deficiency in the agroforestry systems, which was independent of the removal of epiphytic layers. Furthermore, natural pollination differed significantly between sites, suggesting that there are important site specific factors other than epiphyte removal, that influence cacao pollination. The increase in fruit-set after hand-pollination, however, was followed by an increase in harvest loss due to fruit-wilt. Fruit-wilt is a form of abortion when the number of fruits produced exceeds the load that trees can physiologically support (Valle et al. 1990). Therefore, our results demonstrate that increased pollination does not necessarily lead to increases in cacao's yields, as long as other environmental factors remain limiting. The potential fruit load of a cacao tree is restricted by factors such as available nutrients and local shade conditions (Entwistle 1972; Bos et al. 2007).

Conclusion

In conclusion, epiphyte removal is not necessary for improving the productivity of cacao in the study region. We therefore strongly recommend abandoning this practice when such layers predominantly consist of non-vascular epiphytes. In contrast, this study revealed a slightly negative effect of epiphyte removal on the natural pollination of cacao. This may be explained by damage on the cacao tree caused by the practice of epiphyte removal, or even by the possible importance of the epiphyte layers as a substrate for pollinator populations (Fish & Soria 1978). Pollinator availability had the greatest impact on fruit-set success, although total harvest was presumably mainly determined by site-specific factors, which are yet to be studied. In short, this study shows that if farmers consider epiphytic layers on cacao trees as irrelevant in terms of productivity, they may reduce their labour, and, at the same time, enhance the biodiversity supported by these agroforestry systems.

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Chapter

6

Summary and Outlook

Tropical rainforests form the most species rich but also most threatened ecosystems in the world. With ongoing large scale forest conversion into agricultural land, pristine forests become diminished and the unique biodiversity they harbor decreases towards extinction. This is not only a local concern but can have global impact on related ecosystem services on which human health and welfare depend.

In the present study, the impact of ongoing forest degradation and habitat homogenization on epiphytic bryophytes is investigated. Epiphytic bryophytes are particularly sensitive to forest conversion and other environmental changes due to their lacking protective cuticle. The studies include research on diversity, ecology, and relevance for agroforestry management of epiphytic bryophytes in natural forests and different cacao agroforestry systems in Central Sulawesi, Indonesia.

Richness, composition, distribution and ecology (based on life-form inventory) of epiphytic bryophytes in natural forests were investigated to evaluate biodiversity patterns characteristic for pristine forest habitats while building up the information standard of epiphytic bryophytes in Southeast Asia. The results were correlated with microclimate changes within the respective forest structure. Compared with studies in rainforests elsewhere in the tropics, impressively high levels of species richness were found. Species richness peaked in the inner crown of forest canopy trees. In the shady, humid habitats of understorey trees and canopy tree trunks as well as on exposed, dry and sunny outer canopy habitats, species richness was intermediate. Moreover, species composition differed greatly between shaded habitats of understorey trees and canopy tree trunks on one hand and sunny habitats in canopy tree crowns on the other. These two distinct assemblages of epiphytic bryophytes on forest trees were reflected by differences in microclimate between the two forest strata: In the understorey, temperatures were comparably low and humidity high, whereas in tree crowns temperatures were high and humidity low. Indeed, bryophytes communities in the understorey were characterized by species with exposed life-forms, whereas communities in higher canopy layers were increasingly characterized by species with life-forms better adapted to drought. Thus, although bryophytes on understorey trees are less species rich compared to canopy tree crowns, excluding them from inventories would underestimate the importance of a unique group of “shade-epiphytes”.

Because forest conversion and shade removal in cultivated forests result in an increase in temperatures and decrease in humidity in lower vegetation layers, bryophyte assemblages in the understorey are predicted to be among the first to be affected by such acts of human habitat disturbance. Also in our study area, microclimate in the cacao agroforests was clearly warmer and drier than in the understorey habitats in nearby natural forest sites. While in the forest understorey microclimate was comparably stable during the day, microclimate in the agroforests was characterized by a drastic decline in air humidity and temperatures during the afternoon. The impact of this narrower microclimatic “bottleneck” was not significant in terms of species richness of epiphytic bryophytes, but was reflected in a pronounced change in species composition from natural forests to cacao agroforests. Particularly the amount of change in microclimate conditions could be related to the high turnover of epiphytic bryophyte species between the natural and cultivated forest types.

For this purpose the four habitat types “understorey”, “trunk” and “crown” in natural forest and “cacao” in agroforests, were compared in regard to species richness, composition and ecology of epiphytic bryophytes. Whereas microclimate changed drastically from forest understorey to cacao agroforests (see above), microclimate in the agroforests was warm and dry, comparable with that in upper canopy tree crowns of the natural forest sites. Nevertheless, only 30% of the forest bryophytes also occurred on cacao trees in the agroforests, which diminishes the potential of agroforest as refuge for epiphytic bryophyte species from the natural forest. Compositions of bryophyte assemblages in “crown”, “cacao” and “understorey” differed significantly from each other, whereas those on forest canopy tree trunks were similar to those in upper canopy tree crowns. Cacao trees and upper canopy tree crowns each had a characteristic set of indicator species, which on cacao trees mostly had pantropical or asian distributions, and in forest canopies mostly palaeotropical distributions. Similar microclimate conditions within “cacao” and “crown” explain the closer resemblances. However, the majority of species on cacao trees (>70%) seemed to originate from tree crowns of the previous forest over or nearby forested sites. These results suggest that epiphytic “shade-bryophytes” that characterize understorey trees and tree trunks are most sensitive to forest conversion and management intensification, because they cannot cope with the resulting changes in the microclimate.

In this and other studies, it has become evident that cacao trees can harbor species rich and characteristic compositions of epiphytic bryophytes in levels that deserve attention in terms of tropical biodiversity conservation and the development of sustainable land-use. Unfortunately, it is common practice by cacao farmers to rip off epiphytic layers from cacao trees, lead by the assumption that epiphytes impede the tree’s productivity. Fruit-set, pest sensitivity and yield of cacao trees with and with removed epiphytic layers were compared during one season. Within the time frame of the experiment no significant effect of epiphytic layers on the eventual harvest of the cacao trees was found. Differences in fruit-set and yield were related to varying pollinator availability on one hand and site-specific factors that mediate fruit-abortion and occurrence of fungal diseases on the other. Thus, epiphyte removal does not necessarily improve cacao productivity and can be abandoned to save farmer’s labor and, more importantly from a conservation point of view, to maintain the rich and unique biodiversity of forested habitats in regions dominated by deforestation.

Carrying out comparative studies on any plant or animal group at any spatial and temporal scale, needs detailed information on the occurrence, distribution and ecology of species. Unfortunately, this information is mostly hard to access or even non-existing for the tropics, which limits ecological studies throughout the tropics. For Southeast Asia in general and Sulawesi in particular, recent checklists and this dissertation can form the basis for further investigations on the highly diverse group of epiphytic bryophytes and their ecological value and their value as indicator species for forest integrity, and to reveal modes and mechanisms of ancient and recent dispersal.

To shed further light upon the ecological value of epiphytic bryophyte communities in cacao agroforests and the actual potential of agroforests in protecting that value, further studies on species composition in cacao agroforests have to be carried out building further upon the information basis. By comparing inventories between different cacao growing regions, an overview can be reached of native versus non-native elements, which is important for assigning conservation priorities.
Additionally, although the role of nearby forests for bryophyte species richness and composition in cacao agroforests was discussed in this dissertation, more detailed data on the distribution and habitat preferences of epiphytic should increase our knowledge on possible effects of cacao agroforestry on biotic homogenization, which is hypothetically reflected by floristic similarity between agroforests from different regions/continents . Furthermore, effects of habitat fragmentation and distance to source populations on epiphytic bryophytes, which may drive further declines in richness of forest species, remain to be studied.

Lastly, to conduct experiments on the possible impact of epiphytic layers on cacao productivity and on other elements of biodiversity, future studies should aim at longer time ranges and include other study regions. The available time frame covered only one big harvest event, and it is impossible to account for long-term effects of epiphyte removal in this case study. Furthermore, epiphytic layers consisted mostly of bryophytes, lichens and a small number of vascular plants. Because negative effects (such as “epiphytosis”) are only described for vascular epiphytes, possible effects should be investigated in cacao agroforests with differing epiphyte composition, which may result in different implications for cacao growing practices.

Appendix

Appendix 1: Excerpt form Plantationowner-Census conduction in April 2005 by Rosmina and SG Sporn

Land-Use Type	CNS			CPS				L			
No.	1	2	3	1	2	3	4	1	2	3	4
Owner	Abia	Penga	Ambi	Samuel	Abdullah	Dada	Theodoris	Tahir	Rompa	Sony	Ilham
How long ago converted from forest to a plantation?	45 years	10 years	30-40 years	?	20 years	15 years	20 years	20 years	30 years	30 years	>20 years
Has there been coffee/other crop first?	Coffee	Coffee	Coffee	No	Peanut, corn, coffee	5 years coffee	Corn	Coffee	Coffee	5 years coffee	Corn, coffee
First under which shading?	Forest trees	Planted fruit-tree	Forest trees	Forest trees	Planted fruit-tree	Planted fruit-tree	-	-	-	Forest trees	None
Or clearcut?	No	No	No	No	No	No	Yes	-	-	No	Yes
Age of cacao trees?	15, 10, 5, 2 and 1 year	10 and 1 year	10, 5, 3, 2 years	9 years	2, 5 and 13	4 years	2,5 , 3 and 12	>15	10 and 20 years	20, 4 and 1 year	15
Distance between cacao trees?	3x3m	2x2 m	3x3m	3-4m	Different, 3 x 4m is the best	2 m	varying	-		varying	3m
Fertilizing (Method)?	Spreading of litter ash	No	No	No	KCL and Urea (50g per tree)	No	Urea and TSP (50/50)	-	Urea and TSP	KCL and Urea	KCL and Urea
How often Fertilizing?	-	-	-	-	2x / year	-	4X / year	-	Once	1x / year	Once
Use of insectizide or herbizide?	No	No	No	No	No	No	No	Once	No	1x/year	No
How often removing the herb layer?	3x / year	3x / year	2x / year	3x / month	3x / year	2x / year	1x / 3 month	regular	1x / 3 month	1x / month	1x/month
Frequency of regular harvest?	1x / week	2-3x / month	Every 3 weeks	2x / month	1x/month	2x/month	2x/month	Every week		2x/month	every 3 days
Yield from regular harvest?	15kg/ week	5kg/ month	5kg/ 3 weeks	2x 50kg / month	20kg/ harvest	60kg/ harvest	60kg/ month	5kg/ week		120kg/ month	50kg/ month
How often a big harvest?	None	No	No	-	1x/year	-	-	-	3x/year	none	2
Yield from big harvest?	No	-	-	-	1ton/year	-	-	-	150kg	-	70-80kg
How often visit of the plantation per week?	Every day	Every day	1x / month	Every day	Every day	Every day	Every 3 days	Every day	3x /week	Every day	Every day

Vegetation on the plantation beside *Theobroma cacao*?	CNS			CPS				L			
	1	2	3	1	2	3	4	1	2	3	4
Scientific name (assigned by R. Pitopang):											
Neonauclea ventricosa	-	-	-	p	-	-	-			10	15, p
Aleurites mollucana	-	-	-	-	13, f	-	-			?	15, p
Arenga pinnata	15, f	20, f	-	-	>20, f	-	-				
Artocarpus elasticus	-	f	60, f	-	-	-	-	p			
Artocarpus hererophyllus	-	-	-	-	-	-	13, p	p			
Artocarpus vrieseana	-	f	f	-	-	f	-				
Bischoffia javanica	>60, f	>20, f	>60, f	f	-	-	-				
Callamus zollingerii	-	-	-	-	-	-	-	p			
Cananga odorata	-	-	-	-	-	-	15, p				
Ceiba pentandra											
Citrus spp											p
Cocos nucifera	-	-	-	-	-	-	3, p	p		25	
Coffea robusta	15-45, p	8, p	-	p	-	-	-	p			
Durio zibethinus	-	-	3, p	-	-	-	1,5, p		5, p		10, p
Elmerilla ovalis	60, f	-	-	-	6, f	-	-				
Erythrina sp	60, p	-	f	-	-	-	-			20	
Erythrina subumbran	15, p	-	-	f	13, p	20, f	13, f				15, p
Ficus sp	-	-	-	-	-	-	-				
Ficus variegata	-	-	60, f	-	-	-	-				
Glyricidia sepium	-	-	-	-	-	3, p	-				
Gnetum gnemon	-	-	f	-	-	-	-				
Horsfieldia costulata	-	-	f	-	-	-	-	p			10
Jatropa curcas	-	-	-	-	-	p	-				
Lansium domesticum	5, p	-	-	-	-	15, p	-		15, p		
Litsea sp	60, f	-	10, f	-	-	-	-				
Mangifera indica	15, p	-	-	-	-	-	-			10	10

Manihot esculenta	-	-	-	-	-	-	-			
Melicope confusa	-	-	60, f	-	-	-	-			
Musa paradisiaca	3, p	-	2, p	p	13, p	5, p	13, p	20, p		p
Nephelium lappaceum	8, p	8, f	3, p	p	5, p	-	-	15, p		15, p
Pandanus sp	-	-	-	-	-	-	-			
Persea americana	-	-	-	-	5, p	-	-			
Piper aduncum	-	-	-	-	-	-	-		10,p	
Pterospermum celebicum	-	-	60, f	-	-	-	-		30	
Schizostachyum brachycladum	-	-	-	-	-	-	-			
Syzigium aromaticum	-	-	-	-	-	-	-		10	
Syzigium mallacensis	-	-	-	-	-	-	16, p			
Trema orientalis	-	>20, f	60, f	-	-	-	-			

Appendix 2: The height of each of the trees and zones. in meters. from which epiphytic bryophytes were collected on understorey trees (zones U1 to U3) and canopy trees (zones Z1 to Z5) in four forest sites (N1 to N4) in Central Sulawesi. Indonesia.

	Canopy		**Understorey**	
	Tree 1	***Tree 2***	***Tree 1***	***Tree 2***
N1	38.0	35.0	4.5	4.0
N2	28.0	26.0	3.0	6.5
N3	39.0	30.0	4.0	6.5
N4	45.0	39.0	7.5	7.5

	Zone	**Canopy**		**Zone**	**Understorey**	
		Tree 1	***Tree 2***		***Tree 1***	***Tree 2***
N1	***Z1***	1.5	1.5	***U1***	0.6	0.5
	Z2a	6.5	5.0	***U2***	1.6	1.4
	Z2b	11.0	8.0	***U3***	4.5	3.2
	Z3	23.0	17.0			
	Z4	25.0	17.0			
	Z5	26.0	20.0			
N2	***Z1***	1.5	1.5	***U1***	0.5	1.0
	Z2a	6.0	5.5	***U2***	1.4	2.8
	Z2b	10.0	9.0	***U3***	2.0	5.3
	Z3	15.0	14.0			
	Z4	16.0	20.0			
	Z5	18.0	18.0			
N3	***Z1***	1.5	1.5	***U1***	0.7	0.7
	Z2a	6.0	7.0	***U2***	2.0	1.9
	Z2b	10.0	12.0	***U3***	6	5.5
	Z3	15.0	14.0			
	Z4	23.0	14.0			
	Z5	23.0	17.0			
N4	***Z1***	1.5	1.5	***U1***	0.8	0.5
	Z2a	6.5	7.0	***U2***	1.4	1.8
	Z2b	10.5	12.0	***U3***	5.0	5.5
	Z3	18.0	18.0			
	Z4	19.0	21.0			
	Z5	20.0	23.0			

Appendix 3: The liverwort and moss species that occurred in 10% or more of all samples. Amount of samples indicated in which the species occur per tree type and per zone.

	Understorey tree	Canopy tree	U1	U2	U3	Z1	Z2a	Z2b	Z3	Z4	Z5	% of all zones
	n_{total} =12	n_{total} =24	n_{total} =4									n_{total} =72
Liverworts												
Archilejeunea planiuscula	10	17	3	4	3	4	3	3	2	2	3	51.4
Lopholejeunea subfusca	8	18	2	3	3	1	3	4	4	3	3	51.4
Cheilolejeunea vittata	3	14	1	1	1	1	4	3	2	2	2	36.1
Mastigolejeunea auriculata	2	14	0	0	2	0	2	3	3	3	3	31.9
Cheilolejeunea trapezia	5	13	1	2	2	1	4	3	3	0	2	30.6
Lejeunea punctiformis	3	12	0	1	2	1	1	3	3	2	2	29.2
Lejeunea spec 1	5	9	1	2	2	1	2	3	2	1	0	26.4
Lejeunea spec 2	0	15	0	0	0	0	4	4	4	1	2	25.0
Cheilolejeunea trifaria	2	11	1	0	1	0	1	3	3	3	1	23.6
Lejeunea spec 7	1	13	0	1	0	0	3	3	3	2	2	22.2
Metzgeria lindbergii	7	5	2	3	2	1	0	1	1	1	1	18.1
Porella acutifolia	4	4	1	1	2	1	0	0	1	1	1	18.1
Heteroscyphuscf zollingeri	3	9	0	2	1	0	2	2	3	1	1	16.7
Lejeunea flava	2	8	0	2	0	0	1	2	2	2	1	16.7
Lejeunea sordida	0	10	0	0	0	0	2	2	3	1	2	16.7
Thysananthus spathulistipus	2	6	0	1	1	0	1	1	1	2	1	16.7
Radula javanica	5	5	3	1	1	1	0	1	2	1	0	15.3
Frullania apiculata	0	6	0	0	0	0	1	1	1	2	1	13.9
Schiffneriolejeunea tumida	0	8	0	0	0	0	1	1	2	2	2	13.9
Plagiochila bantamensis	1	8	0	0	1	0	0	1	2	3	2	12.5
Acrolejeunea pycnoclada	0	5	0	0	0	0	1	1	1	1	1	11.1
Caudalejeunea recurvistipula	1	7	0	0	1	0	1	0	2	1	3	11.1
Plagiochila spec 4	1	6	0	1	0	0	1	1	2	2	0	11.1

	Understorey tree	**Canopy tree**	**U1**	**U2**	**U3**	**Z1**	**Z2a**	**Z2b**	**Z3**	**Z4**	**Z5**	**% of all zones**
	n_{total} =12	n_{total} =24	n_{total} =4									n_{total} =72
Mosses												
Neckeropsis lepineana	6	17	2	2	2	2	2	3	4	4	2	43.1
Pinatella mucronata	9	13	3	3	3	3	2	3	1	2	2	40.3
Floribundaria floribunda	5	14	2	2	1	1	1	3	4	3	2	30.6
Himantocladium spec 1	6	10	2	3	1	1	3	3	2	1	0	29.2
Chaetomitrium setosum	1	10	0	1	0	1	1	1	2	4	1	20.8
Meteorium miquelianum	2	8	0	0	2	0	0	0	2	3	3	20.8
Atractylocarpus spec	0	8	0	0	0	0	2	2	1	2	1	18.1
Acroporium spec	3	5	0	2	1	0	2	0	1	2	0	15.3
Garovaglia luzonensis	3	7	0	2	1	0	2	2	1	1	1	15.3
Octoblepharum albidum	2	9	1	1	0	2	1	2	2	1	1	15.3
Pinatella kuehliana	3	5	2	1	0	1	2	1	1	0	0	15.3
Chaetomitrium papilifolium	3	6	1	0	2	1	1	0	1	2	1	13.9
Chaetomitrium spec	3	7	0	2	1	0	1	0	3	2	1	13.9
Ectropothecium spec	0	6	0	0	0	1	1	1	1	1	1	13.9
Garovaglia spec 2	4	5	2	1	1	0	1	1	3	0	0	13.9
Meteoriopsis squarrosa	0	9	0	0	0	0	0	1	4	3	1	13.9
Meteorium spec	1	7	0	0	1	0	2	2	2	1	0	13.9
Aequatoriella bifaria	1	5	0	1	0	1	1	1	1	1	0	12.5
Aerobryopsis longissima	0	8	0	0	0	0	1	2	3	2	0	12.5
Leucobryum bowringii	1	6	1	0	0	0	1	1	1	3	0	12.5
Macromitrium spec 4	0	8	0	0	0	0	2	1	1	1	3	12.5
Plagiomnium spec	0	7	0	0	0	0	0	0	1	3	3	12.5
Himantocladium spec 1	0	8	0	0	0	0	1	2	2	2	1	11.1
Pinatella anacamptolepis	0	8	0	0	0	0	1	2	1	2	2	11.1
Syrrhopodon spec 2	3	5	0	1	2	0	1	1	1	2	0	11.1

Appendix 3: Checklist and geographical distribution of epiphytic bryophytes from natural forests and two differently managed cacao agroforests in the Kulawi Valley, Central Sulawesi, Indonesia. Distribution: A= Asian, Pal= Palaeotropic, P=Pantropic; Habitat type: FC= forest canopy crown, FS= forest canopy stem, FU= forest canopy understorey, CPS= cacao agroforests under planted shade trees, CNS= cacao agroforests under natural shade.

Species	Geographical distribution	Habitat type				
		FC	FS	FU	CPS	CNS
Liverworts						
Acrolejeunea pycnoclada (Taylor) Schiffn.	*A*	+	+	-	-	-
Archilejeunea planiuscula (Mitt.) Steph.	*A*	+	+	+	+	-
Caudalejeunea recurvistipula (Gottsche) Schiffn.	*A*	+	+	+	+	+
Ceratolejeunea cornuta (Lindenb.) Schiffn.	n.s.	+	-	-	-	+
Cheilolejeunea ceylanica (Gott.) R.M. Schust. & Kachroo	*A*	+	+	-	-	-
Cheilolejeunea khasiana (Mitt.) N. Kitag.	*A*	+	+	+	-	-
Cheilolejeunea trapezia (Nees) Kachroo & R.M. Schust.	*A*	+	+	+	+	+
Cheilolejeunea trifaria (Reinw. et al.) Mizut.	*P*	+	+	+	+	+
Cheilolejeunea vittata (Steph. ex G.Hoffm.) R.M. Schust. & Kachroo	*A*	+	+	+	+	+
Cololejeunea floccosa (Lehm. & Lindenb.) Schiffn.	Pal	+	-	+	-	-
Cololejeunea haskarliana (Lehm. & Lindenb.) Schiffn.	A	-	-	+	-	-
Cololejeunea inflectens (Mitt.) Benedix	A	+	-	-	-	-
Cololejeunea lanciloba Steph.	A	-	+	-	+	+
Cololejeunea planissima Mitt. (Abeyev)	A	-	-	-	+	+
Cololejeunea sp. 1	n.s.	+	+	-	-	-
Cololejeunea sp. 2	n.s.	-	-	-	-	+
Cololejeunea sp. 3	n.s.	+	-	-	-	-
Diplasiolejeunea cavifolia (Steph.) Steph.	Pal	+	-	-	-	-
Diplasiolejeunea sp.	n.s.	-	-	-	+	+
Drepanolejeunea angustifolia Grolle	A	+	-	-	-	-
Drepanolejeunea dactylophora (Nees et al.) Schiffn.	A	+	+	-	-	-
Drepanolejeunea sp. 1	n.s.	+	+	-	+	+

Drepanolejeunea sp. 2	n.s.	+	+	-	-	-
Drepanolejeunea sp. 3	n.s.	+	+	-	-	-
Drepanolejeunea ternatensis (Gottsche) Steph.	A	+	+	+	+	+
Frullania apiculata (Reinw. et al.) Nees	P	+	+	-	+	-
Frullania berthoumieuii Steph.	A	-	+	-	-	-
Frullania ericoides (Nees) Mont.	P	-	-	-	+	+
Frullania riojaneirensis (Raddi) Ångstr.	P	+	-	-	+	+
Frullania sp. 1	n.s.	+	-	-	-	-
Frullania sp. 2	n.s.	+	-	-	+	+
Frullania sp. 3	n.s.	+	+	-	-	-
Frullania sp. 4	n.s.	+	-	-	-	-
Harpalejeunea filicuspis (Steph.) Mizut.	A	+	+	-	-	-
Harpalejeunea sp.	n.s.	+	-	-	-	-
Heteroscyphus cf zollingeri (Gottsche) Schiffn.	A	+	+	+	-	-
Lejeunea anisophylla Mont.	A	+	+	+	+	+
Lejeunea cf obscura Mitt.	A	+	+	+	+	-
Lejeunea discreta Lindenb.	A	+	-	-	-	-
Lejeunea exilis (Reinw., Blume & Nees) Grolle	A	+	+	-	+	+
Lejeunea flava (Sw.) Nees	P	+	+	+	+	-
Lejeunea punctiformis Taylor	A	+	+	+	-	+
Lejeunea sordida (Nees) Nees	A	+	+	-	+	+
Lejeunea sp. 1	n.s.	+	+	+	+	+
Lejeunea sp. 2	n.s.	+	-	+	-	-
Lejeunea sp. 3	n.s.	-	-	+	-	-
Lejeunea sp. 4	n.s.	-	+	+	+	-
Lejeunea sp. 5	n.s.	-	+	+	+	-
Lejeunea sp. 6	n.s.	+	-	-	-	-
Lepidolejeunea bidentula (Steph.) R.M. Schust.	A	+	+	-	-	-
Leptolejeunea balansae Steph.	A	-	-	-	+	+
Leptolejeunea sp.	n.s.	+	+	-	-	-
Leptolejeunea epiphylla (Mitt.) Steph.	n.s.	+	-	-	-	-

Lopholejeunea eulopha (Taylor) Schiffn.	P	+	+	-	-	-
Lopholejeunea subfusca (Nees) Schiffn.	P	+	+	+	+	+
Lopholejeunea wiltensii Steph.	A	+	+	-	-	-
Mastigolejeunea auriculata (Wils.) Schiffn.	P	+	+	+	+	+
Metalejeunea cucullata (Reinw., Blume & Nees) Grolle	A	+	-	+	+	+
Metzgeria furcata (L.) Dumort	A	+	+	-	-	-
Metzgeria leptoneura Spruce	P	-	+	-	-	-
Metzgeria lindbergii Schiffn.	A	+	+	+	-	-
Plagiochila bantamensis (Reinw. et al.) Mont.	A	+	+	+	-	+
Plagiochila javanica (Sw.) Dumort	A	+	+	+	-	-
Plagiochila junghuhniana Sande Lac.	A	-	+	+	-	-
Plagiochila sp. 1	n.s.	+	+	+	-	-
Plagiochila sp. 10	n.s.	+	+	+	-	-
Plagiochila sp. 11	n.s.	+	-	-	-	-
Plagiochila sp. 12	n.s.	+	-	-	-	-
Plagiochila sp. 2	n.s.	-	-	+	-	-
Plagiochila sp. 3	n.s.	+	-	+	-	-
Plagiochila sp. 4	n.s.	-	+	+	-	-
Plagiochila sp. 5	n.s.	+	-	-	-	+
Plagiochila sp. 6	n.s.	-	-	-	-	+
Plagiochila sp. 7	n.s.	-	-	+	-	-
Plagiochila sp. 8	n.s.	+	-	+	-	-
Plagiochila sp. 9	n.s.	+	-	+	-	+
Porella acutifolia (Lehm. & Lindenb.) Trevis	A	+	+	+	-	-
Porella perrottetiana (Mont.) Trev.	A	-	+	-	-	-
Porella sp. 1	n.s.	+	+	-	-	-
Porella sp. 2	n.s.	-	-	+	-	-
Porella sp. 3	n.s.	+	-	-	-	-
Ptychanthus sp.	n.s.	+	-	-	-	-
Ptychanthus striatus (lehm. & Lindenb.) Nees	A	-	-	+	-	-

Radula falcata Steph.	A	+	+	+	-	-
Radula javanica Gottsche	A	+	+	+	-	-
Radula van-zantenii Yamada	A	+	+	-	-	-
Schiffneriolejeunea cunmingiana (Mont.) Gradst.	A	+	+	-	-	-
Schiffneriolejeunea tumida (Nees) Gradst.	A	+	+	-	-	-
Spruceanthus polymorphus (Sande Lac.) Verd.	A	-	-	+	-	-
Stenolejeunea apiculata (Sande Lac.) R.M. Schuster	A	+	+	+	-	+
Thysananthus convolutus Lindenb.	A	+	+	-	-	-
Thysananthus spathulistipus (Reinw. et al.) Lindenb.	Pal	+	+	+	-	-
Tuyamaella jackii (Steph.) Tixier	A	+	-	+	-	-

Mosses

Acroporium macroturgidum Dixon	A	+	+	+	-	-
Aequatoriella bifaria (Bosch. % Sande Lac.) Touw	A	+	+	+	+	+
Aerobryopsis longissima (Dozy & Molk.) Fleisch.	A	+	-	+	+	-
Aerobryopsis sp.	n.a.	+	+	-	-	-
Aerobryum speciosum (Dozy & Molk.) Dozy & Molk.	A	+	+	-	-	-
Aerobyidium crispifolium (Broth. & Geh.) Fleisch. Ex Broth.	n.a.	-	-	+	-	-
Atractylocarpus novoguineensis (Broth. & Geh.) Norris & T. Kop.	*A*	+	+	-	-	-
Barbella trichophora (Mont.) M. Fleisch.	n.a.	+	+	+	-	-
Brachythecium sp.	n.a.	-	-	-	+	-
Calymperes dozyanum Mitt.	Pal	+	-	+	+	+
Calyptothecium sp.	n.a.	+	+	-	-	-
Calyptothecium subcrispulum Broth.	A	+	-	-	-	-
Chaetomitrium lanceolatum Bosch & Sande Lac.	A	+	-	+	-	+
Chaetomitrium leptopoma (Schwaegr.) Bosch & Sande Lac	A	+	+	+	-	+
Chaetomitrium papillifolium Bosch & Sande Lac.	A	+	+	+	+	+
Chaetomitrium setosum Broth. ex Dixon	A	+	-	+	-	-
Chaetomitrium sp. 1	n.a.	+	+	+	+	+

Chaetomitrium sp. 2	n.a.	-	-	-	-	+
Clastobryum epiphyllum (Renault & Cardot) B.C.Tan & Touw	n.a.	-	-	-	+	-
Clastobryum sp.	n.a.	-	-	-	-	+
Cryptopapillaria fuscescens (Hook.) M. Menzel	n.a.	+	-	-	-	-
Cyathophorum spinosum (C.Muell.) Akiyama	n.a.	-	+	-	-	-
Daltonia sp.	n.a.	+	-	-	+	+
Distichophyllum sp.	n.a.	+	-	-	-	-
Ectropothecium sp. 1	n.a.	+	-	-	-	-
Ectropothecium sp. 2	n.a.	+	+	-	-	-
Ectropothecium sp. 3	n.a.	-	+	-	-	-
Erythrodontium julaceum (Schwaegr.) Par.	Pal	-	-	-	+	-
Floribundaria floribunda (Dozy & Molk.) Fleisch.	Pal	+	+	+	+	+
Floribundaria pseudofloribunda M. Fleisch	A	-	-	+	+	+
Garovaglia luzonensis William	n.a.	+	+	+	+	+
Garovaglia plicata (brid.) Bosch & Sande Lac.	n.a.	+	+	+	-	-
Garovaglia sp.	n.a.	+	-	-	-	-
Garovaglia sp.2	n.a.	+	-	-	-	-
Himantocladium plumula (Nees) Fleisch.	A	+	-	+	-	-
Himantocladium sp. 1	n.a.	+	+	-	-	-
Himantocladium sp. 2	n.a.	+	-	-	-	-
Himantocladium spec 1	n.a.	+	+	+	-	-
Homalia pseudo-exigua Besch.	A	-	+	+	-	-
Hypopterygium aristatum Bosch & Sande Lac	n.a.	+	+	-	-	-
Hypopterygium sp. 1	n.a.	-	-	+	-	-
Hypopterygium sp. 2	n.a.	+	+	-	-	-
Isocladiella sulcularis (Dixon) B.C. Tan & Mohamed	n.a.	-	-	-	-	-
Leucobryum bowringii Mitt.	n.a.	+	+	+	-	-
Leucobryum sp. 1	n.a.	-	-	+	-	-
Leucophanes octoblepharoides Brid.	A	-	-	-	-	-

Macromitrium concinuum Mitt.	A	+	-	-	+	+
Macromitrium sp. 1	n.a.	+	-	+	+	+
Macromitrium sp. 2	n.a.	+	+	-	-	-
Mesonodon flavescens (Hook.) W.R. Buck	Pal	+	-	-	+	-
Meteoriopsis reclinata (C. Muell.) Broth.	A	+	-	-	-	-
Meteoriopsis squarrosa (Hook.) Fleisch.	A	+	+	-	-	-
Meteorium miquelianum (C. Muell.) Fleisch.	A	+	-	+	+	+
Meteorium sp.	n.a.	+	+	+	-	-
Neckera acutata Mitt.	A	+	-	-	-	-
Neckeropsis gracilenta (Bosch & Sande Lac.) Fleisch.	A	+	+	+	+	-
Neckeropsis lepineana (Mont.) Fleisch.	Pal	+	+	+	+	-
Octoblepharum albidum Hedw.	n.a.	+	+	+	-	-
Orthomnion dilatatum (Mitt.) P.C. Chen	n.a.	+	-	-	-	-
Palamocladium leskeoides (Hook.) Britt.	n.a	-	-	-	+	-
Palamocladium nilgheriense (Mont.) Müll.Hal.	n.a.	-	-	-	-	-
Papillaria flexicaulis (Williams) A. Jaeger	A	+	-	+	-	-
Papillaria sp.	n.a.	+	+	-	+	-
Pinatella anacamptolepis (C. Muell.) Broth.	A	+	+	-	-	-
Pinatella kuehliana (Bosch & Sande Lac.) Fleisch.	A	+	+	+	-	-
Pinatella mucronata (Bosch & Sande Lac.) Fleisch	A	+	+	+	-	-
Pterobryopsis sp.	n.a.	+	+	-	-	-
Rhacopilum sp.	n.a.	-	-	-	+	-
Stereodontopsis excavata (Broth.) Ando	A	+	-	-	-	-
Stereodontopsis sp.	n.a.	-	+	-	+	-
Stereodontopsis sp. 2	n.a.	+	+	-	-	-
Syrrhopodon parasiticus (Brid.) Besch	A	+	+	-	-	-
Syrrhopodon sp.	n.a.	+	+	+	+	-
Syrrhopodon trachyphyllus Mont.	Pal	+	-	-	-	-

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List of Publications

Sporn SG, Bos MM, Gradstein SR (2007) Is productivity of cacao impeded by epiphytes? An experimental approach. Agriculture, Ecosystems & Environment 122: 490-493.

Steffan-Dewenter I, Kessler M, Barkman J, Bos MM, Buchori D, Erasmi S, Faust H, Gerold G, Glenk K, Gradstein SR, Guhardja E, Harteveld M, Hertel D, Höhn P, Kappas M, Köhler S, Leuschner C, Maertens M, Marggraf R, Migge-Kleian S, Mogea J, Pitopang R, Schaefer M, Schwarze S, Sporn SG, Steingrebe A, Tsjitrosodirdjo SS, Tjitrosoemito S, Tscharntke T, Twele A, Weber R, Woltmann L, Zeller M (2007) Sociooeconomic context and ecological consequences of rainforest conversion and agroforestry intensification. Proceedings of the National Academy of Sciences U.S.A. 104: 4973-4978.

Kessler M, Abrahamczyk S, Bos M, Putra DD, Gradstein SR, Höhn P, Kluge J, Orend F, Pitopang R, Saleh S, Schulze CH, Sporn SG, Steffan-Dewenter I, Tscharntke T; Alpha and Beta Diversity of Plants and Animals along a Tropical Land-use Gradient. Ecological Applications (in press))

Sporn SG, Bos MM, Hoffstätter-Müncheberg M, Kessler M, Gradstein SR (2009) Microclimate determines community composition but not richness of epiphytic understorey bryophytes of rainforest and cacao agroforests in Indonesia. Functional Plant Biology 36: 171-179.

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)

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Bos MM, Sporn SG, Steffan-Dewenter I, Gradstein SR, Tscharntke T (2005) The influence of pollination, herbivory, non-vascular epiphytes and shade trees on cacao productivity in Central Sulawesi, Indonesia. STORMA Symposium: Linking Ecological, Economic and Social Constrains of Land Use and Conservation, 19-23. September 2005, Göttingen, Germany.

Sporn SG, Gradstein SR (2005) Diversity Comparison of Epiphytic Bryophytes on Cacao Plantations with Different Shading Canopy Layers. STORMA Symposium: Linking Ecological, Economic and Social Constrains of Land Use and Conservation, 19-23. September 2005, Göttingen, Germany

Sporn SG, Gradstein SR (2006) Do epiphytic layers have a negative impact on cacao production? 19th annual meeting of the Society for Tropical Ecology, Kaiserslautern, 21.-24. February 2006, Kaiserslautern, Germany

Sporn SG, Gradstein SR (2006) Comparing the diversity of non-vascular epiphytes in natural forest and cacao agroforests in Indonesia. Annual meeting of the Association for Tropical Biology and Conservation, July 18-21, 2006 Kunming, China.

Sporn SG, Gradstein SR (2007) Impact of rain forest conversion and agroforestry management on bryophyte diversity in Central Sulawesi. 7th Flora Malesiana symposium, June 18-22, 2007 Leiden, Netherland.

Sporn SG, Gradstein SR, Bos M (2007) Is productivity of cacao impeded by epiphytes? An experimental approach. Annual meeting of the Association for Tropical Biology and Conservation, July 15-19, 2007 Morelia, Mexico.

I WAS READING ABOUT HOW COUNTLESS SPECIES ARE BEING PUSHED TOWARD EXTINCTION BY MAN'S DESTRUCTION OF FORESTS.
SOMETIMES I THINK THE SUREST SIGN THAT INTELLIGENT LIFE EXISTS ELSEWHERE IN THE UNIVERSE IS THAT NONE OF IT HAS TRIED TO CONTACT US.
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WATTERSON
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1 Mixed deciduous forest in the Hainich region (Central Germany)
2 Different insect taxa on the flowers of a thistle (*Cirsium* sp.)
3 *Glomeris* sp., a member of the decomposing soil fauna in forest ecosystems
4 *Pleodorina californica* (Chlorophyceae), colony-forming freshwater phytoplankton species
5 Grasshopper *Tettigonia cantans*, distributed from the Pyrenees to Northeastern China
6 *Microcebus berthae* (Cheirogaleidae), the smallest extant Primate species (Madagascar)
7 Tropical rain forest (Greater Daintree, Australia)
8 *Lethocolea glossophylla* (Acrobolbaceae), a liverwort of alpine mountain ranges in South America
9 Part of a coral reef in the Red Sea

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