GEORG-AUGUST-UNIVERSITÄT
GÖTTINGEN

Diversity of vascular epiphytes in jungle rubber agroforests and different land-use systems in Sumatra (Indonesia)

Diversität vaskulärer Epiphyten in Kautschukagroforstsystemen und verschiedenen Landnutzungssystemen in Sumatra (Indonesien)

Masterarbeit an der
Fakultät für Forstwissenschaften und Waldökologie der
Georg-August-Universität Göttingen

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Acknowledgements

I would like to express my gratitude to Prof. Dr. Holger Kreft for giving me the opportunity of writing this thesis and for all the friendly support throughout.

Further I would like to thank Dr. Katja Rembold for all the kind help in basically the entire process of writing this thesis. Thank you Katja!

I also want to thank Lukas Beeretz for being an awesome field buddy and Atok Hardianto Mangopo for being a great host and allowing us to stay in his tiny flat in Bogor.

Special thanks also to the incredibly friendly coordination staff of the EFForTS-Project in Jambi and Bogor.

Additionally I am grateful for the support of the project counterpart, Dr. Sri Sudarmiyati Tjitrosoedirdjo of the Bogor Agricultural University (IPB).

Further thanks to the DAAD for funding my field stay.

Last but not least I would like to thank Annika Dörner for proofreading.

Content

Abstract

As primary forest have almost completely disappeared from central Sumatra and have largely been turned into other land-use systems, this study aimed to assess the consequences of this forest conversion for vascular epiphytes by plot-based species inventories. Species richness, abundance and composition of vascular epiphytes were compared between four land-use systems: natural forest, rubber plantations, oil palm plantations and jungle rubber agroforest. Furthermore, microclimatic conditions were measured in each system. A total of 81 species, belonging to 20 different families were found within 120 plots (30 per system). The highest species richness was recorded in jungle rubber closely followed by the forest, while epiphyte richness was very poor in both plantations. Oil palm plantations had high epiphyte abundance, but the lowest species richness of all systems. Forest, jungle rubber and oil palm plantations did not differ on plot level in terms of richness, diversity, and evenness, but had higher values than rubber plantations. The epiphyte composition in jungle rubber and rubber plantations resembled that of the forest, whereas the composition in the oil palm plantations was markedly different from the other systems. Forest and jungle rubber exhibited a wider range in microclimatic conditions than was the case in the plantations, thus indicating that microclimate conditions are possible drivers of epiphyte diversity. Since jungle rubber agroforest had the highest total epiphyte richness, it could be considered as a significant refuge for epiphyte diversity. Stand structure analysis in jungle rubber showed that rubber densities and presence of large long-lived trees are some of the drivers of the epiphyte diversity in jungle rubber.

Zusammenfassung

Da die primären Regenwälder zentral Sumatras mittlerweile nahezu vollkommen verschwunden sind und zum Großteil in andere Landnutzungssysteme umgewandelt wurden, war das Ziel dieser Arbeit, die Folgen dieser Umwandlung für die Diversität von vaskulären Epiphyten im Rahmen einer plotbasierten Inventur zu untersuchen. Artenreichtum, Abundanz und floristische Zusammensetzung von vaskulären Epiphyten wurde dabei zwischen den folgenden vier Landnutzungssysteme verglichen: Wald, Kautschukagroforst, Kautschukplantagen und Ölpalmplantagen. Zusätzlich wurden die mikroklimatischen Bedingungen in jedem der untersuchten Systeme gemessen. Insgesamt wurden 81 Arten aus 20 Familien, innerhalb von 120 Plots (30 Plots pro System) gefunden. Der höchste Artenreichtum wurde dabei im Wald und in Kautschukagroforsten verzeichnet, während die Artenvielfalt in den Plantagen sehr gering war. Ölpalmplantagen hatten eine hohe Abundanz von Epiphyten aber gleichzeitig war dies das System, in dem die geringste Anzahl von Arten verzeichnet wurde. Wald, Kautschukagroforst und Ölpalmplantagen unterschieden sich auf Plot-Niveau, in Bezug auf Artenreichtum, -vielfalt und -gleichmäßigkeit („Evenness“) nicht signifikant voneinander, hatten aber höhere Werte als die Kautschukplantagen. Die floristische Zusammensetzung von Epiphyten in Kautschukagroforst und Kautschukplantagen ähnelte der des Waldes, während die Zusammensetzung innerhalb der Ölpalmplantagen deutliche Unterschiede zu den anderen Systemen aufwies. Die mikroklimatischen Bedingungen im Wald und Kautschukagroforst wiesen eine deutlich stärkere Variation auf, als dies in den Plantagen der Fall war, somit scheint das Mikroklima ein wichtiger Faktor für die Diversität von Epiphyten zu sein. Da innerhalb des Kautschukagroforstes die höchste Abundanz und der größte Artenreichtum von Epiphyten festgestellt wurde, kann man dieses System als bedeutendes Refugium für Epiphyten betrachten. Eine Analyse der Bestandesstrukturen innerhalb des Kautschukagroforstes ergab, dass die Höhe der Kautschukanteile und das Vorhandensein großer, alter Bäume einige der Faktoren sind, die Epiphytendiversität innerhalb dieses Systems bestimmen.

1. Introduction

1.1 The EFForTS-Project

This thesis is part of the collaborative research project “Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems in Sumatra, Indonesia” (EFForTS). Central aim of the project is to provide science-based knowledge on how to protect and enhance the ecological, as well as socioeconomic functions of tropical forests and agricultural transformation systems. The leading question of the project is how to integrate agricultural land use and conservation issues on a landscape scale at the same time.

For this purpose, the land-use systems oil palm plantations, rubber plantations and jungle rubber agroforests are investigated in comparison to the natural lowland rainforest. The project takes place in two landscapes within the Jambi Province in central Sumatra. The investigated landscapes surround two different forest reserves, which act as natural reference systems, namely the Bukit Duabelas National Park and the Harapan Rainforest. In each landscape, four core plots with a dimension of 50 x 50 m have been established within the three land use systems and the forest. Which means that a total of 16 core plots have been established per landscape.

This thesis is part of the Project Group B (Biota and ecosystem services) and was conducted within the subgroup B06 (Taxonomic, phylogenetic, and biogeographical diversity of vascular plants in rainforest transformation systems on Sumatra – Indonesia).

The following institutes are part of the project: University of Göttingen, the University of Jambi (UNJA), the Bogor Agricultural University (IPB), the Tadulako University (UNTAD) and the Indonesian Institute of Science (LIPI).

1.2 Tropical forests in Indonesia and Sumatra

Tropical rainforests are the most diverse terrestrial ecosystems of the world (FAO 2010a). They harbor an estimated 80 % of all terrestrial species (Carnus *et al.* 2006) and function as enormous carbon sinks, storing around 46 % of the world's living terrestrial carbon (Soepadmo 1993). At the same time, tropical rainforests are the most threatened forests worldwide and one third to one half of these forests have already been converted into other land-use systems during the last few decades (Primack & Corlett 2005).

The Indo-Malayan rainforest of tropical Asia is the second largest rainforest region of the world (Whitmore 1998). It once occupied most of the Malay Peninsula and extends through the Malay Archipelago from Sumatra in the west to New Guinea in the east. The region ranks as one of the highest in the world in terms of species richness and endemism (Myers *et al.* 2000) and this great biological diversity and uniqueness makes it, among other things, one of the earth's biodiversity hotspots (Mittermeier *et al.* 1999). At the same time, the population of the region is growing at a rapid rate. In 2007 it was estimated that 1.9 billion people were living in tropical Asia and this population is expected to grow to 2.6 billion by the year 2050 (Laurance 2007). In combination with a rapidly expanding industrialization and globalization, the continued population growth puts enormous pressure on the native forest (Laurance 2007), resulting in a relative deforestation rate which is the highest of any tropical region (Sodhi *et al.* 2004). The destruction and conversion of primary forest results in the loss of unique tropical forest habitats and poses a tremendous threat to the local biodiversity (Margono *et al.* 2014). The region could lose up to 42 % of its biodiversity by the turn of the next century (Sodhi *et al.* 2004).

Indonesia occupies most of the Malay Archipelago and accounts for the majority of the region's forest area (Achard *et al.* 2002). The total forest area of Indonesia is estimated to be 94 million ha (FAO 2010a) of which 45 million ha are still considered primary forests (FAO 2010b). But the forest cover in Indonesia is declining at an alarming rate. In fact Indonesia has the highest deforestation rate in the world and is at the same time the country which exhibited the largest increase in forest loss from 2000 to 2012 worldwide (Hansen *et al.* 2013; Margono *et al.* 2014).

The Indonesian island of Sumatra underwent a dramatic deforestation in the last couple of decades. In 1985 Sumatra was still covered with 25 million ha of natural forest, spreading across 58 % of the island (Uryu *et al.* 2010). The remaining primary forest extent in the year 2010 was only 13.6 million, covering just 30.4 % of the island area (Margono *et al.* 2012). Thus the primary forest cover was nearly halved in a period of only 25 years.

The vast majority of deforestation took place in the lowlands of Sumatra. Uryu *et al.* (2010) stated that between the years 1985 and 2008/9 81 % of all forest loss was below 150 m elevation. Today almost all primary forests have completely disappeared from the lowlands of the Sumatra peneplain (Beukema *et al.* 2007). They have largely been replaced by monoculture plantations of oil palm (*Elaeis guineensis*), rubber (*Hevea brasiliensis*) and pulp & paper plantations of acacia or eucalyptus trees (Beukema *et al.* 2007; Margono *et al.* 2012).

1.3 Epiphytes in rainforest ecosystems

The enormous diversity of vascular epiphytes is striking. According to Zotz, there are nearly 28,000 different species of vascular epiphytes worldwide (Zotz 2013a). Together they account for almost 10 % of all extent vascular plants species on earth. Their diversity is one of the key characteristics of tropical forests and a fundamental component to tropical biodiversity (Flores-Palacios & García-Franco 2001; Gradstein *et al.* 2003). Vascular epiphytes can represent one third to one half of the total vascular flora in some tropical forests (Gentry & Dodson 1987a), which makes epiphytes a central feature of tropical forests and differentiates them from most temperate forests (Gradstein *et al.* 2003).

By definition epiphytes are plants which germinate and root non-parasitically on other plants (Benzing 1990). They are divided into two major groups, namely holoepiphytes (true epiphytes) and hemiepiphytes. Holoepiphytes germinate on their host trees and grow on them throughout their whole life cycle without any connection to the ground (Benzing 1990). On the contrary, hemiepiphytes maintain a vascular connection with the ground soil over a part of their life (Benzing 1990). Hemiepiphytes are further subdivided into primary hemiepiphytes and secondary hemiepiphytes depending whether their epiphytic stage occur early in their life cycle or late (Benzing 1990). Primary hemiepiphytes germinate on other plants first and establish contact with the ground via aerial roots later (Kress 1986; Putz & Holbrook 1986). Secondary hemiepiphytes climb up their hosts after germination on the ground. Later they show diebacks of their older stems and in the final stage sever all connections to the soil (Kress 1986).

However, Zotz argues that the term secondary hemiepiphytes can be misleading and that its definition is hard to impossible to apply in the field (Zotz 2013b). Furthermore, secondary hemiepiphytes should be separated from epiphytes because of major differences in their ecology (Zotz 2013a). Hence secondary hemiepiphytes were excluded from this study and only primary hemiepiphytes and holoepiphytes were included. Accidental epiphytes, which are typically terrestrial species that coincidentally occur anchored in tree crowns (Benzing 1990) were also not considered in this study.

The highly diverse community of animals in tropical forest canopies depends largely on vascular epiphytes. Epiphytes contribute significantly to the structural complexity of the tree crowns and provide food, shelter and energy resources for numerous vertebrates and countless invertebrates and microorganisms (Nadkarni & Matelso 1989; Benzing 1990; Nadkarni 1994; Stuntz *et al.* 2002). Arthropods in particular benefit from the microhabitats created by epiphytes in form of stored water, leaf litter, dead organic matter, and foliage (Nadkarni & Matelso 1989; Nadkarni 1994). Epiphytes also contribute considerably to the diversity of birds by providing a diverse array of fruits and nectar (Nadkarni & Matelso 1989).

Epiphytes are capable of growing in all forest layers from the understory all the way to the periphery of the tree crowns. Thus they have to cope with a wide variety of growing sites and different environmental constrains.

The most relevant abiotic constraint for the growth of epiphytes is the scarcity of water in their habitat (Johansson 1974; Laube & Zotz 2003). The limited availability of substrate as water source and a high transpiration rate due to exposure to sun and wind makes drought the most serious threat to epiphytic life (Johansson 1974). Therefore adaptions to water stress are critical for the survival of epiphytic species. Typical drought adaptions among epiphytes are poikilohydry, succulence (Ng & Hew 2000), shootlessness (Benzing *et al.* 1983), drought-deciduousness (Benzing 1990) and crassulacean acid metabolism or water tanks, which are common for epiphytic bromeliads (Benzing 1990).

With no root contact to the soil, another major constraint for epiphytes is the lack of access to nutrients (Benzing 1990; Zotz & Hietz 2001). As a consequence they mainly rely on atmospheric inputs, such as rain, dust and mist (Benzing 1990). Minerals and organic matter imported by ants and other animals (Treseder *et al.* 1995; Stuntz *et al.* 2002) or nutrients released from ground rooted plants through leaching or decomposition can be further nutrient sources (Benzing 1990). Morphological adaptions such as phytotelmata, litter trapping leafs, bromeliad trichomes and orchid velamen radicum also improves nutrient scavenging but usually promote water uptake as well (Zotz & Hietz 2001).

The limitations and exposure of their habitat in the forest canopy makes epiphytes very vulnerable to changes in their environment (Benzing 1990). They are strongly effected by variations in microclimate conditions and reported susceptible to forest disturbances (Hickey 1994; Benzing 1998; Hietz *et al.* 2006). Therefore they are regularly proposed as model group to study levels of human disturbance and/or ecosystem health (Hietz 1998, 2005; Barthlott *et al.* 2001; Nadkarni & Solano 2002; Haro-Carrión *et al.* 2009).

1.4 Jungle Rubber agroforestry systems

Jungle Rubber is an extensive rubber (*Hevea brasiliensis*) agroforest in which the wild species are growing between rubber trees and that can structurally resemble secondary forest (Beukema *et al.* 2007).

The cultivation of rubber was first introduced to Indonesia by Dutch colonial officials in the 1890s. The first smallholder rubber in the Jambi province was planted around 1904 (Joshi *et al.* 2002) and the first account of a jungle rubber agroforest in Jambi was reported in 1918 (Joshi *et al.* 2002).

Jungle rubber agroforests are either established after a slash and burn of secondary vegetation or rubber seedlings are directly planted in between secondary forest areas (Wibawa *et al.* 2006). Seedlings are sometimes planted together with food and cash crops, such as rice, maize, soybean, pineapple, mungbean or banana (Gouyon *et al.* 1993; Joshi *et al.* 2002; Beukema & Van Noordwijk 2004; Wibawa *et al.* 2006). These annual intercrops are planted in between rubber rows for the first 2-3 years (Beukema & Van Noordwijk 2004; Wibawa *et al.* 2006) until soil depletion, grass weeds and the shade of the developing rubber trees prevent further cultivation of these crops (Gouyon *et al.* 1993). However, these intercropping practices have not been observed for the jungle rubber areas studied in this present work.

In the initial stage management is mainly limited to occasional weeding and slashing of extensive forest regrowth. After completion of any annual intercropping systems the famers abandon the land until the rubber reaches its tappable size, which is usually between 8 – 12 years after rubber planting (Wibawa *et al.* 2006). During this period most wild species are now allowed to grow with the rubber trees, until a complex forestlike vegetation develops (Beukema *et al.* 2007). Once mature, rubber trees can be tapped by the farmers for more than 30 years and apart from tapping further management is only limited to maintaining paths between the rubber trees (Beukema *et al.* 2007).

After rubber trees become unproductive farmers usually start a new agroforest cycle by slashing and burning the old jungle rubber (Joshi *et al.* 2002). As an alternative to this, rotational rejuvenation gap replanting is used by some farmers (Joshi *et al.* 2000, 2002), a practice more common in the study area. In this system which does not require slashing and burning new rubber seedlings are planted in between gaps left by dead trees or by the removal of unproductive or unwanted trees. This method can significantly prolong the productive stage of the jungle rubber and results in a more varied age structure of trees than in a rotational rubber agroforest (Joshi *et al.* 2000, 2002).

Due to its complex vegetation structure and extensive management, mature jungle rubber is defined as a complex agroforest (de Foresta *et al.* 2000). Stand structure in older jungle rubber agroforests can resemble that of secondary forest and trees in mature jungle rubber can reach heights of 20-40 m in the Jambi lowlands (Beukema *et al.* 2007). The percentage of rubber trees does vary and declines with the age of the agroforest but typically account for an average of 40-50 % and less than 70 % of trees above 10 cm DBH (diameter at breast height) (Hardiwinoto *et al.* 1999; Beukema *et al.* 2007; Vincent *et al.* 2011).

With regards to the dramatic deforestation and forest conversion transformation in Sumatra, jungle rubber might become the most extensive forestlike vegetation in the region (Gouyon *et al.* 1993; Wibawa *et al.* 2006; Beukema *et al.* 2007). It is thus regularly proposed as a possible refuge and reservoir of the original forest biodiversity (Gouyon *et al.* 1993; Joshi *et al.* 2002; Penot 2004; Wibawa *et al.* 2006; Beukema *et al.* 2007).

However, jungle rubber agroforests themselves are under growing pressure and experience an accelerated conversion to more intensive agricultural systems like monoculture plantations (Ekadinata & Vincent 2011).

1.6 Sampling for biodiversity in jungle rubber

As jungle rubber is a land-use system which is predominantly used by smallholder farmers sampling in jungle rubber is bound to be complicate. Farmers usually own several small and scattered jungle rubber agroforests of different ages, which can vary in size from less than one hectare up to a few (Beukema *et al.* 2007). Furthermore, management activities and intensities can differ greatly between famers. The consequence is a rubber landscape that is a mosaic of jungle rubber agroforests of different appearances, ages, rubber densities and management intensities (Beukema *et al.* 2007). Additionally, succession and regrowth of wild species in jungle rubber is strongly influenced by source populations in surrounding areas, by selective activities of farmers and by the cultivation history of the agroforest (Beukema *et al.* 2007). Therefore species composition are likely to differ greatly within this mosaic of jungle rubber agroforests.

1.5 Aims of the study

As the last natural rainforests continue to disappear from the lowlands of central Sumatra and with the vast majority of these forests already converted to the land-use systems jungle rubber, rubber and oil palm plantations, this work aims at investigating the effects of this transformation on the diversity of vascular epiphytes by plot based species inventory. Since vascular epiphytes are a key feature of tropical forests and a fundamental component of tropical biodiversity, they can be seen as an ideal model group to study possible consequences of forest conversion on ecosystem health.

Special emphasis in this work was put on the epiphyte diversity in jungle rubber agroforest systems with the aim to investigate the system’s potential to serve as a refuge for epiphytes as well as overall biodiversity.

The hypotheses of this study were: (H1) Epiphyte diversity and species richness is higher in jungle rubber than in rubber or oil palm plantations, but lower than in the natural forest, (H2) Floristic composition of epiphytes differs between land-use systems, (H3) Changes in epiphyte diversity between the land-use systems are linked to different microclimatic conditions in the systems, (H4) The stand structure of jungle rubber agroforests has an influence on epiphyte diversity.

2. Materials & Methods

2.1 The study area

The field work took place in the Bukit Duabelas landscape of EFForTS-Project, situated in the Jambi Province in central Sumatra (Indonesia).

With a surface of 473,606 km² (Barber *et al.* 2005), Sumatra is the largest island of Indonesia and the sixth largest in the world. It was formed during the early Tertiary period, approximately 70 million years ago, by the collision of the Indian and Asian continental plates. The island spans 1760 km form its northwestern to its southeastern tip and is up to 400 km wide (Barber *et al.* 2005). The Strait of Malacca separates the island from the Malay Peninsula in the northwest and the Sunda Strait separates it from Java in the southeast. The backbone of the island is formed by the Barisan Mountain chain, which extends the whole western length of Sumatra in a narrow belt (Barber *et al.* 2005). Mount Kerinci is with 3805 m the highest peak of the island. East of the Barisan Mountains the island is covered by broad coastal plains. Near the coastline these lowlands would naturally be dominated by swamps and mangrove forest, while dipterocarp-dominated lowland rainforests would naturally cover the landscape further inland (Laumonier 2012; Damanik & Whitten 2013).

The Jambi Province is located on the east coast of central Sumatra (Fig. 1). Its capital is Jambi City. The province covers an area of 49 578 km^2 (Murdiyarso *et al.* 2002) and was inhabited by 3 092 265 people in the year 2010 (Statistics Indonesia 2015). Jambi Province experiences on average an annual rainfall in the range of around 3000 mm with 7-8 wet months (> 200 mm rainfall/month) and no dry months (< 100 mm rainfall/month) per year (Laumonier 2012).

The transformation of the natural forest has been particular severe in the Jambi region over the last decades. Between 1985-2009 the total forest cover loss has been estimated to be 1.6 million ha, which represents 53 % of its natural lowland rainforest (Uryu *et al.* 2010). Today primary forest have been almost completely disappeared from the lowlands of Jambi Province and turned into monocultural oil palm and rubber plantations or jungle rubber agroforests (Beukema *et al.* 2007).

The Bukit Duabelas National Park, which is located 50-90 km west from Jambi City (Fig. 1), covers an area of 60 500 ha and was established in 2000 (Kusuma & Hendrian 2011). Elevation in the park ranges from 50 to 438 m a.s.l. (Kusuma & Hendrian 2011). As a result of selective logging and other human disturbances the forest cover of the park has to be considered as a primary degraded forest, which suffered partial canopy loss and altered forest composition and structure (Margono *et al.* 2014).

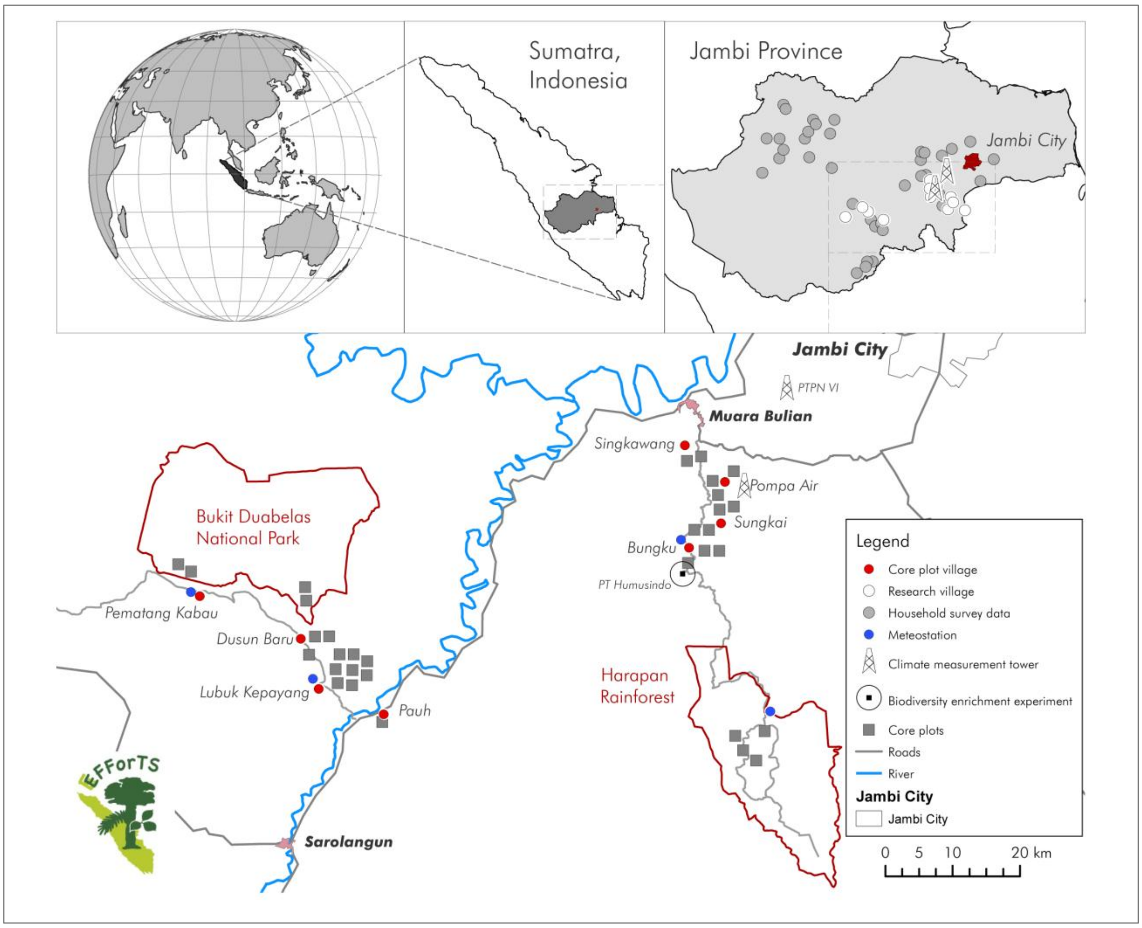

Fig. 1: Study area of the EFForTS-Project in the Jambi Province in central Sumatra. Forest reserves are framed in red. Core plot locations are indicated with grey squares. This work was conducted around the Bukit Duabelas National Park which is located in the east of the region. Source: (Drescher *et al.* in prep).

2.2 Epiphyte inventory

A total of 30 plots were established in jungle rubber areas along a 30 km long transect between the southern border of the Bukit Duabelas National Park and the village Batu Kucing (Fig 2). Each plot contained one large host tree (phorophyte) which was investigated for the presence and abundance of vascular epiphytes by using single rope climbing techniques. Only native trees species were examined.

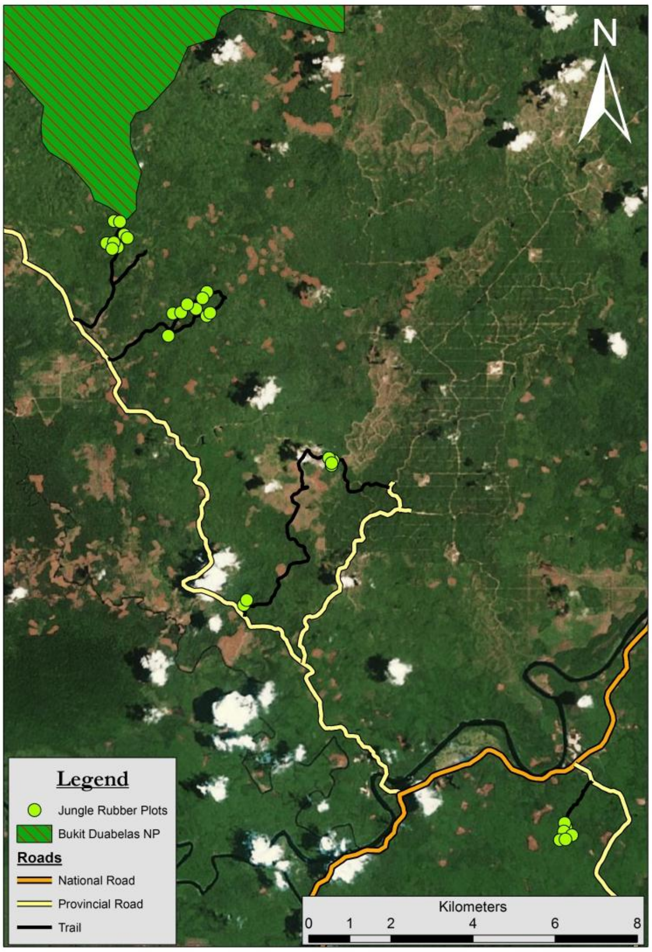

Fig. 2: Positions of jungle rubber plots in the southeastern area of the Bukit Duabelas landscape. Modified after Beeretz (2015).

Phorophytes were randomly selected but had to have a minimum DBH of 40 cm to ensure a suitable stability for climbing. If this requirement could not be met, ground based observations using binoculars were conducted following the ground based observation protocol of Flores-Palacios and García-Franco (Flores-Palacios & García-Franco 2001). Additionally, investigated trees had a minimum distance of 60 m to each other. At least one phorophyte was investigated in each of the 4 jungle rubber core plots already established by the EFForTS project.

The position of all investigated phorophytes was determined and marked with a GPS device (*Garmin*^{TM} *62s*). In addition to the location, total tree height and the base of the tree crown (lowest branch) were documented, as well as the DBH and bark roughness (smooth, medium, heavy). All distance and height measurements were conducted with an ultra-sonic measuring device (*Vertex*^{TM} *IV – Haglöf Schweden AB*). Specimens of each investigated phorophyte were collected and later identified to species level.

To sample epiphytes in the tree canopy, single rope climbing techniques were used (Perry & McCarthy 1978). Although ground based observations are faster and safer, Flores-Palacios & García-Franco showed that these methods underestimate species richness and frequency and that climbing based methods are much more accurate (Flores-Palacios & García-Franco 2001).

At first a throw bag, weighing 400 g, was attached to a 2 mm thick and 100 m long rope. Then the throw bag was shot over a thick branch in the upper canopy by using a 2m long slingshot (*Big Shot®*). The thin rope was then used to pull the 50 m long and 10 mm thick climbing rope over the branch. One end of the climbing rope was tied to the trunk of the phorophyte while the other end could then be used to ascent into the canopy. A hand ascender in combination with a foot loop was used for climbing.

A complete inventory of all occurring vascular epiphytes was taken for each investigated phorophyte. For every single epiphytic individual the position in the tree, the size and its relative coverage of the trunk area was recorded. In cases where single epiphyte species were particularly abundant these characteristics were summarized for large groups of individuals. Their total number was estimated by counting all individuals growing within a small sample area first and then projecting the result to the total area covered by the particular species. In the case of clonal plants each cluster of clones was counted as just one individual.

As the epiphytic flora usually shows usually a pronounced stratification on their host trees (Morris 1968), epiphyte sampling was divided in five vertical tree zones following a subdivision after Johansson (Johansson 1974). This allows for comparisons between phorophytes and reflects possible zones of environmental conditions and thus potential ecological preferences of epiphytic species. Johansson-Zone 1 (JZ1) stretches from the base up to 2 m, JZ2 from 2 m above the ground to the first major ramification, JZ3 comprises major branches in the inner crown, JZ4 branches in middle crown and JZ5 thin branches in the outer crown (Fig 3). To compensate for the small surface area of JZ1 compared to JZ2 – JZ5 an additional 400 m² plot (20 x 20 m) was established around the phorophyte[1]. Within this plot all epiphytic individuals growing in the JZ1 of other trees and scrubs with a DBH >10 cm were documented and sampled as well. They were recorded as occurring in JZ1 of the original phorophyte (after Gradstein *et al.* 2003).

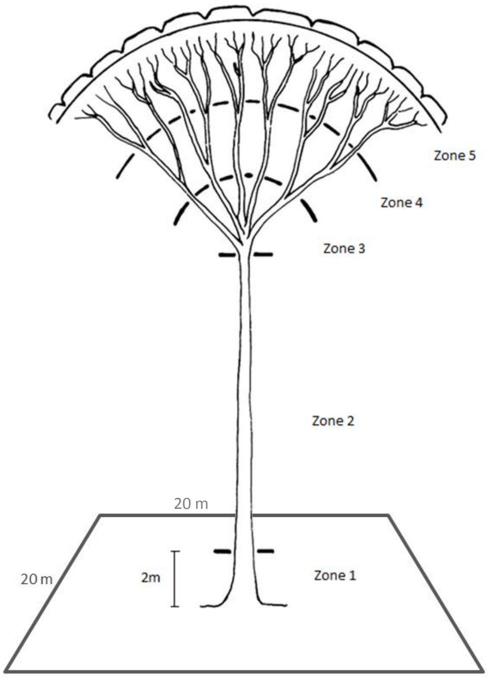

Fig. 3: Plot design with central phorophyte divided into 5 zones after Johansson (1974) within a 20 x20 m plot.

Three specimens were collected for each epiphytic species for later identification and a long-term deposition in the Herbarium Bogoriense. To further facilitate identification, in-situ photographs were taken and numerous close-up photographs were shot from each collected specimen before pressing. All photographs were shot with a digital single lens reflex camera (*Canon EOS 550D*). A macro-lens (*AF-S Micro Nikkor 60 mm 1:2.8 G ED*) in combination with a ring flash (*Canon Ringlite MR-14 EX*) was used for close-up photos and a telephoto lens (*Tamron AF 70-300mm*) for longshot pictures.

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[1] The terms of phorophyte and plot will be used synonymously in the following text.

Epiphytes in the outer canopy that could not be reached by climbing could sometimes be collected by using a 4 - 5 m long wooden or bamboo stick. If epiphytes could not be reached at all they were photo documented with the telephoto lens.

Identification of collected species in the field was limited to the division of morphospecies. The final identification was done in the herbarium at SEAMEO BIOTROP in Bogor. The following literature was used in the classification: Ferns of Malaysia in colour (Piggott 1988), Ferns of the tropics (Wee 1998), Ferns of Thailand, Laos and Cambodia (Lindsay & Middleton 2012 onwards), Kew garden (The Herbarium Catalogue 2015), Orchids of Sumatra (Comber *et al.* 2001). The nomenclature of the scientific names of the plants follows APG (2009) and The Plant List (2013).

To be able to analyze and compare epiphytic community compositions in the four land-use systems, recorded species were grouped into 3 taxonomic groups after Barthlott *et al.* (2001): orchids (family Orchidaceae), ferns (Monilophytes incl. Lycophytes) and other angiosperms (flowering plants excluding Orchidaceae).

The fieldwork took place from the 6th of August until the 18th of September 2014. The identification of collected specimens was carried out in Bogor between the 19th and 29th of October 2014.

2.5 Additional Data

The data on epiphyte diversity in jungle rubber was compared to data on epiphyte diversity in rubber plantations, oil palm plantations and lowland rainforest in Bukit Duabelas National Park and its surroundings from Böhnert (2013) and Altenhövel (2013).

They applied the same study design as described in the present study in jungle rubber, with minor exceptions: because of the smaller height of the phorophyte in the oil palm and rubber plantations, climbing was not necessary and epiphytes were surveyed following the ground based observation protocol of Flores-Palacios and García-Franco (2001) using binoculars and cameras. Because of their lack of a real crown, Johansson-Zones 4 and 5 were absent in oil palm plantations.

Altenhövel and Böhnert established 30 plots in each of the investigated land-use systems, i.e. 90 plots in total. Since 30 additional plots were established in jungle rubber during the course of this study, it was possible to include the data of 120 plots, belonging to 4 land-use systems, in the final evaluation.

They also recorded microclimatic conditions for one tree per land-use system over a period from 15 March – 4 April 2013 in the forest and 9 April – 15 April 2013 in oil palm and rubber plantations.

2.6 Epiphyte data analysis

To analyze the observed epiphytic diversity and abundance numerous descriptive and statistical methods were performed by using the free software for statistical computing and graphics, *R*, version 3.2.1 (R Core Team 2013). Most figures were created in *R* by using the package *ggplot2*.

Alpha diversity, which refers to the diversity within a particular area or ecosystem (within-habitat diversity) was calculated by using the Simpson diversity index and Pielou’s evenness (Simpson 1949; Pielou 1969).

The Simpson index is regarded as one of the most meaningful and robust diversity measures available (Magurran 2004). It describes the probability that two individuals, drawn at random from an infinitely large community belonging to the same species as:

$$D = \sum p_i^2$$

where p_i represents the proportion of individuals in the *i*th species. For a finite community the index is calculated as:

$$D = \sum \left(\frac{n_i\,[n_i - 1]}{N\,[N - 1]} \right)$$

where n_i represents the number of individuals in the *i*th species and N represents the total number of individuals. Since *D*, in this form, indicates low diversities with high values, which is counterintuitive, Simpson index was expressed as the reciprocal of *D* (1/*D*; “inversed Simpson index”) in this study.

Pielou’s Evenness is calculated based on the long-established Shannnon index *H’*, which is calculated from the equation:

$$H' = -\sum p_i \ln p_i \quad \text{with} \quad p_i = \frac{n_i}{N}$$

where p_i represents the proportion of individuals found in the *i*th species. Although the Shannon index takes the degree of evenness in species abundance already into account it is nevertheless possible to calculate a separate evenness measure, in the form of Pielou’s Evenness (Magurran 2004). Pielou’s Evenness describes the ratio of observed diversity to maximum diversity ($H_{\max}$), which is the diversity that would occur if all species had equal abundances. Pielou’s Evenness is therefore calculated as:

$$J' = H'/H_{\max} = H'/\ln S$$

with *S* representing the number of different species within the population. The values for Pielou’s evenness can range between 0 and 1, where 0 is standing for a low and 1 is representing a high evenness.

Simpson index as well as Pielou’s Evenness were calculated on overall landscape level, i.e. the overall systems, as well as on plot level. Indices were calculated in *R* by using the package *vegan*.

To estimate the total species richness per system species accumulation curves were calculated for each system. Species accumulation curves plot the cumulative number of recorded species as a function of sampling effort, i.e. number of plots (Colwell & Coddington 1994). As long as new species are discovered with increased sampling effort the species accumulation curve will rise. When no new species are found despite a further increase in sampling effort the curve will reach an asymptote, indicating that the species inventory was sufficient to detect the total species richness of the corresponding system. Randomized species accumulation with 100 permutations were calculated in this study for each of the four land-use systems by using the *R* function *specaccum* and Kindt’s exact accumulator method according to Ugland *et al.* (2003). The function *specaccum* is available within the *vegan* package.

Total species richness per system was also calculated using the Chao 2 estimator (Chao 1987). It is based on the number of rare species in a sample and assumes that the number of unseen species is related to the number of species seen only once or twice (Colwell & Coddington 1994; Magurran 2004). Chao 2 estimator is calculated as:

$$S_{\text{Chao 2}} = S_{\text{obs}} + \frac{Q_1^2}{2Q_2}$$

Where S_{obs} represents the number of species in the collection, Q_1 stands for the number of species that occur in one sample only (uniques) and Q_2 represents the number of species that occur in two samples (duplicates). Chao 2 values were calculated for each system in *R* by using the function *specpool* of the *vegan* package.

Plot based epiphyte species richness, abundance, alpha-diversity and evenness were tested for normality using the Shapiro-Wilk-test (Shapiro & Wilk 1965). Since test results indicated that the plot based epiphyte data was not normally distributed, the land-use systems were compared using the non-parametric Kruskal-Wallis one-way analysis of variance (Kruskal & Wallis 1952). Additional post hoc tests using multiple comparisons were conducted to detect pairwise differences within the epiphyte data between land-use systems. The *R* functions *shapiro.test*, *kruskal.test*, *kruskalmc* and the package *pgirmess* were used in the statistical tests.

To examine possible changes in the epiphyte community structure and composition in the four land-use systems rank-abundance curves were compiled for each individual system. Rank abundance curves, also known as Whittaker plots after their inventor (Whittaker 1965), plot recorded species in sequence from most to least abundant along the x axis. Whilst their abundances are displayed on the y axis, usually in form of proportional or percentage abundances. Abundances are also typically displayed in a $\log_{10}$ format to accommodate all recorded species on the same graph even if their abundances span several orders of magnitude (Magurran 2004). Rank abundance curves clearly display contrasting patterns of species richness as well as highlighting differences in evenness amongst assemblages (Magurran 2004). To calculate species accumulation curves for the four systems, the *R* function *specaccum* of the *vegan* package was used.

Beta diversity, which describes changes in species composition between different ecosystems (between-habitat diversity) was determined by computing the Bray-Curtis dissimilarity index for all pairwise combinations of the 30 plots per system. The Bray-

Curtis dissimilarity is regarded as one of the most effective similarity measures (Southwood & Henderson 2000). As it was first devised by Sørensen it is also known as Sørensen index (Sørensen 1948). Three parameters are used in its calculation: the total number of shared species occurring in both samples (a), the number of species only occurring in sample 1 (b) and the number of species only occurring in sample 2 (c):

$$C_s = \frac{2a}{2a + b + c}$$

The resulting value ranges between 1 and 0. While 0 shows that the compared sites have all species in common, 1 means that sites do not share any species at all. The function *vegdist*, also available within the *vegan* package, was used in *R* to calculate the Bray Curtis dissimilarities for all possible pairwise plot combinations per system. Results were tested for significant differences between systems by using Kruskal-Wallis one-way analysis of variance and additional post hoc tests, in form of multiple comparisons.

To assess the floristic composition of vascular epiphytes between the investigated land-use systems non-metric multidimensional scaling (NMDS) ordination was used. The aim of an ordination graph is to plot sites in a way that distances between them in the graph also reflect their ecological distances, i.e. the ecological differences (Leps & Smilauer 2003; Zuur *et al.* 2007). Ecological distances between plots were expressed with the Bray-Curtis dissimilarity index, which was calculated for all possible plot combinations, but only plots with more than one individual were included. The result is a distance matrix, which contains the ecological distance for every given pair of plots. Each plot was then assigned coordinates in two dimensions according to its scores in the distance matrix. Additionally, 95 % confidence ellipses were calculated for each land-use system to visualize the core distribution of its corresponding plots. If confidence ellipses of two land-use systems do not overlap, the systems are probably significantly different from each other (Oksanen 2009). The NMDS ordination was compiled in *R* with the function *metaMDS* of the *vegan* package. Confidence ellipses were calculated by using the function *ordiellipse*.

2.3 Agroforest stand structure

To evaluate possible relations between the agroforest stand structures of jungle rubber and epiphyte diversity, central structural features of trees growing in the understory of the investigated phorophytes were determined. We measured the height and DBH of all trees, with a DBH ≥ 10 cm, within the 20 x 20 m plot, surrounding the central phorophyte. To determine rubber densities within the plots, all measured trees were identified and either recorded as rubber or native trees.

DBH measurements were later used to calculate the basal area of each individual tree. The basal area is defined as the area covered by the cross section of tree trunks at their base. Individual basal areas can then be summed up to determine the total basal area of the plot. The basal area was also calculated for only rubber and only native trees separately.

To investigate possible correlations between epiphyte diversity and agroforest stand structures, simple linear regression analyses where carried out. Simple linear models examine the relationship between a scalar dependent variable *y* and a single explanatory variable *x* (Weisberg 2005). Stand characteristics, separated by phorophyte structures and understory structures, were modeled as explanatory variables against the dependent variables species richness and abundance. Models were performed in *R* by using the function *lm(y ~ x)*.

2.4 Microclimatic measurements

To investigate possible influences of microclimatic conditions on epiphyte diversity, data loggers (*iButton®, Hygrochron temp/relative humidity logger, 8 kb storage*) were installed in each Johansson-Zone of 3 different phorophytes (Tab. 1). The surveyed phorophytes were located inside the jungle rubber core-plots BJ3, BJ4 and BJ5. In the plots BJ3 and BJ5 the investigated phorophytes were the same as in the epiphyte inventory. This was not possible in BJ4 because of the inaccessibility of the higher Johansson-Zones of the initially sampled phorophyte. Instead data loggers in BJ4 were installed on a neighboring tree with similar properties but better access to the upper canopy.

Tab. 1: Positions (height in m) of data loggers within the Johansson-Zones of the 3 investigated phorophytes. Phorophytes are identified by corresponding plot names.

Plot	JZ1	JZ2	JZ3	JZ4	JZ5
BJ3	1.5	9	19	24	26.5
BJ4	1.5	9.2	20	24.8	27.3
BJ5	1.4	5.1	10.2	14.1	17.6

Data loggers measured and recorded temperature (°C) and relative humidity (%) in intervals of 10 minutes. The microclimate was measured in BJ4 over a period from 15 August – 25 August 2014 (10 days). In BJ4 the measurement took place between 26 August – 12 September 2014 (14 days) and in BJ3 the investigated period was between 13 September – 25 September 2014 (12 days). It was not possible to conduct parallel measurements because of the limited amount of available data loggers.

Mean diurnal temperature and humidity curves for jungle rubber were calculated over the three sites from the resulting measurements. Curves for the highest and lowest data logger were plotted using *R* and the package *ggplot2*.

3. Results

The application of the before mentioned methods allowed for the finding of interesting and insightful results, which will be presented in the following chapter.

3.1 Species richness & abundance

A total of 3955 individuals of vascular epiphytes belonging to 81 different species were found in the 120 investigated plots (Appendix 1). The highest abundance was found in jungle rubber (1933 individuals) followed by oil palm plantations (1385 individuals) and forest (549 individuals). The lowest abundance was recorded in the rubber plantations (88 individuals). Species richness was highest in jungle rubber (46 species), closely followed by forest (44 species). However, the number of families was higher in forest (15 families) than in jungle rubber (9 families). Despite the high abundance of epiphytes in oil palm plantations, overall species richness was very poor (10 species, 7 families) and in terms of species richness even slightly poorer than rubber plantations (11 species, 6 families).

Inverse Simpson's index values for overall alpha diversity were highest in the forest (14.9), followed by jungle rubber (7.1) and rubber plantations (6.2), while oil palm plantations showed the lowest inversed Simpson's index value (3.4).

The highest values for Pielou's Evenness were calculated for rubber plantations (0.856) and forest (0.798), the lowest for oil palm plantations (0,693) and jungle rubber (0.638).

Epiphyte communities showed strong differences in their composition at higher taxonomic levels between investigated systems (Fig. 4). Rubber and oil palm plantations were strongly dominated by ferns both in terms of abundance and number of species, while other angiosperms were almost completely absent. Although jungle rubber had the highest overall species richness and abundance its composition mainly consisted of ferns and orchids while other angiosperms were underrepresented. Forest was the only system where all 3 taxonomic groups were almost evenly distributed at species level.

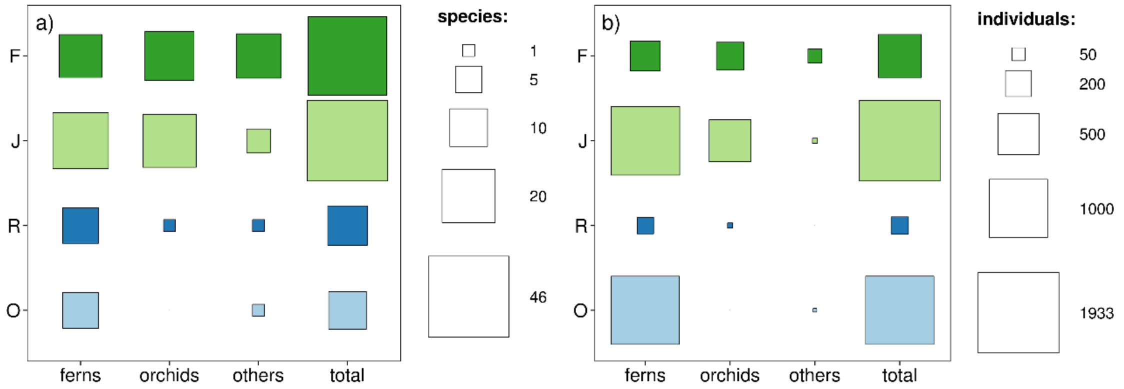

Fig. 4: Species richness (a) and abundance (b) of vascular epiphytes divided into three taxonomic groups (orchids, ferns, other angiosperms) in four different land-use systems: forest (F), jungle rubber (J), rubber plantations (R), oil palm plantation (O).

Ferns were the most abundant taxonomic group in all four investigated systems and with the exception of forest also the group with the highest number of species per system. In the forest, where ferns actually had the lowest species richness, orchids were the most species rich group. High numbers of orchids were also found in jungle rubber while only one orchid species (*Dendrobium crumenatum*, 7 individuals) was found in rubber plantations and none in oil palm plantations. Species richness of other angiosperms was also poor in the plantations and was represented by only one species each: *Dischidia imbricata* (Apocynaceae, 1 individual) in rubber and *Cyrtandra oblongifolia* (Gesneriaceae, 3 individuals) in oil palm plantations. By far the highest number of other angiosperms was recorded in the forest while this group was also barely featured in jungle rubber. *Ficus deltoidea* (Moraceae, 2 individuals), *Freycinetia cf. sumatrana* (Pandanaceae, 1 individual) and two unidentified Melastomataceae species were the only other flowering plants found in jungle rubber.

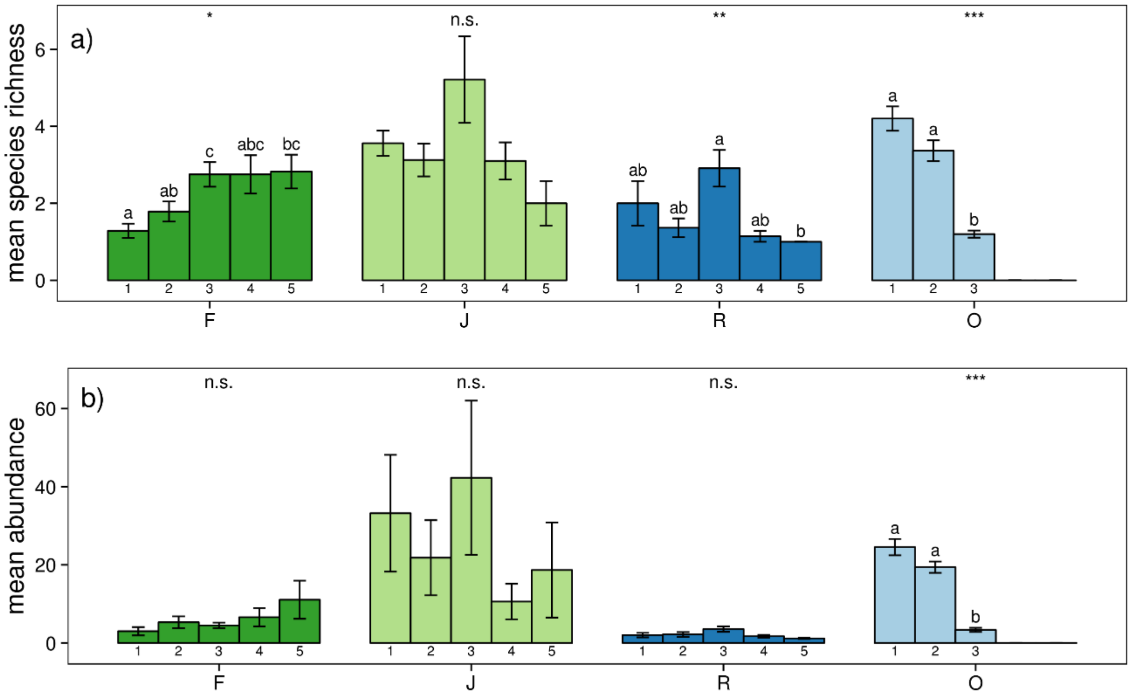

Fig. 5: Mean species richness (a) and mean abundance (b) of vascular epiphytes per Johansson-Zone in the four land-use systems. Error bars indicate standard error. Kruskal-Wallis significance levels: $p > 0.05$ n.s, $p \leq 0.05$ *, $p \leq 0.01$ **, $p \leq 0.001$ ***. Means with different letters, within one system, are significantly different from each other (post hoc multiple comparisons).

Differences in the distribution of epiphytes along the phorophyte zones were also observed (Fig. 5). In the forest, mean species richness was highest within JZ5 and lowest in JZ1. In jungle rubber and rubber plantations, however, this distribution was almost inversed with the second highest mean species richness occurring within JZ1 and the lowest in JZ5, although differences between Johansson-Zones in jungle rubber were not significant. Both rubber and jungle rubber had the highest mean species richness in JZ3. An almost identical distribution pattern occurred in terms of epiphyte abundance. While the abundance in forest steadily increases with every JZ, its distribution in jungle rubber and rubber plantations is centered around JZ3, with an additional peak in JZ1 of jungle rubber. In oil palm plantations highest species and individual numbers were found in JZ1 decreasing towards JZ2 and JZ3 while JZ4 and JZ5 were absent. However, differences between epiphyte abundances per Johansson-Zone were only significant in oil palm plantations.

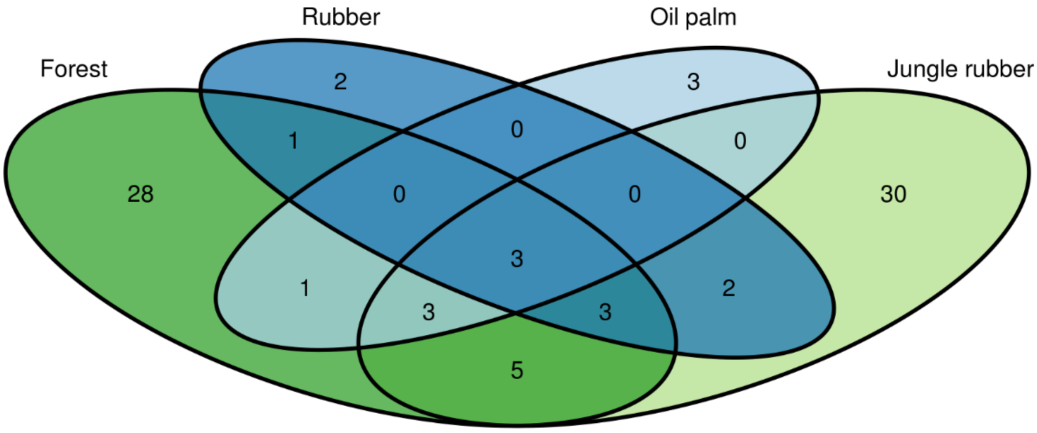

Fig. 6: Venn diagram showing numbers of epiphyte species in the different land-use systems. Sizes of ellipses are proportional to the total species richness per land-use system.

Out of the 81 total species found in this study, 30 species were exclusively recorded in jungle rubber and 28 only occurred in forest (see Fig. 6). On the contrary, only 2 species were unique to rubber plantations (*Myrmecophila sinuosa, Pyrrosia cf. lingua*) and 3 to oil palm plantations (*Asplenium longissimum, Cyrtandra spec., Stenochlaena palustris*). Thus the majority of recorded species were restricted to the systems forest or jungle rubber, while the larger share of species in the plantations also occurred in other systems.

In this study species which were restricted to a single system were categorized as specialists and species that occurred in two or more systems were classified as generalists. Therefore the systems forest (64%) and jungle rubber (65%) were mainly composed by specialist species, while the species composition in the plantations was dominated by generalist species (rubber plantations: 82 %, oil palm plantations: 70 %). Three species were found in all 4 systems: *Asplenium nidus, Davallia denticulata* and *Vittaria elongate*.

Species-accumulation curves for all four systems revealed clear differences between monoculture plantations and forest and jungle rubber (Fig. 7). While the species-accumulation curve of oil palm plantations reached an early saturation, the curves for forest and jungle rubber are clearly not yet saturated. The curve of rubber plantations appears almost saturated, but is still slightly rising. Accumulation-curves indicate that the sampling effort of 30 plots was sufficient for a complete inventory of epiphyte species in oil palm plantations and for an almost complete inventory in rubber plantations. Nevertheless, accumulation-curves further indicate, that sampling effort failed to depict the maximum species richness in forest and jungle rubber. A higher overall species richness could therefore be expected by further sampling in forest and jungle rubber.

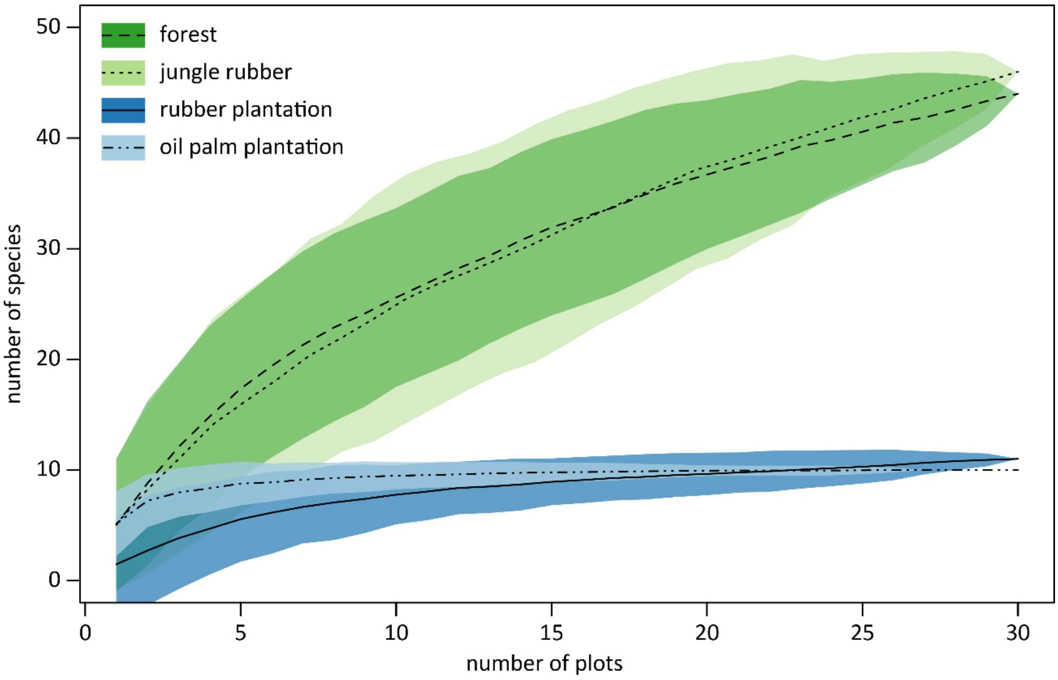

Fig. 7: Species-accumulation curves for vascular epiphytes in four land-use systems. Mean values (lines) and standard deviations (colored areas) from 100 permutations are shown.

These findings were mainly supported by the estimated species richness. Calculated Chao 1 estimates for the total number of species were highest in forest (71.62) and jungle rubber (71.57), but were considerably lower in oil palm plantations (10). Estimated species richness in rubber plantations (16.8) though, was considerably higher as first indicated by the course of the corresponding accumulation-curve. According to

Chao 1 values, epiphyte inventory revealed 61.4 % of the predicted total species richness in the forest and 64.2 % in the jungle rubber. In the rubber plantations 65.4 % of the estimated total species number was observed, while the inventory in oil palm plantations resulted in a complete inventory of the estimated species richness (100%).

On plot level, the four systems showed significant differences both in terms of species richness and abundance (Kruskal-Wallis one-way analysis of variance, $p < 0.001$). Post-hoc multiple comparisons revealed significant lower species richness in rubber plantations (mean: 1.5 ± 1.6 *SD*), while forest (18.3 ± 25.4 *SD*), jungle rubber (5.4 ± 3.6 *SD*) and oil palm plantations (46.1 ± 11.8 *SD*), were indistinguishable in terms of species richness per plot (see Fig. 8). With respect to abundance per plot post-hoc comparisons showed no significant difference between forest (mean: 18.3 ± 25.4 *SD*) and jungle rubber (64.4 ± 116.6 *SD*), while the abundance per plot was significantly lower in the rubber plantations and higher in the oil palm plantations (46.1 ± 11.8 *SD*). However, the abundance per plot in jungle rubber had some extreme outliners (Fig. 8).

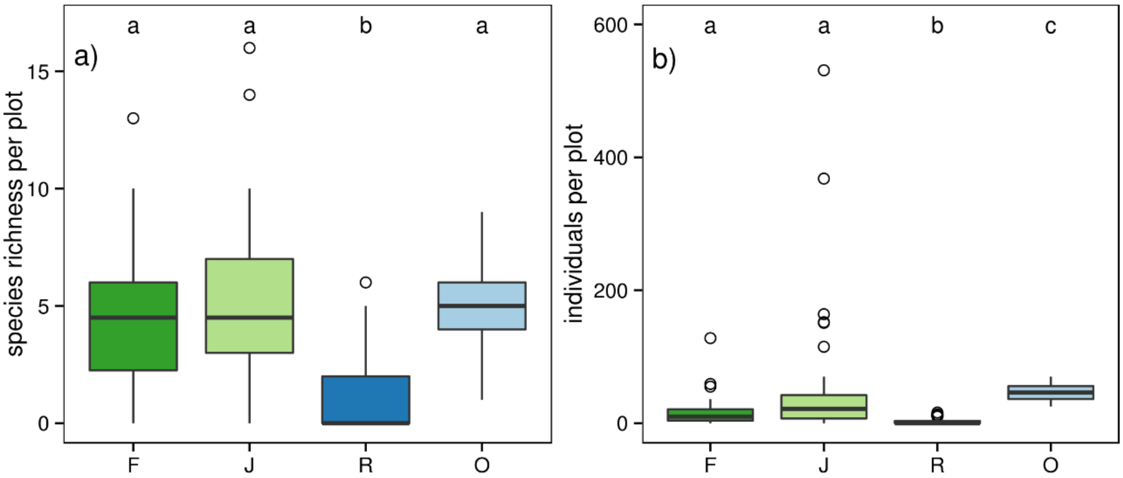

Fig. 8: Epiphyte species richness (a) and abundance (b) in 30 plots per land-use system. Kruskal-Wallis one-way analysis of variance showed significance level of $p \leq 0.001$ (a) & (b). Letters indicate significant differences between systems (post hoc multiple comparisons after Kruskal–Wallis).

Inverse Simpson's index values on plot level (Fig. 9) were significant different between systems (Kruskal-Wallis one-way analysis of variance, p < 0.001). Additional post-hoc tests revealed similarities between forest (mean: 3.11 ± 1.79 *SD*), jungle rubber (2.91 ± 1.39 *SD*) and oil palm (2.95 ± 1.3 *SD*), while values are significantly lower in rubber plantations (1.2 ± 1.6 *SD*).

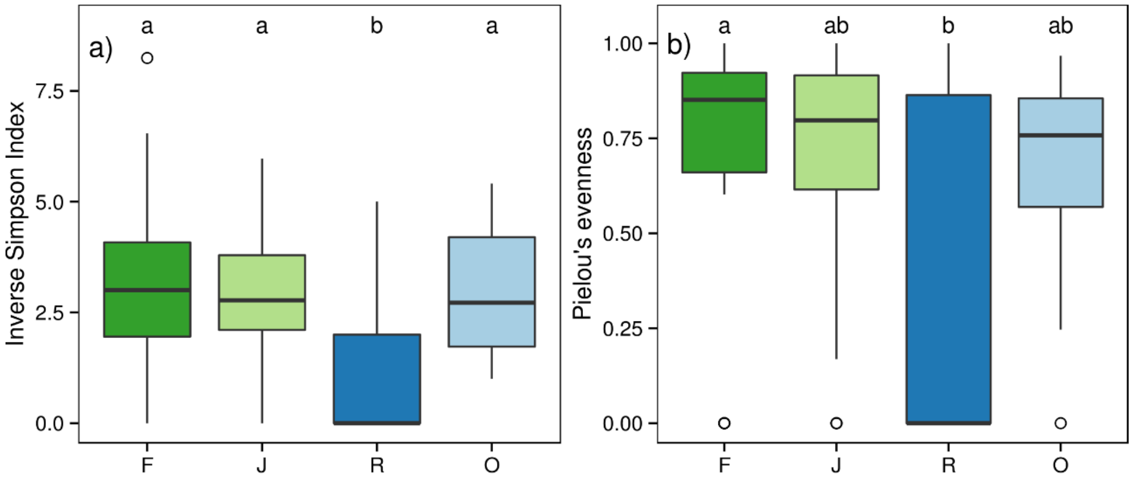

Fig. 9: Inverse Simpson index values (a) and Pielou's evenness in 30 plots per land-use system. Kruskal-Wallis one-way analysis of variance showed significance level of p ≤ 0.001 (a), p ≤ 0.01 (b). Letters indicate significant differences between systems (post hoc multiple comparisons after Kruskal-Wallis).

Pielou's Evenness (Fig. 9) was significantly different between the forest (mean: 0.7 ± 0.34 *SD*) and rubber plantations (0.3 ± 0.44 *SD*), whereas jungle rubber (0.7 ± 0.3 *SD*) and oil palm (0.69 ± 0.22 *SD*) showed similarities to the forest, as well as to rubber plantations (post hoc multiple comparisons after Kruskal-Wallis).

3.2 Floristic composition

Rank-abundance curves plotting the relative abundance against the abundance rank of each species showed distinct differences in appearance between the four systems (Fig. 10), indicating an individual floristic composition of epiphytes in each system. The rank-abundance curves for forest and jungle rubber had a long, slowly descending shape, hinting at high species richness and a high evenness within these systems. On the contrary, the curves for the plantations were shorter and had a very steep descent, pointing to a lower number of species and to a high dominance of few highly abundant species.

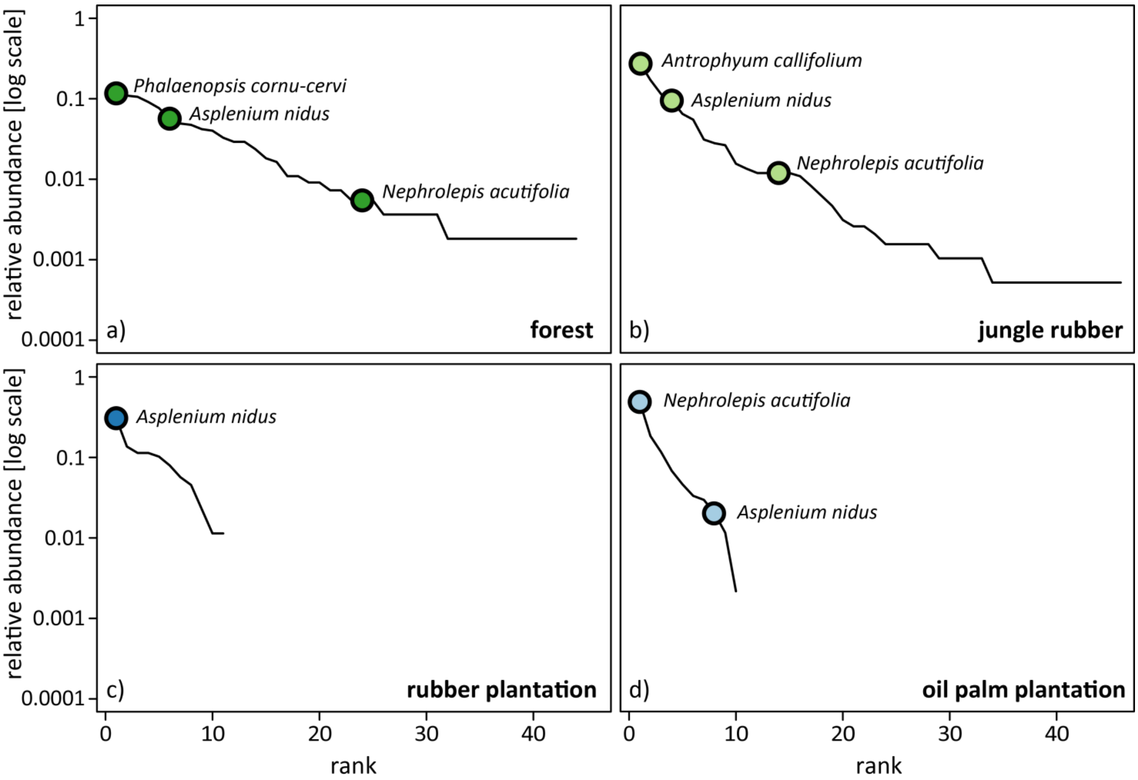

Fig. 10: Rank-abundance plots for forest (a), jungle rubber (b), rubber plantation (c) and oil palm plantation (d). Vertical axis (log10 scale) shows the relative abundance of the species. Horizontal axis ranks each species from most to least abundant. The abundance of all 81 collected species is designated as 1.0 and the relative abundance of each single species is given as a proportion of the total.

Species also varied in importance in regard to their abundance between the systems. The most abundant species in forest (*Phalaenopsis cornu-cervi*) and jungle rubber (*Antrophyum callifolium*) for instance were completely absent in the rubber and oil palm plantations. Whereas *Nephrolepis acutifolia*, which had an intermediate abundance in forest and jungle rubber was the most abundant species in oil palm plantations but did not occur in the rubber plantations at all. Furthermore, the most abundant species in the rubber plantations (*Asplenium nidus*), which was also very common in the forest and jungle rubber, was only of minor importance in the oil palm plantations.

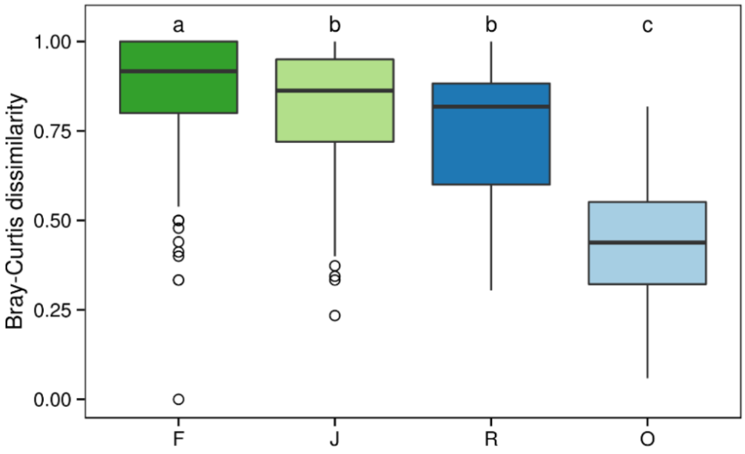

Fig. 11: Bray-Curtis dissimilarity values for 30 plots in the four land-use systems. Kruskal-Wallis one-way analysis of variance showed significance level of $p \leq 0.001$. Letters indicate significant differences between systems (post hoc multiple comparisons after Kruskal-Wallis).

Bray-Curtis dissimilarity, computed for all possible pairwise plot combinations (Fig. 11), had the highest mean values in the forest (0.87 ± 0.15 *SD*) and jungle rubber (0.82 ± 0.16 *SD*), indicating a high variation in epiphyte species composition within these systems. Average Bray-Curtis dissimilarity was slightly lower within rubber plantation plots (0.76 ± 0.16 *SD*), while mean dissimilarity values were the lowest within in the oil palm plantations (0.44 ± 0.19 *SD*), hinting to a strong similarity in epiphyte composition and a high amount of shared species within the oil palm plots.

Post-hoc multiple comparisons after Kruskal-Wallis revealed a strong overlap between the dissimilarity values of jungle rubber and rubber plantations, while the forest and oil palm plantations were each significant different from the other systems (see Fig. 11).

An NMDS ordination based on the Bray-Curtis dissimilarity index showed that the epiphyte communities in jungle rubber had strong similarities to the forest communities

(Fig. 12). Overlapping confidence areas of these two systems indicate a strong similarity in epiphyte composition. This finding is further supported by the fact that the majority of jungle rubber outliers, which appeared outside the confidence area of jungle rubber, were nevertheless still inside the confidence area of the forest. Furthermore the ordination shows partly overlapping confidence areas of the forest and rubber plantations, which also points to a close resemblance in epiphyte communities between the forest and rubber. However, the ordination also revealed that communities in oil palm plantations were clearly distinct from the other land-use systems.

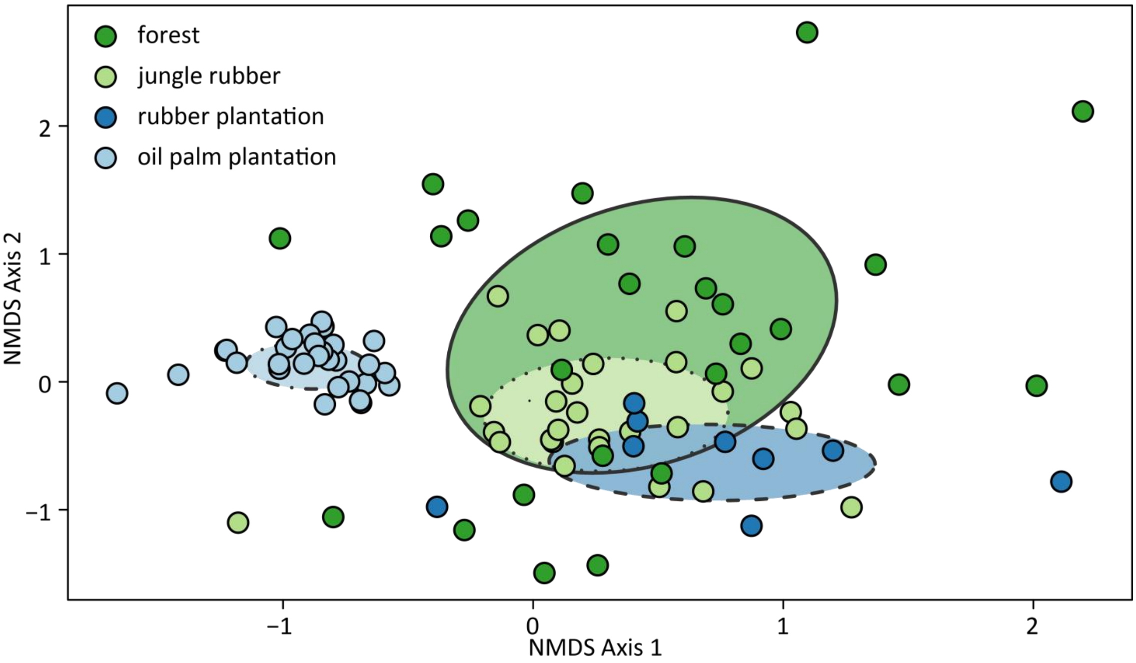

Fig. 12: NMDS ordination based on Bray-Curtis dissimilarity of species numbers between plots. Only plots with more than 1 individual have been included. Colored ellipses show the 95 % confidence areas of each system. Analysis of Similarity (ANOSIM) tests showed a significance level of p = 0.001. Stress-value: 0.179.

3.3 Microclimatic conditions

Mean diurnal temperature and humidity curves revealed clear differences in microclimatic conditions between the four land-use systems (see Fig. 13). While forest and jungle rubber showed a wide range of temperature and humidity conditions, the conditions in both plantation systems were much narrower.

During the night, values for temperature and relative humidity showed initially no distinct differences between the systems or between the data logger positions within the individual systems. In all four systems, temperatures reached their minimum values (23-25 °C) around 6 a.m., shortly after sunrise. Values for relative humidity were highest in all systems around 8-9 a.m. (95-100 %). Relative humidity measurements reaching above 100 % at that time, which indicate fog formations, were exclusively recorded in the forest.

Over the course of the day the temperatures rose in all four systems and temperature values measured by the data loggers near ground level were in general lower than the values measured near the tree crowns. In the forest and jungle rubber however, the differences between the upper and lower data loggers were very distinct, with up to 5 °C temperature and 30 % humidity difference in the forest, whereas plantations just showed minor differences in microclimatic conditions between data logger positions. The highest temperatures and lowest relative humidity were reached in the jungle rubber and the plantations around 2 p.m. and thus 2 hours earlier than in the forest, where the values peaked at around 4 p.m.

With temperatures never exceeding 34 °C and humidity not falling below 88 % near the ground level the forest had a generally cooler and more humid climate than the other land-use systems (see Fig. 13 a & b). The microclimate in the jungle rubber showed similarities to the forest but reached higher total temperatures and lower humidity values (see Fig. 13 c & d). Both the highest overall temperature (36 °C) and the lowest total humidity (55 %) were measured in the rubber plantations (see Fig. 13 e & f). Conditions in the oil palm had the lowest microclimatic variation between the upper and lower data loggers (see Fig. 13 g & h).

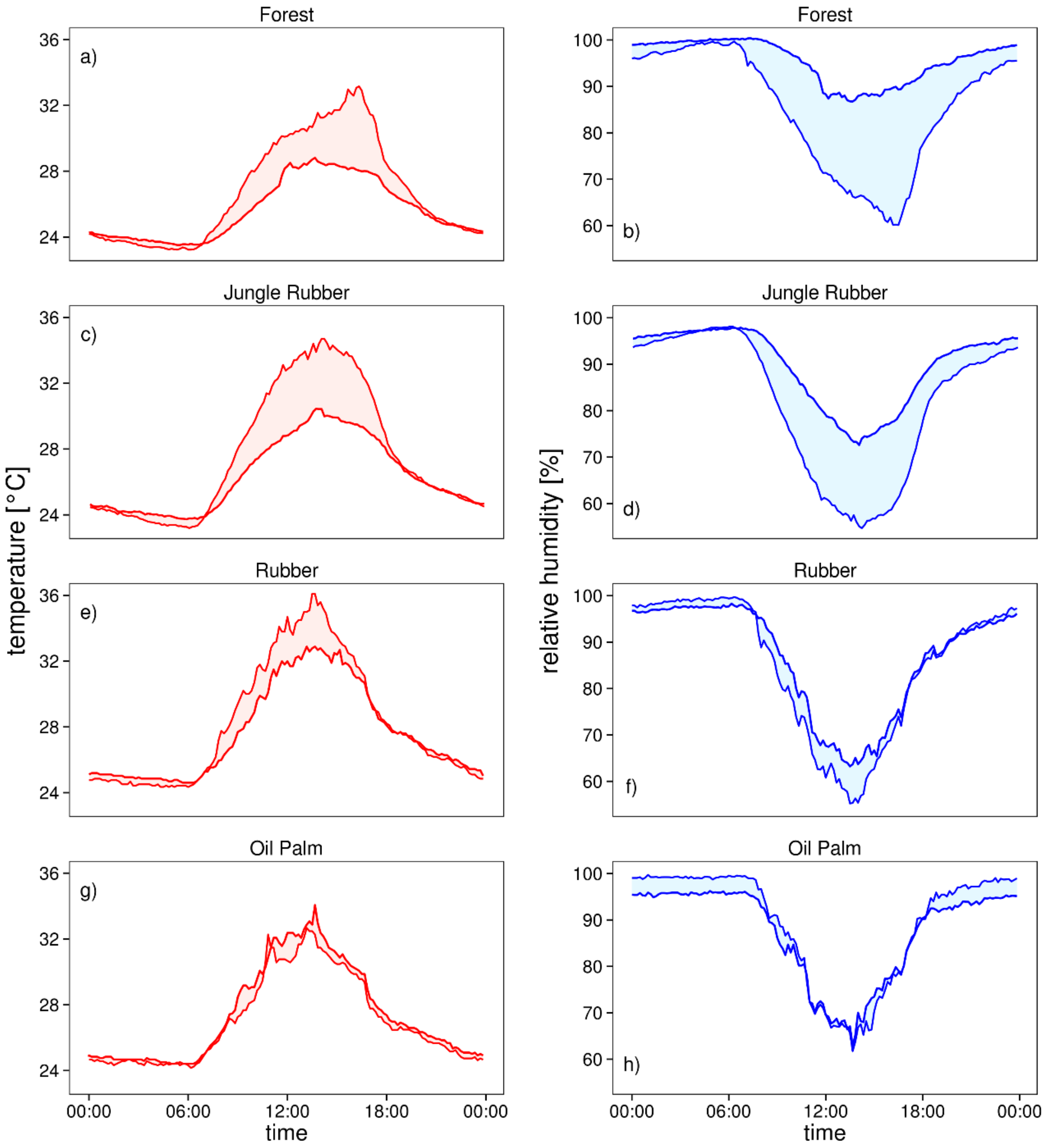

Fig. 13: Mean diurnal temperature (°C, left figures) and relative humidity curves (%, right figures) recorded in 10-min intervals in the four land-use systems. The curves show the values for data loggers installed in Johansson-Zone 1 and Johansson-Zone 5 (respectively JZ3 in Oil Palm). Measurements were conducted over a period from 15 March – 4 April 2013 in forest, 9 April – 15 April 2013 in oil palm and rubber plantations, and from 15 August – 24 September 2014 in jungle rubber.

3.4 Agroforest structure

The measurement of central structural features in the 30 jungle rubber plots showed that an average of 22.7 (± 7.15 *SD*) trees with a DBH ≥ 10 cm were growing in the understory within a single plot (Appendix 3). These trees had a mean height of 13.46 m (± 1.38 *SD*) and mean total basal area of 0.95 m^2 (± 0.37 *SD*). Native trees usually outnumbered rubber trees with an average percentage of 40.7 % (± 23.09 *SD*) rubber trees and 59.3 % native trees. Mean overall basal area of rubber trees was 0.38 m^2 (± 0.28 *SD*) while the mean basal area of native trees in the understory was distinctively higher with 0.57 m^2 (± 6.78 *SD*).

The 30 investigated phorophytes had an average height of 23.9 m (± 4.73 *SD*) and a mean basal area of 0.33 m^2 (± 0.27 *SD*). Phorophyte crowns started on average in a height of 11.91 m (± 4.03 *SD*) and had a mean length of 11.98 m (± 3.43 *SD*).

Simple linear regression models revealed that measured understory stand structures were unable to explain total plot-based species richness and abundance of vascular epiphytes (Appendix 4). Neither the heights and the basal area of understory trees nor the basal area of rubber and native trees helped to explain richness or abundance patterns. Densities of rubber or native trees were also unable to predict epiphyte diversity on plot level.

However, if understory structures were just modeled against the epiphyte diversity in Johansson-Zone 1, models showed a positive correlation (see Fig. 14 a) between epiphyte species richness in JZ1 and rubber densities ($F = 9.5$, $P = 0.0046$, adjusted $R^2 = 0.22$) or respectively a negative correlation to native tree densities. A positive correlations was also found between species richness in JZ1 and the basal area of rubber trees ($F = 22.33$, $P = 5.872 \times 10^{-05}$, adjusted $R^2 = 0.42$).

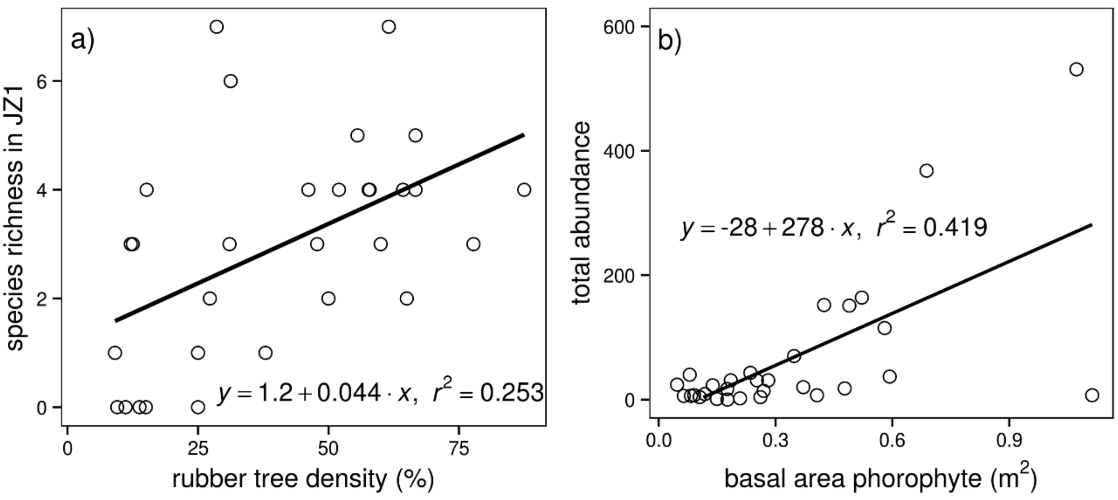

Fig 14: Simple linear regression models: basal area of investigated phorophytes plotted against the total plot abundances (a), rubber tree densities (%) plotted against species richness in Johansson-Zone 1 (b).

Phorophyte basal area did explain 42 % of epiphyte abundance (*F* = 20.16, *P* = 0.0001, adjusted R^2 = 0.42) and the corresponding regression line revealed a positive correlation between the two variables (see Fig. 14 b). Thus a higher number of individuals can be expected growing within plots with an increased phorophyte basal area. However, phorophyte basal area failed to explain epiphyte species richness. Phorophyte crown height and length did also not help to make predictions about epiphyte abundance or richness.

4. Discussion

4.1 Epiphyte diversity & abundance

Plot-based inventories of vascular epiphytes in the four land-use systems in central Sumatra revealed clear differences between the systems, both in terms of epiphyte diversity and abundance.

Epiphyte species richness was, as predicted in H1, higher in jungle rubber than in the plantation systems, where species richness was found to be very poor (11 in rubber, 10 in oil palm). The same was true for epiphyte abundance, although epiphyte abundance was, despite the low species richness, extremely high in oil palm plantations (88 in rubber, 1385 in oil palm). Altenhövel (2013) discusses the accumulation of organic litter in the dead leaf axils of the oil palms as possible explanation why some epiphyte species are so abundant in oil palm plantations, while Böhnert (2013) speculate that the deliberate destruction of epiphytes by farm workers might explain the low abundance within the rubber plantations.

The findings of this study are in line with Danielsen *et al.* (2009) and Beukma et al. (2007), who found that the flora of oil palm and rubber plantations is impoverished compared to that of the natural forest. Prescott et al. (2015), however, claimed to have found a taxonomically diverse epiphyte community of 58 species from 31 families in oil palm plantations, which would contradict the findings of this study. However, they also included accidental epiphytes in their evaluation and if these were subtracted, epiphyte diversity would actually be very poor, as well.

Numerous studies in coffee and cocoa plantations in the Neotropics suggest that epiphyte diversity is higher in natural forest than in plantations (Hietz 2005; Haro-Carrión *et al.* 2009; Moorhead *et al.* 2010; Toledo-Aceves *et al.* 2012). At the same time epiphyte diversity was shown to be strongly dependent on management intensity and was, for instance, very similar to the forest in case of polycultural plantations, while it was generally very poor in monocultures (Hietz 2005; Moorhead *et al.* 2010). This would explain the clear differences between rubber and jungle rubber found in this study.

The most remarkable result of this study though was that the highest total species richness and abundance was recorded inside jungle rubber agroforests and not inside the natural forest as predicted in H1. Although the difference in terms of species richness was relatively small (46 in jungle rubber, compared to 44 in forest) the two systems nevertheless showed a very distinct difference in regards to epiphyte abundance. In fact the abundance of epiphytes in jungle rubber was more than 3.5 times higher than in forest (1933 individuals in jungle rubber, compared to 549 in forest) and accounts for almost 50 % of the total 3955 individuals found in all four land-use systems combined. Gouyon *et al.* (1993) also found a high plant diversity in jungle rubber, similar to that of old growth secondary forest. The same was found by Beukma *et al.* (2007), who also included epiphytic pteridophytes and orchids in their survey. But none of them detected an abundance or species richness as high in comparison to the natural forest as found in this present work.

What has to be taken into account when evaluating these results though is the strong internal variability and heterogeneity of jungle rubber agroforests, as described earlier. Furthermore, sampling in jungle rubber was done along a 30 km transect, as can be seen in figure 2, while the sampling in the forest was limited to 2 comparably small areas. The same also applies for the oil palm and rubber plantations. Hence plots were clustered in the forest and in the plantations, whereas plots were largely wide spread in jungle rubber. Studies have shown that epiphytes and in particular orchids are not distributed at random but rather have a highly patchy and clumped spatial distribution with a large proportion of rare species (Nieder *et al.* 2000; Jacquemyn *et al.* 2005; Köster *et al.* 2009; Zotz & Bader 2011). A larger sampling scale, as was the case for jungle rubber in this study, would therefore increase the possibility to include more epiphyte species in the sample.

These circumstances make a direct comparison between jungle rubber and forest, but also between jungle rubber and the plantations difficult. Therefore H1 should neither be accepted nor rejected solely on the base of the total number of species or individuals.

The forest for instance harbored the highest number of families (15) and was the only system in which all 3 taxonomic groups, ferns, orchids and other angiosperms, were evenly distributed at species level. Jungle rubber on the contrary harbored only 9 families and its community was dominated by ferns, while other angiosperms were almost completely absent. These findings highlight that there certainly is a difference between forest and jungle rubber in terms of epiphyte diversity.

Jungle rubber did shelter a high amount of orchids, which hardly occured in the plantations. Both plantations systems were dramatically dominated by ferns, while the numbers of families were lower as well (6 in rubber, 7 in oil palm). A high dominance of fern species and absence of orchids in oil palm plantations was also observed by Danielsen & Beukema (2009).

The results of the taxonomic evaluation would therefore support the hypothesis (H1), that epiphyte diversity in jungle rubber is lower than in the forest but higher than inside the plantations.

The evaluation of species richness and abundance per Johansson-Zone further indicated differences between the systems. The forest, for instance, found to be the only systems in which abundance and species richness increases with every JZ, while jungle rubber and rubber plantation had the highest values within the lower zones, especially in JZ1 and JZ3. Although differences between Johansson-Zones were largely not significant, results nevertheless point to differences in the vertical distribution of epiphytes. Thus, species that are more adapted to the outer canopy might be rare or absent in jungle rubber and plantations. The orchid *Phalaenopsis cornu-cervi* for example, which was the most abundant species in the forest and occurred mainly in JZ5, was completely absent in the other systems. This finding shows again that epiphyte richness and abundance should not, as total numbers might initially suggest, be equated between forest and jungle rubber.

Inversed Simpsons Index values for alpha diversity were more than twice as high in the forest (14.9) than in the jungle rubber (7.1), again underlining a significant difference between these two systems and pointing to a higher diversity in the forest.

Concurrently, alpha diversity in jungle rubber was slightly higher than in the rubber plantations (6.2) and twice as high as in the oil palm plantations (3.4).

Pielou's Eveness was closer to 1 in the forest (0.85) than in jungle rubber (0.79), which shows that the abundance of epiphyte species on the individual phorophyte was more equally distributed in the forest. Thus, hinting once again at a difference between the two systems. Simultaneously, the evenness in jungle rubber was higher than in the plantations (0.69 in rubber, 0.3 in oil palm), where the abundance of epiphyte had a very unequal distribution.

Barthlott *et al.* (2001) found similar results, regarding alpha diversity, when they investigated epiphyte diversity in primary montane rainforest and tree plantations of the Venezuelan Andes (Shannon-Index H': 3.15 in forest, 1.61 in plantations).

Both the results of the Inversed Simpsons Index, as well as the results of Pielou's Eveness further support H1.

The majority of epiphyte species in the plantations were generalist species which also occurred in at least one other land-use system. In contrast to that, the majority of species recorded in forest and jungle rubber were specialist, only occurring once. Consequently it is likely that the plantations favor common, wide spread epiphytes, whilst forest and jungle rubber species are more likely to harbor rare, specialized species. Admittedly, the terms generalist and specialist were, in this study, solely defined on the base of the shared abundances between systems, without taking any ecological properties of species into account. Conclusions drawn from these results should therefore be interpreted with caution. Nevertheless, the corresponding results emphasized once more the clear differences between the plantations and jungle rubber/forest.

However, in terms of abundance of specialists jungle rubber was very similar to the forest (64 % specialist in forest, 65 % in jungle rubber). As jungle rubber can be seen as a secondary forest, such a high number of specialist seems unlikely and would partly oppose H1. Yet again though, these numbers might be caused by the strong internal heterogeneity of jungle rubber and the larger sampling scale. Since sampling effort was not yet sufficient to produce a complete inventory of epiphytes in jungle rubber and forest, as shown by the species accumulation curves, it also seems likely that the number of shared species between forest and jungle rubber would further increase with increased sampling effort.

While species accumulation curves reveal that sampling in the jungle rubber and forest was not sufficient they showed a completely different appearance for the plantations. In oil palm for instance only around 5 plots were sufficient to detect all 11 species found within the system. This emphasizes clearly how poor the epiphyte diversity in this system really is, despite the high abundance. The majority of epiphyte species in rubber plantations can also be detected with a comparatively low sampling effort. Although the accumulation curve for rubber does not reach full saturation, it nevertheless showed a distinct difference to the forest and jungle rubber. While the curves for forest and jungle rubber were almost undistinguishable, the accumulation-curves did overall highlight the differences between the plantations on one hand and the forest and jungle rubber on the other, as predicted in H1.

Estimated total species richness for the four systems confirmed this trend, with only 61.4 % and 64.2 % of the overall species richness discovered in forest and jungle rubber, whereas 100 % of species have been detected in oil palm plantations. Remarkably was albeit that rubber plantations had an estimated 16.8 species, from which only 65.4 % were found. Following these results it could be concluded that rubber plantations have a higher epiphyte diversity than oil palm plantations even despite the higher abundance in oil palm and the similar species richness found in this study (11 rubber, 10 oil palm).

On plot level forest and jungle rubber did not differ both in terms of epiphyte abundance per plot and epiphyte richness per plot. Although jungle rubber had a slightly higher mean abundance and species richness per plot, differences were not significant. The differences between forest and jungle rubber on plot level are therefore not as clear as first indicated by the overall landscape abundance or to a lesser amount richness.

Furthermore, as illustrated by figure 9 b jungle rubber had some extreme outliers, which certainly had an influence not only on the mean values per plot but also on the overall richness and abundance. In fact 531 individuals were recorded within just a single plot in jungle rubber, which represents 27 % of the total abundance in this system. Another plot featured 15 species which alone constitute 32 % of epiphyte species in jungle rubber. On the contrary some plots did not feature a single epiphytic individual, clearly demonstrating the extreme heterogeneity in jungle rubber.

Species richness and abundance of epiphytes was significantly lower in the rubber plantations than in the other systems, which was also caused by the fact that 16 plots did not have any epiphytes at all. However, species richness per plot did not differ significantly between the forest/jungle rubber and the oil palm plantations. This is probably caused by the high abundance of epiphytes in the oil palm plantations, which also explains the significant differences in plot abundances between oil palm plantations and the other systems. It has been shown though, that the overall species richness on landscape level is very poor in oil palm, hence the epiphyte richness and abundance on plot scale did not reflect the diversity patterns found at the landscape scale.

Plot values of the Inversed Simpson Index and Pielou’s Evenness showed in general the same pattern as the plot richness and abundance, with differences between systems not as distinct on plot level as they were on the landscape level. The relatively high alpha diversity of oil palm on plot level indicates a low beta diversity.

Beukema *et al.* (2007) also observed different patterns between the plot level and the overall landscape scale when they compared epiphyte diversity between jungle rubber, rubber and the primary forest. While all three systems did not differ on plot level, they nevertheless found jungle rubber and rubber to differ significantly on the landscape level. Hence, they concluded that plot level species richness is not fully indicative of the richness of a land-use type at the landscape scale.

Overall it can be concluded that the detailed evaluation of the epiphyte diversity in the four land-use systems revealed that H1 can be confirmed and that diversity is indeed highest in the forest closely followed by jungle rubber. Whilst the plantations have to be consider as poor in epiphyte diversity.

4.2 Floristic composition

Rank-abundance plots compiled for each land-use system showed short steeply descending curves for rubber and oil palm plantations (Fig. 10). This does not only indicate a poor species richness, but also shows that the epiphyte communities of both plantations are dominated by a few highly abundant species. Rank-abundance curves for forest and jungle rubber on the other hand were smoother and longer, thus pointing to a higher evenness within these systems, as well as a higher species richness. Furthermore, both curves for forest and jungle rubber featured a flat "tail", indicating the presence of singletons, i.e. rare species represented by only a single individual, which is not the case in the plantations. Although curves for forest and jungle rubber showed similarities, the forest nevertheless exhibited a higher evenness than jungle rubber.

Overall, it is apparent that community structures of vascular epiphytes change considerably between land-use systems. This is further emphasized by the fact that the importance of species in regard to their abundance also changes significantly between systems. All systems differed, for instance, in regard to their most abundant species, i.e. the species ranked as 1 on the horizontal axis. Furthermore, the most abundant species of forest and jungle rubber were completely absent in the plantations and species, which just had intermediate abundances in forest and jungle rubber became very abundant in the plantations. Remarkable was also the absence of *Nephrolepis acutifolia* in rubber plantations, which was a common species in the other systems.

Altogether, these findings strongly support the proposition postulated in H2, that floristic compositions change between land-use systems.

This is further supported by the evaluation of the beta diversity in form of the Bray-Curtis dissimilarity index. Calculated values were significantly different between the land-use systems. The highest dissimilarity values were computed for forest plots (mean: 0.87), the lowest for oil palm plantations (mean: 0.44), while jungle rubber and rubber plantations lay in between (means: 0.82 & 0.76). Since the Bray-Curtis dissimilarity describes changes in species composition between sites, the results indicate that forest plots differed greatly in terms of their individual epiphyte composition, whereas oil palm plots were very uniform in their composition.

Dissimilarities were lower in jungle rubber and rubber plantations than in the forest, but nevertheless still significantly higher than in oil palm plantations. These findings highlight once more the poor epiphyte diversity in oil palm plantations and at the same time show that epiphyte compositions, as predicted in H2, differ between land-use systems.

As the positions of plots within the NMDS ordination are also based on the Bray-Curtis index, it does illustrate the previous results nicely (Fig. 12). Oil palm plots, for instance, are positioned very close to each other, while the forest and, to a lesser amount, jungle rubber and rubber plots are widely scattered. The 95 % confidence ellipse of oil palm plantations is markedly separated from the other systems. Hence, it can be concluded that the epiphyte composition does change significantly in oil palm plantations compared to the other systems. Confidence ellipses of forest and jungle rubber are completely overlapping, thus pointing to a very close resemblance in floristic composition between these two systems. The fact that the majority of jungle rubber outliers, i.e. plots outside the confidence ellipse, are nevertheless still within the confidence ellipse of the forest, further emphasizes the resemblance between forest and jungle rubber. Similarities in composition also seem to exist between rubber plantations and forest as well as jungle rubber, as suggested by the partly overlapping confidence areas.

Changes in epiphyte composition between land-use systems were also observed by Barthlott *et al.* (2001) for montane rainforests and tree plantations in Venezuela, as well as by Hietz (2005), who found that epiphyte communities were more homogeneous in coffee plantations than in natural forests.

Taking all of the above into consideration, it could be confirmed that the floristic composition does change between land-use systems, as predicted in H2. While the species composition in rubber plantations and, in particular, jungle rubber showed similarities to the forest, the composition in oil palm was significantly different from the other systems.

4.3 Microclimatic conditions

The microclimatic conditions measured in this study showed distinct differences between the four land-use systems. Microclimatic conditions in the forest and jungle rubber, for instance, were cooler and more humid than the climate in oil palm and rubber plantations. Especially the microclimate measured in the lower canopy of the plantations was significantly warmer and drier than the corresponding conditions in forest and jungle rubber. Furthermore, forest and jungle rubber showed a wide variation in microclimatic conditions between JZ1 and JZ5, while conditions showed almost no difference between data logger positions in both plantation systems.

As drought is assumed to be the greatest threat to epiphytic life (Johansson 1974) and since epiphytes have been shown to favor areas with a high humidity (Benzing 1990; Kreft *et al.* 2004), as well as to decrease tremendously in richness and abundance in drier habitats (Gentry & Dodson 1987b), it seems obvious that the higher temperatures and the lower humidities in the plantations have a negative impact on the epiphyte diversity. The limited variation in conditions found within the plantations further suggests a reduced niche availability in oil palm and rubber compared to forest and jungle rubber, where conditions were much more heterogeneous.

These results are supported by the findings of Sporn *et al.* (2009) and Luskin & Potts (2011), who as well found the microclimate in oil palm plantations to be significantly hotter and drier than in natural forest. This was further shown by Foster *et al.* (2011), who concluded that extreme microclimatic conditions are more challenging for most organisms and can account for a large proportion of the biodiversity loss when forests are converted to oil palm plantations. Hence it can be concluded that the differences found for epiphyte diversity between plantations on the one hand and forest and jungle rubber on the other can largely be explained by the extreme microclimatic conditions within the plantations.

Although the differences in microclimate between forest and jungle rubber are not as distinct as they are in comparison to the plantations, forest was, nevertheless, the only system in which fog formations were observed, where temperatures never exceeded 34 °C and where humidity never fell below 88 %. Microclimatic conditions can not only influence epiphyte abundance and richness, but also the epiphytic community composition, which was shown by Sporn *et al.* (2009) for epiphytic bryophytes. Beukema

& Van Noordwijk (2004) also discussed altered microclimatic conditions as an explanation for differences in epiphyte diversity and composition between primary forest and disturbed secondary vegetation.

Thus it seems likely that the microclimatic differences between forest and jungle rubber found in this study can not only account for differences in terms of their epiphyte diversity, but also in regards to their species composition.

However, microclimatic conditions in the land-use systems might be influenced by seasonal differences. Since measurements were not conducted parallel to each other the corresponding results might not reflect seasonal variabilities or different weather conditions. Furthermore, with the exception of jungle rubber, only one phorophyte per land-use system was investigated for microclimatic conditions, which raises the question how representative the measurements are for their corresponding system.

Nevertheless, the results of the microclimatic measurements suggest that differences in the diversity of vascular epiphytes between the four land-use systems are, as predicted in H3, linked to differences in microclimate. It is thus possible to accept H3 as true.

4.4 Agroforest structure

Stand structures, measured within the jungle rubber plots, helped little to explain abundance and diversity of vascular epiphytes in jungle rubber agroforest and most simple linear regression models tested did not reveal significant results.

But once more, it is necessary to take the strong internal variability and heterogeneity of jungle rubber into account, when evaluating these results. The use of different management practices and intensities by smallholders obviously affects stand structures and the resulting jungle rubber landscape is a mosaic of agroforests, which differ greatly in appearance. This internal variability was well reflected by the measured stand structures in this work. Hence it seems likely to have had negative influences on the outcome of regression models. It can be expected that a larger sampling size, i.e. more plots, would have possibly helped to detect more patterns between the agroforest structure and the epiphyte diversity.

Furthermore, it is likely that investigation of stand structures limited to the relatively small 20 x 20 m plots was too small in scale and thus insufficient to explain larger patterns of epiphyte diversity.

Nevertheless, models revealed a positive correlation between epiphyte richness in JZ1 of understory trees and rubber densities, which means that the number of epiphyte species in JZ1 increases with an increased proportion of rubber trees. This relationship could be connected to the daily incisions made by the farmers on the rubber trees for latex harvest. These create large wounds on the tree trunk, which are, due to their rough surface, an ideal hotbed for juvenile epiphytes. Since more of these hotbeds are available with an increased rubber density, epiphyte species richness increases simultaneously. However, conservation implications drawn from this are limited, since epiphytes rarely seem to reach maturity, growing in these wounds, which is reflected by the fact that the vast majority of epiphytes recorded within JZ1 were juveniles.

Models further indicated a positive relationship between phorophyte size, expressed as basal area, and epiphyte abundance. This may partly be due to the simple fact, that large trees also have a large surface area, thus offering more room for epiphytes.

Furthermore, it can be assumed that large trees are also of old age, thus giving epiphytes more time for recruitment and establishment, as well as to multiply locally.

Since the biggest share of epiphyte individuals was recorded growing on just a handful of large phorophytes, as illustrated by some extreme outliers, the presence or absence of large veteran trees seems therefore to be an important component of the epiphyte diversity in jungle rubber.

A positive relationship between tree size and epiphyte diversity and abundance was also observed in multiple other studies (Flores-Palacios & Garcia-Franco 2006; Zotz & Schultz 2008; Haro-Carrión *et al.* 2009; Köster *et al.* 2011) and the importance of large long-lived trees for epiphyte diversity was also described by Hietz (2005) in Mexican coffee plantations.

Numerous studies have also investigated the diversity of multiple taxa in a series of different agroforestry systems so far (Round *et al.* 2006; Beukema *et al.* 2007; Bos *et al.* 2007; Harvey & González Villalobos 2007; Bhagwat *et al.* 2008). Although, these studies did not examine stand structures and their influence on biodiversity in great detail, they nevertheless all suggest that the overall species richness is positive correlated to canopy cover, agroforest complexity and a forest-like appearance of the agroforest.

Despite the fact that most regression models did not reveal significant results. It was possible to show that rubber densities in the understory as well as phorophyte size had an influence on the diversity of vascular epiphytes. Thus it is possible to accept H4 as true. Although it would be desirable to increase the sampling effort, as well as the plot scale in future examinations.

With small confinements all hypothesis (H1-4) can be accepted as true after carefully and critically discussing the results and taking into consideration not only the research practice as such but also findings by other studies.

5. Conclusion

The overall findings of this study showed that the conversion of natural forests to other land-use systems, in central Sumatra, leads to a loss of vascular epiphyte diversity.

This loss was particular severe in the investigated plantation systems and both rubber and oil palm plantations were found to be very poor in epiphyte diversity. With regard to oil palm plantations, this finding is of particular interest. Because of the high abundance of epiphytes in oil palm plantations, one could get the false impression that epiphytes could benefit from conditions in oil palm plantations. However, the detailed examination of the epiphyte diversity in oil palm, conducted in this study, clearly revealed that this is not the case at all. In comparison to the forest species composition was extremely altered and only very common and widespread species were able to profit from conditions in the oil palm plantations. Since these species are of low conservation concern, it must be concluded that oil palm plantations have no conservation implications for vascular epiphytes. The same has to be concluded for rubber plantations. Although, species composition in rubber plantations showed more similarities to the forest then it did in oil palm plantations, epiphyte diversity was nevertheless very poor. As it was further possible to show that the poor epiphyte diversity could largely be explained by the extreme microclimatic conditions in the plantations, it can be summarized that both plantations systems cannot be considered a substitute for the natural forest and have to be considered to be of almost no conservation value.

The remarkable result of this study was the high richness and abundance of vascular epiphytes in jungle rubber, which were even higher than in the natural forest. However, the detailed evaluation of the epiphyte data showed distinct differences to the forest. The forest, for instance was the only system in which all four taxonomic groups were evenly distributed, while in particular other angiosperms were underrepresented in jungle rubber. Furthermore, alpha diversity, beta diversity and evenness were all higher in the forest than in jungle rubber. Nevertheless, epiphyte diversity in jungle rubber was still found to have strong similarities to the forest, especially in terms of community structures and floristic composition. Moreover, measured microclimatic conditions in jungle rubber showed also similarities between the two systems. Thus it can be concluded that jungle rubber has a great potential to act as a refuge for a large number of forest-dependent epiphyte species. Although, jungle rubber agroforests cannot replace the natural forest and forest reserves, as there are still significant differences in epiphyte diversity between the systems, they can nevertheless be crucial for the preservation of many epiphyte species and associated animals and ecosystem functions. Altogether, jungle rubber agroforests contribute to maintain a species rich forest ecosystem within an increasingly hostile agricultural landscape matrix.

This conservation value, though, is likely influenced by management practices and the resulting stand structures. Stand structure analysis in this study was not as informative and significant as initially hoped, but indicated that the presence or absence of large long-lived trees might be an essential component for the epiphyte diversity in jungle rubber. Although, it would be desirable to validate and quantify this finding in an additional study, it could nevertheless be very useful in developing practical conservation approaches.

A further conclusion that can be drawn from this study is, that the taxonomic group of other angiosperms is the group which is most threatened by forest conversion, as the forest was the only system where other angiosperms presence in larger numbers, while they were almost completely absent in all other systems.

6. Literature

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7. Appendix

Appendix 1: List of recorded vascular Epiphytes

No.	Family	Species	Author	Group	System	Indiv.
1	Orchidaceae	*Acriopsis densiflora*	Lindl.	Orchid	1,2	27
2	Orchidaceae	*Acriopsis liliifolia*	(J.König) Seidenf.	Orchid	1,2	7
3	Polypodiaceae	*Aglaomorpha speciosa*	(Blume) M.C. Roos	Fern	2	3
4	Vittariaceae	*Antrophyum callifolium*	Blume	Fern	2	540
5	Aspleniaceae	*Asplenium glaucophyllum*	Alderw.	Fern	1,4	17
6	Aspleniaceae	*Asplenium longissimum*	Blume	Fern	4	46
7	Aspleniaceae	*Asplenium nidus*	L.	Fern	1,2,3,4	265
8	Orchidaceae	*Bulbophyllum spec. 1*		Orchid	1	5
9	Orchidaceae	*Bulbophyllum spec. 2*		Orchid	1	3
10	Orchidaceae	*Bulbophyllum spec. 3*		Orchid	1	26
11	Orchidaceae	*Bulbophyllum spec. 4*		Orchid	1	4
12	Orchidaceae	*Bulbophyllum spec. 5*		Orchid	2	1
13	Orchidaceae	*Bulbophyllum spec. 6*		Orchid	2	23
14	Orchidaceae	*Bulbophyllum spec. 7*		Orchid	2	3
15	Orchidaceae	*Bulbophyllum spec. 9*		Orchid	2	51
16	Orchidaceae	*Cleisostoma subulatum*	Blume	Orchid	2	21
17	Clusiaceae	*Clusia spec.*		Other	1	1
18	Gesneriaceae	*Cyrtandra spec.*		Other	4	3
19	Davalliaceae	*Davallia denticulata*	(Burm. f.) Mett.	Fern	1,2,3,4	375
20	Davalliaceae	*Davallia triphylla*	Hook.	Fern	1,2	19
21	Orchidaceae	*Dendrobium aloifolium*	(Blume) Rchb.f.	Orchid	2	9
22	Orchidaceae	*Dendrobium compressistylum*	J.J.Sm.	Orchid	1	50
23	Orchidaceae	*Dendrobium crumenatum*	Sw.	Orchid	1,2,3	61
24	Orchidaceae	*Dendrobium indragiriense*	Schltr.	Orchid	1,2	21
25	Orchidaceae	*Dendrobium leonis*	(Lindl.) Rchb.f.	Orchid	2	330
26	Orchidaceae	*Dendrobium spec. 1*		Orchid	1	10
27	Orchidaceae	*Dendrobium spec. 2*		Orchid	2	1
28	Orchidaceae	*Dendrobium spec. 3*		Orchid	2	1
29	Apocynaceae	*Dischidia imbricata*	(.Blume) Steud	Other	1,3	23
30	Polypodiaceae	*Drynaria quercifolia*	(L.) J. Sm.	Fern	1,2,3	177
31	Orchidaceae	*Eria spec.*		Orchid	2	1
32	Moraceae	*Ficus deltoidea*	Jack	Other	2	2
33	Moraceae	*Ficus spec. 1*		Other	1	2
34	Moraceae	*Ficus spec. 2*		Other	1	2
35	Moraceae	*Ficus spec. 4*		Other	1	1
36	Moraceae	*Ficus spec. 5*		Other	2	2
37	Pandanaceae	*Freycinetia* cf. *sumatrana*	Hemsl.	Other	1	1
38	Polypodiaceae	*Goniophlebium verrucosum*	J.Sm.	Other	1,2,4	165
39	Orchidaceae	*Grammatophyllum speciosum*	Blume	Orchid	1	5
40	Apocynaceae	*Hoya* cf. *revoluta*	Wight	Other	1	13

No.	Family	Species	Author	Group	System	Indiv.
41	Davalliaceae	*Humata heterophylla*	(Sm.) Desv.	Fern	2	1
42	Davalliaceae	*Humata repens*	(L. f.) J. Small	Fern	2	2
43	Lycopodiaceae	*Huperzia* cf. *carinata*	(Desv. ex Poir.) Trevis.	Fern	1	6
44	Lycopodiaceae	*Huperzia phlegmarioides*	Rothm.	Fern	1	1
45	Lycopodiaceae	*Huperzia spec.*		Fern	2	60
46	Rubiaceae	*Hydnophytum* cf. *formicarum*	Jack	Other	1	2
47	Orchidaceae	*Liparis spec.*		Orchid	2	1
48	Orchidaceae	*Luisia spec.*		Orchid	1	4
49	Melastomataceae	Melastomataceae *spec. 1*		Other	1	6
50	Melastomataceae	Melastomataceae *spec. 2*		Other	1	1
51	Melastomataceae	Melastomataceae *spec. 3*		Other	1	2
52	Melastomataceae	Melastomataceae *spec. 4*		Other	1	2
53	Melastomataceae	Melastomataceae *spec. 5*		Other	2	1
54	Melastomataceae	Melastomataceae *spec. 6*		Other	2	1
55	Polypodiaceae	*Microsorum punctatum*	(L.) Copel.	Fern	2	30
56	Vittariaceae	*Monogramma spec.*		Fern	2	12
57	Polypodiaceae	*Myrmecophila sinuosa*	(Hook.) T. Nakai	Fern	3	12
58	Nephrolepidaceae	*Nephrolepis acutifolia*	(Desv.) Christ	Fern	1,2,4	703
60	Orchidaceae	Orchidaceae *spec. 4*		Orchid	1	1
61	Orchidaceae	Orchidaceae *spec. 8*		Orchid	1	1
62	Orchidaceae	Orchidaceae *spec. 9*		Orchid	2	1
59	Orchidaceae	Orchidaceae *spec. 10*		Orchid	2	1
63	Piperaceae	*Peperomia spec.*		Other	1	2
64	Orchidaceae	*Phalaenopsis cornu-cervi*	(Breda) Blume & Rchb.f.	Orchid	1	64
65	Araceae	*Philodendron spec.*		Other	1	1
66	Polypodiaceae	*Phymatosorus scolopendria*	(Burm. f.) Pic. Serm.	Fern	2	5
67	Polypodiaceae	*Platycerium coronarium*	(Mull.) Desv.	Fern	2,3	11
68	Polypodiaceae	*Polypodiaceae spec.*		Fern	2	1
69	Orchidaceae	*Pomatocalpa diffusum*	Breda	Orchid	2	16
70	Orchidaceae	*Pomatocalpa spec.*		Orchid	2	2
71	Orchidaceae	*Pteroceras spec.*		Orchid	1	1
72	Polypodiaceae	*Pyrrosia angustata*	(Sw.) Ching	Fern	1,2	21
73	Polypodiaceae	*Pyrrosia* cf. *lingua*	(Thunb.) Farw.	Fern	3	2
74	Polypodiaceae	*Pyrrosia* cf. *longifolia*	(Burm. f.) C.V. Morton	Fern	2,3	7
75	Polypodiaceae	*Pyrrosia lanceolata*	(L.) Farw.	Fern	2	4
76	Polypodiaceae	*Pyrrosia piloselloides*	(L.) M.G. Price	Fern	1,2,3	93
77	Blechnaceae	*Stenochlaena palustris*	(Burm. f.) Bedd.	Fern	4	41
78	Orchidaceae	*Thelasis spec.*		Orchid	2	1
79	Orchidaceae	*Trichotosia cf. ferox*	Blume	Orchid	1	1
80	Vittariaceae	*Vittaria elongata*	Sw.	Fern	1,2,3,4	177
81	Vittariaceae	*Vittaria ensiformis*	Sw.	Fern	1,2,4	337

Appendix 2: List of investigated phorophytes in jungle rubber

Plot	Phorophyte species	Familie	Height (m)	Canopy start (m)	Basal area (m²)	Canopy length (m)	Bark roughness	Longitude	Latitude
J1	*Macaranga cf sumatrana*	Euphorbiaceae	23.3	8.7	0.175866	14.6	smooth	102.85138	-2.143024
J2	*Prunus arborea*	Rosaceae	27.5	10	0.235422	17.5	medium	102.75368	-2.016026
J3	*Durio ziberthinus*	Malvaceae	34	20	0.687836	14	medium	102.75291	-2.015719
J4	*Endospermum diademum*	Euphorbiaceae	21	11.8	0.079577	9.2	smooth	102.8008	-2.063084
J5	*Alstonia angustifolia*	Apocynaceae	18	8	0.047181	10	smooth	102.80044	-2.064144
J6	*Macaranga hosei*	Euphorbiaceae	19	10	0.064458	9	smooth	102.79986	-2.062524
J7	*Myristica sp. I*	Myristicaceae	24.9	14.5	0.118443	10.4	medium	102.85116	-2.144847
J8	*Rubiaceae sp. I*	Rubiaceae	23.4	10	0.261157	13.4	medium	102.85296	-2.145676
J9	*Endospermum diadenum*	Euphorbiaceae	19	11.3	0.091108	7.7	smooth	102.80048	-2.063628
J10	*Koompassia malaccensis*	Fabaceae	20.6	12.9	0.082792	7.7	medium	102.85167	-2.143965
J11	*Neolitsea cf javanica*	Lauraceae	20.8	10	0.371277	10.8	heavy	102.77388	-2.030513
J12	*Durio ziberthinus*	Malvaceae	21	10	0.105241	11	medium	102.77082	-2.029654
J13	*Callerya atropurpurea*	Fabaceae	25	12.5	0.138656	12.5	smooth	102.77317	-2.031196
J14	*Macaranga cf conifera*	Euphorbiaceae	21	10.3	0.347706	10.7	smooth	102.8503	-2.146706
J15	*Parkia speciosa*	Fabaceae	23.3	13.4	0.17667	9.9	smooth	102.85153	-2.146601
J16	*Artocarpus elasticus*	Moraceae	26	14.3	1.072704	11.7	medium	102.75125	-2.015146
J17	unidentified tree species	unidentified tree species	24.2	16	0.269417	8.2	smooth	102.75286	-2.015026
J18	*Teisjmanniodendron*	Lamiaceae	17.6	11.9	0.185073	5.7	medium	102.7525	-2.016385
J19	*Terminalia foetidissima*	Combretaceae	26.7	13.7	0.477664	13	medium	102.76578	-2.030625
J20	*Durio ziberthinus*	Malvaceae	27.2	14.3	0.489433	12.9	medium	102.7558	-2.014005
J21	*Dacryodes costata*	Burseraceae	26.6	10	0.521519	16.6	medium	102.75516	-2.013262
J22	*Durio ziberthinus*	Malvaceae	30.8	19	0.58012	11.8	medium	102.75293	-2.010257
J23	*Artocarpus integer*	Moraceae	16.9	4	0.252181	12.9	smooth	102.75419	-2.010423
J24	*Artocarpus sp.*	Moraceae	28.4	16.3	0.281259	12.1	medium	102.76754	-2.030428
J25	*Artocarpus cf elasticus*	Moraceae	27.4	14.2	0.40645	13.2	smooth	102.76889	-2.028619
J26	*Artocarpus anisophyllus*	Moraceae	19.1	5.2	0.424633	13.9	smooth	102.7732	-2.0259
J27	*Prainea limpato*	Moraceae	21.8	4.4	0.593083	17.4	smooth	102.77226	-2.027303
J28	*Dialium indum*	Fabaceae	22.8	6.9	0.149359	15.9	medium	102.76476	-2.035557
J29	*Ixonanthes petiolaris*	Ixonanthaceae	22.5	16.7	0.208843	5.8	smooth	102.7812	-2.094827
J30	*Koompassia malaccensis*	Fabaceae	37	17.1	1.113098	19.9	smooth	102.78184	-2.0938

Appendix 3: List of understory stand structures

Plot	Mean DBH (cm)	Mean height (m)	Basal area (m^2)	No. of tress	Rubber density (%)	Native density (%)
J1	23.07	13.54	1.19	25	48.0	52.0
J2	27.69	15.94	1.35	18	33.3	66.7
J3	16.46	12.78	0.63	26	42.3	57.7
J4	17.66	13.47	0.80	25	40.0	60.0
J5	15.86	12.81	0.86	33	87.9	12.1
J6	18.45	13.66	0.91	28	35.7	64.3
J7	18.31	12.43	0.68	20	85.0	15.0
J8	15.54	12.17	0.84	40	35.0	65.0
J9	17.38	12.92	0.91	33	84.8	15.2
J10	20.36	12.59	1.01	23	52.2	47.8
J11	25.16	12.39	1.23	18	44.4	55.6
J12	20.08	16.3	0.70	18	88.9	11.1
J13	21.83	12.88	0.85	19	42.1	57.9
J14	18.77	13.35	0.80	16	68.8	31.3
J15	18	14.38	0.84	29	86.2	13.8
J16	24.37	14.63	0.76	12	33.3	66.7
J17	23.8	13.03	1.71	24	50.0	50.0
J18	16.63	10.22	0.73	29	69.0	31.0
J19	15.93	11.91	0.40	18	22.2	77.8
J20	18.63	11.77	1.07	32	12.5	87.5
J21	19.21	15	0.92	22	90.9	9.1
J22	33.98	14.87	1.43	8	75.0	25.0
J23	32.37	13.26	2.21	14	71.4	28.6
J24	21.44	16.55	1.05	21	90.5	9.5
J25	19.5	14.16	0.69	16	87.5	12.5
J26	17.71	13.56	0.78	26	38.5	61.5
J27	15.53	11.99	0.37	13	53.8	46.2
J28	20.22	13.63	1.13	29	62.1	37.9
J29	20.2	13.91	0.95	22	72.7	27.3
J30	17.9	13.86	0.71	24	75.0	25.0
Mean	**20.40**	**13.47**	**0.95**	**22.70**	**59.3**	**40.7**

Appendix 4: Results of simple linear regression models between epiphyte diversity and agroforest stand structures

	Species richness			Abundance		
	F	**P**	**R^2**	**F**	**P**	**R^2**
Phorophyte characteristics						
Height	0.48	0.496	-0.018	3.35	0.08	0.075
Basal area	2.42	0.13	0.047	20.16	0.0001	0.0398
Canopy start	0.07	0.79	-0.033	1.94	0.175	0.031
Canopy length	1.67	0.2	0.022	0.66	0.42	-0.012
Understory characteristics						
No. of trees	0.83	0.37	-0.006	1.4	0.24	0.01
Rubber density	1.53	0.23	0.018	2.79	0.11	0.058
Total basal area	0.44	0.51	-0.019	0.47	0.49	-0.019
Basal area rubber	3.59	0.06	0.082	0.06	0.81	-0.033
Basal area natives	0.64	0.43	-0.012	0.94	0.34	-0.001
	Species richness JZ1			Abundance JZ1		
No. of trees	0.18	0.67	-0.029	2.03	0.16	0.034
Rubber density	9.45	0.004	0.227	2.54	0.12	0.05
Total basal area	1.05	0.315	0.001	0.4	0.53	-0.02
Basal area rubber	22.33	>0.0001	0.424	0.05	0.83	-0.034
Basal area natives	4.05	0.054	0.095	0.81	0.38	-0.007

Persönliche Erklärung

Ich versichere, dass ich die Arbeit „Diversity of vascular epiphytes in jungle rubber agroforests and different land-use systems in Sumatra (Indonesia)“ selbständig und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Alle Stellen, die wörtlich oder sinngemäß aus Veröffentlichungen oder anderen Quellen entnommen sind, sind als solche kenntlich gemacht.

(Datum, Unterschrift)