GEORG-AUGUST UNIVERSITÄT GÖTTINGEN

Diversity of vascular epiphytes in lowland rainforest and oil palm plantations in Sumatra (Indonesia)

Diversität vaskulärer Epiphyten im Tieflandregenwald und in Ölpalmenplantagen auf Sumatra (Indonesien)

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

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Contents

1 Abstract

As primary forests have almost completely disappeared from the lowlands of Sumatra, Indonesia, and have been replaced by large scale monoculture plantations, our aim was to assess the consequences of transformation from lowland rainforest into oil palm (*Elaeis guineensis*) plantations for vascular epiphyte diversity by plot-based species inventories. We investigated the epiphyte diversity of the two systems by climbing 30 trees in the primary rainforest of the Bukit Duabelas National Park in Jambi, Sumatra, and by ground based observation of 30 oil palms in surrounding mid-aged oil palm plantations. Additionally we examined, if changes in the epiphyte diversity of the transformation system are linked to changes in the microclimatic conditions by measuring the temperature, the relative humidity and the light intensity. Rank/abundance, species accumulation and species estimation curves were compiled for the two systems. The dissimilarity of forest and oil palm plantation was assessed by calculating the evenness, the alpha and beta diversity as well as running an ordination for all 60 plots. To investigate a possible correlation between species richness and microclimate, simple and multiple linear regression models were performed. An overall number of 1935 individuals of 48 epiphytic species and 18 families were recorded. In the oil palm plantations, we found 1386 individuals of 11 species while the forest plots harboured 549 individuals of 44 species. 7 of the 48 epiphytic species occurred in both systems. The forest species were evenly distributed among the three taxonomic groups of *Orchidaceae*, *Ferns* and *other Angiosperms*. In the oil palm plantation the fern species were extremely dominating (10 fern species, 1 other Angiosperm). Species of the family Orchidaceae were completely lacking in the plantations. Average plot level species richness was not significantly different amongst the two systems. At the landscape level the rank/abundance curve of the forest had a significantly shallower slope than the curve for the oil palm plantation, indicating higher evenness in the forest. The lower dissimilarity value in the plantation hinted at more shared species on the oil palms and therefore at a significantly lower beta diversity. The results of our study showed that the transformation from lowland rainforest to oil palm plantations leads to a considerable loss in epiphyte species richness and to a significant lower evenness and higher similarity in species composition.

Abstract

Da Primärwälder nahezu vollkommen aus den Tiefländern Sumatras verschwunden und durch großflächig angelegte Monokultur-Plantagen ersetzt worden sind, lag unser Ziel darin, die Konsequenzen der Transformation von Tieflandregenwald in Ölpalmenplantagen (*Elaeis guineensis*) für die Diversität vaskulärer Epiphyten im Rahmen einer plotbasierten Inventur zu untersuchen. Wir erforschten die Epiphytendiversität der beiden Systeme durch Beklettern von 30 Bäumen im Primärregenwald des Bukit Duabelas Nationalparks in Jambi, Sumatra und durch Bodenbeobachtung von 30 mittelalten Ölpalmen in den Nationalpark umgebenden Plantagen. Zusätzlich wurde festgestellt, ob Änderungen in der Epiphytendiversität mit Variationen der mikroklimatischen Bedingungen zusammenhängen, indem die Temperatur, die relative

Luftfeuchte und die Lichtintensität gemessen wurden. Rang/Abundanz-, Arten-Akkumulations- und Artenschätzungskurven wurden für die beiden Systeme erstellt. Die Unähnlichkeit von Wald und Ölpalmenplantage wurde durch Berechnung der Evenness, der Alpha- und Beta-Diversität und durch eine Ordination aller 60 Plots untersucht. Um einen möglichen Zusammenhang zwischen Artenreichtum und Mikroklima zu überprüfen, wurden einfache und multiple lineare Regressionsmodelle berechnet. Wir fanden eine Gesamtzahl von 1935 Individuen aus 48 epiphytischen Arten und 18 Familien. In den Ölpalmenplantagen fanden wir 1386 Individuen aus 11 Arten, während der Wald 549 Individuen aus 44 Arten beherbergte. 7 von 48 Arten traten in beiden Systemen auf. Die Wald-Arten waren gleichmäßig verteilt auf die 3 taxonomischen Großgruppen der *Orchidaceae*, der *Farne* und der *übrigen Angiospermen*. Die Ölpalmen wurden erheblich dominiert von den Farnen (10 Farnarten, 1 übrige Angiosperme). Arten aus der Familie der Orchidaceae fehlten gänzlich in den Plantagen. Der durchschnittliche Artenreichtum pro Plot unterschied sich nicht signifikant voneinander. Auf Landschaftsebene wies die Rang/Abundanz Kurve des Waldes einen deutlich flacheren Abfall auf als die extrem steile Kurve der Ölpalmenplantage und deutet somit auf eine höhere Evenness im Wald hin. Der niedrigere Unähnlichkeitswert der Plantage wiederum zeugt von einer Vielzahl gemeinsam auftretender Arten auf den Ölpalmen und somit zu einer signifikant niedrigeren Beta Diversität. Die Ergebnisse unserer Studie zeigten, dass die Transformation von Tieflandregenwald zu Ölpalmenplantagen zu einem erheblichen Verlust des epiphytischen Artenreichtums und zu einer deutlich geringeren Evenness und höheren Ähnlichkeit in der Artenzusammensetzung führen.

2 Introduction

2.1 Context of the thesis

This thesis is part of the project *"Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems in Sumatra, Indonesia (EFForTS)"*, which is a collaborative research project funded by the *Deutsche Forschungsgemeinschaft* (*DFG*). This *Collaborative Research Centre* (*CRC 990*) is organized in close cooperation between the University of Göttingen and the University of Jambi (*UNJA*), the Bogor Agricultural University (*IPB*), the Tadulako University (*UNTAD*) and the Indonesian Institute of Science (*LIPI*).

The CRC 990 program aims at analyzing the ecological, as well as socioeconomic functions of the transformation systems jungle rubber, rubber and oil palm plantation in comparison to the reference system of tropical lowland rainforest. While rubber and oil palm plantations have to be considered as intensively used monocultures, jungle rubber can be seen as an agroforestry system that resembles secondary forests in its structure and in which wild species are tolerated by the farmer (Beukema *et al.* 2007). Numerous project groups of the CRC investigate ecological, economic, social, cultural and political aspects in relation to rainforest transformation, to provide information on how to arrange the intensive agricultural land use with nature conservation. As tropical lowland rainforests are undergoing the strongest decline worldwide (Achard *et al.* 2002), the research takes place in one of the largest regions of tropical lowland rainforest in Southeast Asia, namely the Jambi Province in east Sumatra, Indonesia. Within the Jambi Province two landscapes have been chosen for the research, which provide a nearly natural and untouched forest. On the one hand the *Bukit Duabelas National Park* and on the other hand the *Harapan Rainforest*, which is managed by a group of NGOs. Within each of the two sites, there are four core plots with a dimension of 50 x 50 m each, representing the study area for the reference system of lowland rainforest. Additionally, four villages per landscape were selected to contain the core sites for the transformation systems. In each village, there is one core site each for jungle rubber, rubber plantation and oil palm plantation, which leads to a total of 16 core sites per landscape.

This thesis is part of the CRC 990 *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)*, under the supervision of Prof. Dr. Holger Kreft, principle investigator of the *Biodiversity, Macroecology, and Conservation Biogeography Group* at the University of Göttingen. This subproject aims at investigating the effects of rainforest transformation on plant diversity on taxonomic, phylogenetic, functional and biogeographical levels and at different spatial scales (alpha, beta, gamma diversity). The present work examines the diversity patterns of vascular epiphytes in tropical lowland rainforest in comparison to oil palm plantations. Data collection in Sumatra happened in cooperation with Tim Böhnert, former Bachelor's student of the Eberswalde University of Applied Sciences, who additionally investigated the transformation system rubber plantation (Böhnert 2013).

2.2 Threats to tropical rainforests in Southeast Asia

The tropics are in terms of surface area the largest climate and vegetation zone of the world. The three greater tropical humid regions are the northern South America and Amazonia, the western Central Africa (Congo Basin and coastal areas) and Southeast Asia (southern India, Malaysia and Malay archipelago, New Guinea, northern tip of Australia) (Bresinsky *et al.* 2008). As the most biologically diverse terrestrial ecosystem of the world (MA 2005), tropical primary forests harbour a major part of the global biological diversity (MacKinnon 1997) including an estimated 80 % of all terrestrial species (Carnus *et al.* 2006). Even though tropical forests are home to countless endangered species and function as enormous carbon sinks, storing around 46 % of the world's living terrestrial carbon (Soepadmo 1993), they are at the same time the most threatened forests worldwide (Laurance 2007, Sodhi *et al.* 2004). Especially Southeast Asia's tropical lowland forests, which represent the largest extent amongst all forest ecosystems of the eastern tropics (Whitmore 1998), are experiencing high and acute rates of forest loss (Curran *et al.* 2004, Hansen *et al.* 2009).

Indonesian forests represent 2.3 % of global forest cover (FAO 2010) and account for 39 % of Southeast Asian forest extent (Achard *et al.* 2002). In the context of high economic and population pressure, Indonesia is undergoing the world's second highest deforestation rate, right after Brazil (FAO 2001), with annual emission rates of 502 million t CO_2 equivalent (MoF 2008).The fact that 25 % of total net carbon emissions result from ongoing deforestation and forest degradation (Skutsch *et al.* 2007) shows the paradox approach of destroying tropical forests to transform them into crops for carbon-neutral fuels.

Over the past few decades, the oil palm (*Elaeis guineensis*) has become the most rapidly expanding equatorial crop worldwide (Clay 2004, Koh & Wilcove 2007). As the global demand for palm oil, processed in products like food additives, cosmetics and biodiesel (Corley & Tinker 2003, Clay 2004), increases, it leads to a rapid agricultural expansion of plantations in the major oil palm producing countries (Koh 2007). Because oil palm gives high vegetable oil yields relatively cheaply (Carter *et al.* 2007, Corley 2009), in recent years oil palm plantations have replaced large areas of forest in Southeast Asia, which represent 11% of the world's remaining tropical forests (Koh & Wilcove 2007). Additionally the request for convenient infrastructure has increased at the cost of the forest sites to move palm oil from the plantations to their market destinations (Butler *et al.* 2009). Nature conservation is complicated, due to the fact that the oil palm industry is highly profitable, while funds for conserving Southeast Asia's lowland forests are lacking (Fritzherbert *et al.* 2008, Curran *et al.* 2004, Venter *et al.* 2009). Additionally, the establishment of plantations has been simplified for oil palm companies, due to corruption and the increasing regional autonomy (Laurance 2007). Because of their suitable climate and the rich soils allowing for year-round harvesting, Malaysia and Indonesia are two of the most cost-efficient countries in the world for oil palm agriculture (Casson 1999). As a matter of course, these two countries currently lead the world in oil palm production, accounting for almost 50% of global oil palm cultivated area. Unfortunately Malaysia and Indonesia are located within two of the world's 34 biodiversity hotspots, which contain extraordinarily high concentrations of endemic species and are undergoing widespread deforestation (Koh 2008).

The overall impacts of converting forests into oil palm plantations on biodiversity are negative, leading to a frequently lower biodiversity in disturbed forests and plantations (Fritzherbert *et al.* 2008, Danielsen & Beukema 2009). This is indicated by a significant decrease of the species richness (total number of occurring species) and changes in species composition. Hence, plantations are mostly lacking of forest specialists, which are of a high conservation concern, while generalists, which are of a quite low conservation concern, are dominating (Danielsen & Heegaard 1995, Fritzherbert *et al.* 2008). The main reason for this difference is the lower complexity of the ecosystem oil palm plantation. Plantations normally have a uniform tree age structure, a lower canopy, almost no undergrowth and a less stable microclimate. A clearing and a replanting on a 25-30 year rotation (Corley & Tinker 2003) indicates the high human disturbance in oil palm plantations (Danielsen & Heegaard 1995, Fritzherbert *et al.* 2008). Major components of the forest vegetation, like forest trees, lianas and epiphytic orchids are completely lacking in the monoculture plantations (Danielsen & Beukema 2009).

The natural lowland rainforest in Sumatra has been cleared and turned into large scale monoculture plantations of rubber (*Hevea* brasiliensis) and oil palm (*Elaeis* guineensis) since the early 20th century (Beukema *et al.* 2007). In 1985 Sumatra was covered by 25 million ha of natural forest, spreading across 58 % of the island (Fig. 1). Just 23 years later, already half of the forest (i.e. 12.5 million ha) had been cut down with an annual deforestation rate of 2.1 %, resulting in a decrease of natural forest cover to 29 % of the island. In the study site in the Jambi Province the deforestation of lowland forest, followed by expansion of plantations, led to a total forest loss of 53 % since 1985 (Uryu *et al.* 2010) and most of today's remaining lowland rainforest fragments of Sumatra are mainly located in national parks (Gaveau *et al.* 2009; Laumonier *et al.* 2010). Even though these areas are highly protected, illegal logging and oil palm development within these protected sites has been reported frequently (Clay 2004, Buckland 2005)

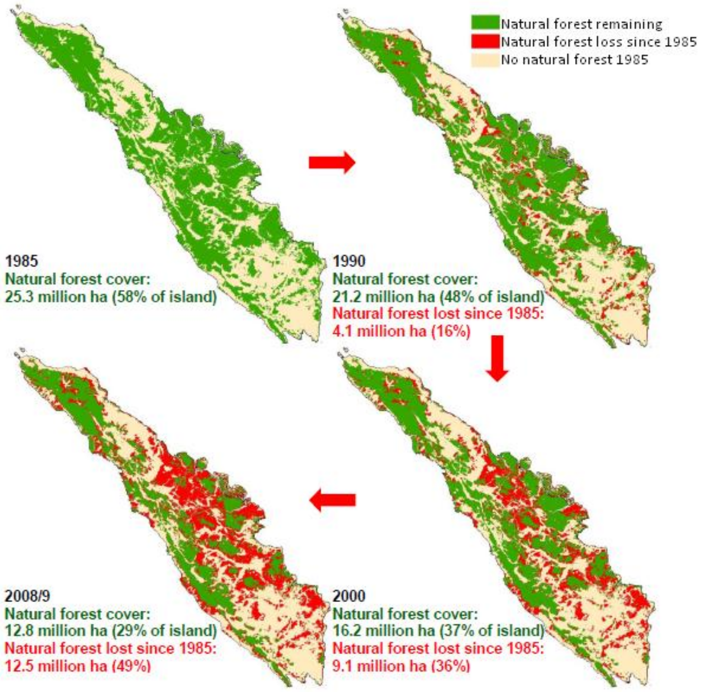

Figure 1: Loss of natural forest in Sumatra. Natural forest in Sumatra in 1985, 1990, 2000 and 2008/2009 (green) and lost since 1985 (red). Taken from Uryu *et al.* 2010 (p. 15, map 4).

2.3 The role of epiphytes in rainforest ecosystems

Vascular epiphytes are plants, which grow non-parasitically on other plants, mainly on other trees (Benzing 1990). Ontogenetically, there are two types of epiphytes, namely *holoepiphytes* (true epiphytes) and *hemiepiphytes*. While holoepiphytes germinate and grow on their host plant (*phorophyte*) throughout their whole life cycle, hemiepiphytes just spend a part of their life on other plants. Hemiepiphytes are subdivided into *primary* and *secondary hemiepiphytes* depending on their site of germination. Primary hemiepiphytes begin their life cycle germinating on other plants and developing roots afterwards, which allow contact to the ground. On the contrary, secondary hemiepiphytes germinate on the ground, climb up afterwards and loose contact to the ground finally (e.g. species of the genus *Ficus*) (Zotz 2013a). Following Zotz (2013b), primary hemiepiphytes were included in and secondary hemiepiphytes were excluded of this work, as the latter do not share the early ontogenetic phases of epiphytic germination and seedling establishment with true epiphytes. Additionally, accidental epiphytes, which occurred highly abundant in the oil palm plantations, were excluded, because they just grew epiphytically in the dead leaf axils of the palms without necessarily completing their life cycle there (Zotz 2013b). As the present work deals with vascular epiphytes, all non-vascular plants like lichens, liverworts and mosses were also excluded.

Occurring from the understory of the forest to the outer tree canopy, epiphytes have to deal with a wide range of abiotic restrictions, among others water and nutrient shortage. The most limiting factor for the growth of vascular epiphytes is the irregular availability of water (Zotz & Hietz 2001). Adaptations against the resulting water stress in rainless periods can be a minimized water loss through poikilohydry, leaf, stem and root succulence (Ng & Hew 2000), shootlessness (Benzing *et al.* 1983)or drought-deciduousness (Benzing 1990). As a consequence of the lacking root contact to the soil, epiphytes have to compensate the nutrient deficiency by absorbing nutrients out of dust and mist (Benzing 1990). Also imported mineral and organic material by associated animals, for instance ants living in the epiphyte leaves, can be used to derive nutrients (Stuntz *et al.* 2002, Davidson & Epstein 1989, Treseder *et al.* 1995). Slightest variations in the microclimatic conditions can have negative affects on epiphytic diversity (Hietz *et al.* 2006) and lead to a high rate of species loss (Sala *et al.* 2000). Due to their enormous sensitivity to changes in the environment (Benzing 1990), epiphytes can be used in diversity research as ecological indicators, to investigate the effects of deforestation and replacement of primary forest by secondary vegetation or plantations (Hietz *et al.* 2006).

The tremendous diversity of epiphytes is the key feature of humid tropical forests and differentiates them from most temperate forests (Gradstein *et al.* 2003). Epiphytes represent about 10% of all plant species globally (Nieder & Barthlott 2011) and are therefore an extremely important part of the flora. As they are responsible for much of the biotic diversity, they make humid tropical forests the most complex terrestrial ecosystems of the world (Gentry & Dodson 1987). According to Zotz (2013b), there are in fact 27,614 species of vascular epiphytes (incl. primary hemiepiphytes) representing 913 genera in 73 families. One of the most important epiphytic plant groups are the orchids. With almost 19,000 epiphytic species in 543 genera, 68 % of all epiphytes are orchids and within the family Orchidaceae, 69 % of all species are epiphytes (Zotz 2013b). Besides being important components of tropical forests, epiphytes play also important roles in ecosystem processes like water and nutrient cycling (Benzing 1990). As an indirect positive effect on the forest diversity, epiphytes provide ressources for tree dependent fauna. They provide food and habitat for numerous vertebrates and offer shelter to a large number of invertebrates and microorganisms (Remsen & Parker 1984, Nadkarni & Matelson 1989, Stuntz *et al.* 2002).

Looking at the global distribution of epiphytes throughout the tropics, it can be noticed that the majority of epiphytic species occurs in the neotropical zones (Gentry & Dodson 1987). One reason for the higher epiphytic species richness in the neotropics might be the absence of the highly abundant family of Bromeliaceae in Africa and Southeast Asia (Givnish *et al.* 2011). Within the context of this unequally distributed diversity pattern of epipyhtic species, it becomes apparent that most of current research projects deal with the epiphyte diversity of the neotropics (e.g. (Freiberg 1996, Barthlott *et al.* 2001, Nieder & Barthlott 2001, Kreft *et al.* 2004, Köster *et al.* 2009, 2011). In fact there are only a handful research projects and publications dealing with the vascular epiphyte diversity of Southeast Asia (e.g. Beukema *et al.* 2007, Mojiol *et al.* 2009, Zhang *et al.* 2010).

2.4 Aim of the study

Humid tropical forests are the most biodiverse terrestrial ecosystems of the world. At the same time, the climatic conditions in the tropics are ideal for cultivating oil palms. As monoculture plantations are expanding and repressing the last primary forest fragments in the tropics in general and in Indonesia in particular, biodiversity is extremely threatened. This leads to a conflict between conservation issues on the one side and greed for profit on the other side. Vascular epiphytes play a key role in humid tropical forests, and due to their sensitivity to changes in the environment, epiphytes are optimal ecological indicators to investigate the effects of deforestation. As relatively little research to that subject has been carried out in the rainforests of Southeast Asia, this scientific work is the first project in Sumatra, Indonesia, investigating the effects of transformation from tropical lowland rainforest into oil palm plantations for vascular epiphyte diversity by plot-based species inventory.

Because epiphytic diversity has been found to be higher in primary forest than in disturbed areas (Hickey 1994, Hietz 1998, Barthlott *et al.* 2001, Flores-Palacios & Garcia-Franco 2001), we expected vascular epiphyte diversity and species richness to be higher in the undisturbed natural forest plots than in the oil palm plots (H1). As oil palm plantations are structurally less complex habitats with a lack of major components of forest vegetation, we assumed changes in the epiphyte diversity to be linked to changes in the different microclimatic conditions (H2). Associated with the different complexities of the two systems and as shown by previous investigations (Danielsen & Heegaard 1995, Fritzherbert *et al.* 2008), we expected high rates of specialists (e.g. orchids) in the forest sites (H3) and at the same time high rates of generalists and accidental epiphytes in the oil palm plantations (H4).

3 Study Area

Sumatra is an island in the western part of Indonesia. With a surface of 473,606 km², it is the largest island of the country and the sixth largest island of the world. The equator runs midway through Sumatra, which spans over 1,700 km from northwest to southeast direction and has a maximum width of 400 km (Barber *et al.* 2005). The Indian Ocean borders the west, northwest and southwest sites of Sumatra. On the northeastern side the Strait of Malacca separates the island from the Malay Peninsula. In the southeast, Sumatra is separated from Java by the Sunda Strait (Fig. 2, left).

By the period of the early Tertiary, approximately 70 million years ago, Sumatra was formed by the colliding of the Indian and the Asian continental plates. As a result of this geomorphological movement and the associated tectonic pressure, the Barisan Mountains were built up, extending over the whole west side of Sumatra. The impact of the moving plates can be observed until today, being expressed in numerous earthquakes and volcanic eruptions. The mountainous areas of the island are streaked by a range of volcanoes, like the *Lembuh* in Aceh and the *Merapi* in West Sumatra. In contrast to that, the northeastern parts of Sumatra are relatively flat and nearly completely covered by swampy plains and mangrove forests at the coast, while the lowland in the eastern parts of the island is naturally dominated by rainforest (Whitten *et al.* 2000).

Very important for the plantation industry in the east, are the prevalent hydromorphic soils. The region of the study sites, which were situated in the lowlands of the Jambi province, is covered by the yellow podzolic soils. The soils of the mountainous areas are predominated by various forms of red-yellow podzolic soils, associated with altosols or litosols (Whitten *et al.* 2000). The FAO classifies the podzolic soils to the group of the "*Acrisols*", which are tyicially distributed in humid tropical and subtropical regions with an undulating landscape. The natural vegetation type on acrisols is forest (FAO 2006).

Distinctive for the climate in Sumatra are frequent rainfalls throughout the whole year. Transition from wet to dry season is relatively smooth and less abrupt in comparison to Java and eastern Indonesia. Rainfall in Sumatra is highly influenced by the Barisan Mountains, which act as a natural barrier and block rain clouds and humid winds. The result is a high range of annual precipitation, ranging from 6,000 mm per year in areas west of the Barisan Mountains to less than 1,500 mm per year in some areas of the east. Additionally, the rainfall is affected by the northeasterly monsoon between December and March and the southwesterly monsoon, which lasts from May to September, so that the main rainy season occurs between September and December. A second rainy period happens in April, during the transition of northeasterly and southwesterly monsoon (Whitten *et al.* 2000). In the Jambi province annual rainfall is about 3,000 mm per year and there are 7-8 wet months (> 200 mm rainfall/month) per year and no months with less than 100 mm of rainfall. The driest months occur from May to September. The average daytime temperature in Sumatra ranges from 22 °C - 32 °C with greatest daily variations in the drier months (Beukema *et al.* 2007). The differences in temperature are mainly caused by the differences in altitude. There are two main winds in Sumatra, blowing from the north from December to March, and from the south from May to September. In addition to that, strong winds, associated with the monsoon, occur regularly (Whitten *et al.* 2000).

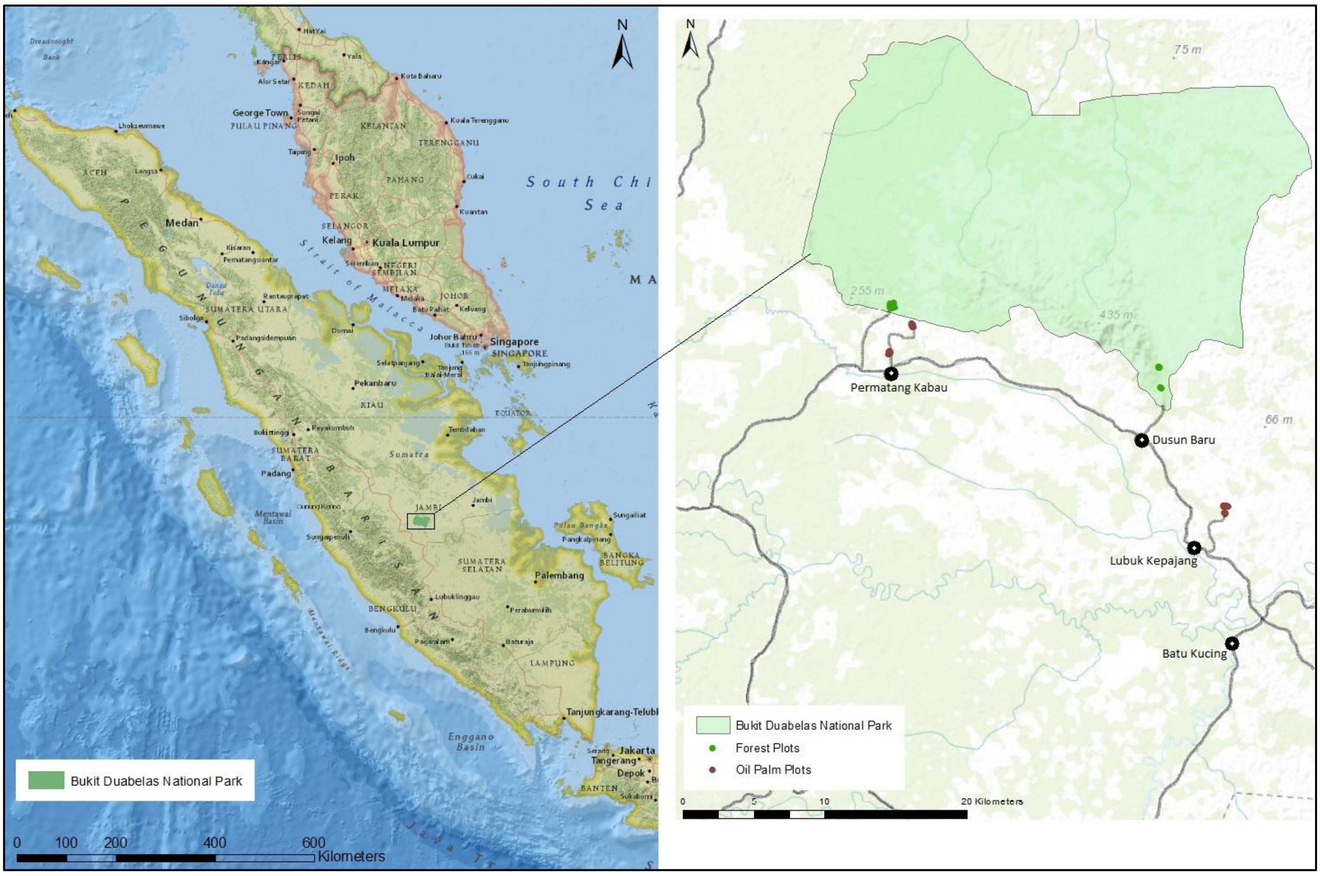

Figure 2: Study area in Sumatra. Left: General map of Sumatra with the east province Jambi and the study area in and around the Bukit Duabelas National Park. At the North Malaysia, in the South the northern tip of Java with the Indonesian capital Jakarta. Right: Detail view of the 30 forest plots (green) in the south of the Bukit Duabelas National Park and the 30 oil palm plots (brown) north of the village Permatang Kabau and east of the village Lubuk Kepajang Source: ESRI, National Geographic; modified by the author

The Jambi province is located in the east of central Sumatra and has a total surface of 50,058.16 km^2. The undisturbed lowland forest in this area has been transformed into rubber plantations since the early 20th century (Beukema *et al.* 2007). Since the late 1960's the oil palm sub-sector has experienced an enormous growth (Casson 1999), so that until now the natural lowand rainforest has almost completely disappeared (Lambert & Collar 2002) and is replaced today by large scale monoculture plantations (Beukema *et al.* 2007). This transformation in Jambi is resulting in a total forest loss of over 1.6 million ha since 1985. Expressed as a percentage, since 1985 Jambi has lost 53 % of its natural lowland rainforest over the short period of 28 years (Uryu *et al.* 2010).

The Bukit Duabelas National Park (Indonesian: "*Taman Nasional Bukit Duabelas*") is located at 102°31'37" – 102°48'27" E and 1°44'35" – 2°03'15" S in the middle of the Jambi province in central Sumatra (see Fig. 2). The relatively small national park, covering 60,500 ha, was established in 2000, and is a representative of a tropical lowland rainforest. The topography of the Park ranges from rather flat (50 m a.s.l.) to slightly hilly with a few higher hills (438 m a.s.l.). The temperature varies from 24 °C – 29 °C with a relative humidity between 71 % - 100 % (Kusuma *et al.* 2011). According to the MoFEC (2012), the last parts of the natural primary lowland rainforest remained in the northern areas of the national park, while the rest must be considered as secondary forest, as a result of previous logging. For many years the indigenous people of the Anak Dalam tribe (*Orang Rimba*) have been living inside the forest area of the national park. The forest provides them all daily needs, i.e. they collect honey, hunt pigs and fish, and tap the sap from rubber trees to sale it in the surrounding villages (MoFEC 2012).

4 Methods

4.1 Study Design

In each of the two investigated systems of primary tropical lowland rainforest and oil palm plantation, 30 host trees for epiphytes (phorophytes) were examined for presence and abundance of vascular epiphytes. As shown in the right map of Fig. 2, 25 of the 30 rainforest trees were investigated in the area of the Bukit Duabelas National Park next to the village Permatang Kabau (01°95'S 102°58' E), the five remaining trees near the village Dusun Baru (02°04'S 102°74' E). 15 of the 30 oil palms were investigated on two plantations around the village Permatang Kabau, the 15 remaining palms were examined on two of the CRC 990 project plots near the village Lubuk Kepajang (02°11'S 102°79'E).

To ensure a random selection of phorophytes in the oil palm plantations, the palms were chosen based on a 50x50 m grid, resulting in a minimum distance of 50 m between all investigated palms. Due to their relatively small size, there was no need in climbing up the palms, but the epiphytes were visible to the unaided eye (*ground-based observation* based on Flores-Palacios & García-Franco 2001) or could be observed by using binoculars (*Nikon Monarch 10x42 DCF*). For the random selection of phorophytes in the study area of the lowland rainforest, additional tree attributes were specified. Due to their enormous size, the forest trees had to be climbed by using single rope climbing techniques (Perry, 1978), especially to reach epiphytes in the upper canopy. To guarantee a sufficient stability and climbability of the phorophyte, only trees with a minimum diameter at breast height (DBH) of 40 cm were chosen. In addition to that, we tried to satisfy a minimum distance of 100 m between all investigated trees. This limit had to be reduced a few times to a minimum distance of 60 m, due to the relatively small size of the investigation area.

For all 60 phorophytes of the two transformation systems the coordinates were marked with a GPS device (*Garmin™ 62s*). In addition to that, the following tree characteristics were documented as well: DBH (trunk circumference at 1.30 m, divided by pi), height, lower beginning of the canopy and bark roughness (smooth, medium, heavy). To measure the tree's height and the beginning of its canopy, a laser-based distance measuring device (*Leica© Disto™ D8*) was used.

To climb the phorophytes, at first a throw bag, weighing 200 g, and an attached 100 m fishing line had to be shot over a thick branch in the canopy by using a 2 m slingshot (*BigShot©*). After releasing the lowered throwback, a 4 mm thick rope was knotted to the fishing line and pulled over the thick branch down to the other side. To the one end of this thicker and more stable rope, the actual 80 m long and 10 mm thick climbing rope was tied and pulled to the other side. One end of the climbing rope was attached to the phorophyte trunk, whilst the other end could be climbed by using ascenders for both hands and the left foot (Fig. 3d).

A complete inventory of all vascular epiphytes (ferns and angiosperms) growing on the 60 sampled phorophytes was taken. For each single epiphytic individual the growth height in the tree, the size and the coverage compared to trunk-/branch-surface were documented.

Figure 3: Field work in the lowland rainforest of Jambi (Sumatra). a) View over the canopy layer of the Bukit Duabelas National Park. b) Tim Böhnert climbs up a phorophyte. c) The author preparing the Big Shot$^{©}$. d) The author attached to the climbing rope with the ascenders. e) Climbing up a phorophyte, using the single rope technique. f) *Asplenium nidus* (Aspleniaceae), diameter 300 cm. g) *Phalaenopsis-cornu-cervi* (Orchidaceae).
Photos: Tim Böhnert (c-e, g), Christian Altenhövel (a, b, f)

Each of the 30 phorophytes in the rainforest was divided into five Johansson-Zones (JZ1-JZ5), while the 30 phorophytes in the oil palm plantations were just divided in three JZ, because of their lack of a real canopy (Fig. 4).

To compensate the difference in size between JZ1 and the larger tree canopy of the rainforest phorophytes, a 20x20m plot was established, surrounding the large host tree. Within this 400 m^2 plot all vascular epiphytes occurring in JZ1 of the remaining trees with a DBH ≥ 10 cm were recorded as well and counted as growing in JZ1 of the examined phorophyte which was standing in the center of the plot (modified after Gradstein 2003 and Rembold 2011). On that account, the terms of *phorophyte* and *plot* will be used synonymously in the following text.

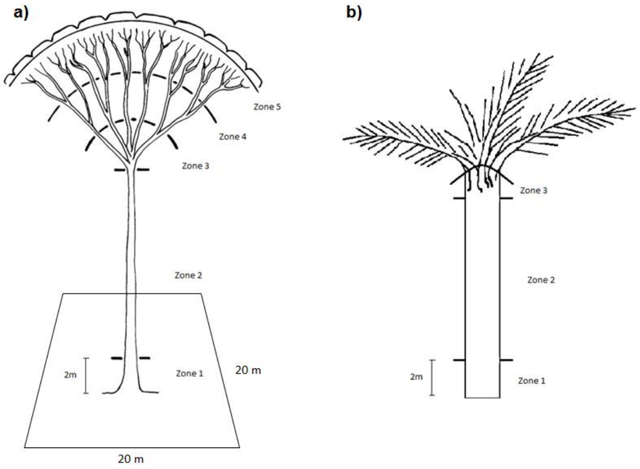

Figure 4: Johansson zones. a) Phorophyte in rainforest divided into five Johansson zones, standing in the center of a 20x20 m plot. b) Oil palm divided into three Johansson zones.

All epiphytes that could not be reached by climbing, especially those in the outermost canopy zones, were observed with binoculars and photo documented with a camera and a telephoto lens (*Pentax ist DL2*, *Tamron AF 18-200 3.5-6.3 XR* and *Nikon D300s*, *AF-S Nikkor 16-85 mm 3.5-5.6 G ED*).

Three herbarium specimens per epiphytic species were collected for a later identification and a long-term retention in the herbariums in Bogor (Herbarium Bogoriense and the Asian Regional Center for Tropical Biology, BIOTROP). Furthermore, close-ups of all collected epiphytic species were taken at the end of each field day by using a tripod, a black cloth as background, a ruler and a close-up lens (*AF-S Micro Nikkor 60 mm 1:2.8 G ED*) in combination with a ring flash. The close-up photos facilitated the plant identification considerably.

While working in the field, the different epiphyte- and tree-species were divided into morphospecies. The final classification took place in the herbariums in Bogor using the following literature: Backer & Backhuizen v. d. Brink 1963: Flora of Java, Vol. I; Backer & Backhuizen v. d. Brink 1963: Flora of Java, Vol. III; Piggott 1988: Ferns of Malaysia in color; Wee 2005: Ferns of the Tropics; Comber 2001: Orchids of Sumatra. The nomenclature of the scientific names of the plants is following: APG (2009) and The Plant List (2010).

The epiphyte sampling in the rainforest took place in the four established CRC plots in the Bukit Duabelas National Park (two plots north of Permatang Kabau and two plots north of Dusun Baru). To reach the defined number of 30 forest trees, we examined a total area in the national park of approximately 50 ha near Permatang Kabau and 10 ha near Dusun Baru. The sampling in the plantation was situated in the four oil palm plantation plots of the CRC 990 next to Lubuk Kepayang. We completed the investigated oil palm plots by additional plots in plantations around Permatang Kabau (Fig. 2 right).

The field work started in the four project plots in the lowland rainforest of the Bukit Duabelas National Park. At first we began the epiphyte sampling in Permatang Kabau from 6 March 2013 until 4 April 2013. After that we moved to the village Batu Kucing and worked in the rainforest plots near Dusun Baru and in the plantations next to Lubuk Kepayang from 5 April 2013 until

14 April 2013. The final species identification of the collected epiphytes lasted from 21 April 2013 until 01 May 2013 and took place in Bogor (see above).

Photos of the field work in the oil palm plantations are shown in Fig. 5.

Figure 5: Oil palm plantations in Jambi (Sumatra). a) Recently grubbed-up area on the way to the investigated oil palm plantations. b) Tim Böhnert in front of one of the 30 examined oil palms. c) Newly planted oil palms (in the foreground) and older oil palm plantation (in the background). d) View into an oil palm plantation near Permatang Kabau.
e) *Cyrtandra spec.* (Gesneriaceae).
Photos: Christian Altenhövel

4.2 Measurement and analysis of the microclimate

To examine the hypothesis that the changes in the epiphyte diversity in the two transformation systems are linked to changes in the microclimatic conditions, we installed data loggers (*iButton®, Hygrochron temp/relative humidity logger, 8 kb storage*) in each JZ of one forest tree (Fig. 6) and one oil palm, recording the parameters temperature and relative humidity.

We attached the loggers in the forest to Phorophyte No. 5 (PF05), standing in the national park area near Permatang Kabau. This tree was one of the few forest trees, where all JZ could be reached by climbing, so that it was possible to install a data logger also in the upper canopy. For the transformation system oil palm plantation we installed three loggers in the JZ of oil palm 19 (OPP19), growing in the project plot BO2 near Lubuk Kepayang. Heights of the forest loggers were: 1.5 m (JZ1), 5 m (JZ2), 23 m (JZ3), 27 m (JZ4) and 32 m (JZ5). The data loggers of the oil palm were attached in the following heights: 0.7 m (JZ1), 2.2 m (JZ2), 3.4 m (JZ3).

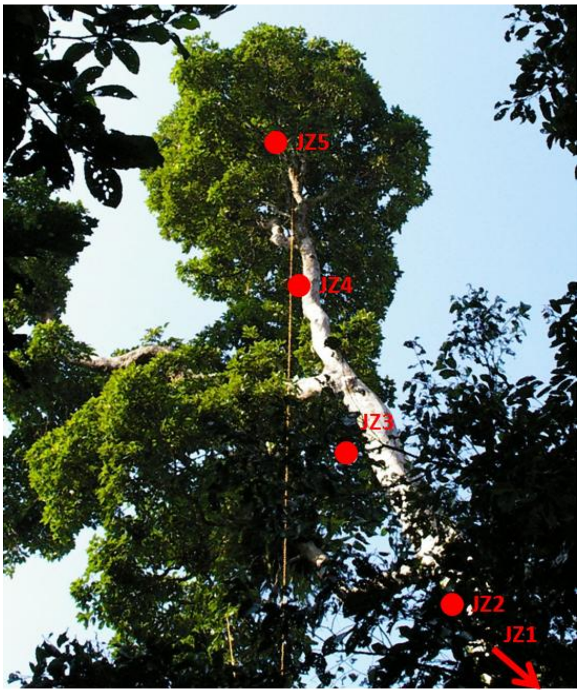

Figure 6: Data loggers in PF05. Position of the data loggers in each Johansson zone (JZ) in forest phorophyte "PF05".

The loggers recorded the actual temperature and relative humidity in intervals of 10 minutes over the period from 15 March 2013 until 4 April 2013 in the forest and from 9 April 2013 until 15 April 2013 in the oil palm plantation. Because of organizational reasons the installation in the plantation happened later and the recording period was a bit shorter. Out of these measurement periods we calculated the average temperature and humidity over the day for every JZ of both trees and plotted the climate values vs. the time of the day.

Additionally, the light intensity in the Johansson zones of the same two phorphytes PF05 and OPP19 was measured with further data loggers (*Li-Co, LI-1400 Datalogger*). In both systems, three measurements per JZ were executed with intervals of 20 seconds between each measurement. To make the light intensities in the trees more informative and to see variances in the different light conditions, we measured reference values simultaneously in a clearing near the investigated tree/palm. While hanging in the forest tree, the three measurements per JZ were made on 13 March 2013 by holding the data logger into sunlight in the following heights: 1.5 m (JZ1), 9 m (JZ2), 22.8 m (JZ3), 26 m (JZ4), 30 m (JZ5). In the oil palm the light intensity was measured on 9 April 2013 in 0.7 m (JZ1), 2.2 m (JZ2) and 3.4 m (JZ3).

To investigate a possible correlation between species richness and microclimate (cf. H2, p. 7), we performed simple and multiple linear regression models with one single or multiple predictor variables. The main goal of a linear regression model is to find the relationship between a dependent variable y and one or more explanatory variables x (Fahrmeir *et al. 2007*). In these models the mean values of temperature, relative humidity and light intensity (explanatory variables x) were involved, as well as the total number of species occurring in each JZ (dependent variable y). The results of the linear regression can be shown in scatterplots together with the corresponding regression line, adjusted r-squared and the p-value, to represent the quality of the linear model. The regression models were performed in the statistical analysis program *R*, version *i386 3.0.2*, using the command *lm= y ~ x*.

4.3 Analysis of epiphyte richness and diversity

To analyze the differences in the epiphytic richness and diversity between the two systems of lowland rainforest and oil palm plantation, numerous descriptive and statistical methods were performed.

For the quantitative description of vascular epiphyte richness, the programs of the *Microsoft Office 2010* package were used. Species lists were organized in *Microsoft Access* and graphically visualized in *Microsoft Excel*. Due to clear analyses and strongly related to Hypotheses H3 and H4, the observed species were divided into three taxonomic groups (cf. Barthlott *et al.* 2001): *Orchidaceae* (Orchids), *Ferns* (Pteridophytes, incl. club mosses) and *other Angiosperms* (flowering plants without the family Orchidaceae).

Statistical analyses were performed with the free software for statistical computing and graphics, *R*, version *i386 3.0.2*.

A very well suited graphical medium to give a quick overview on the distribution of the data, is the Boxplot (*Box-Whisker-Plot*). Boxplots are always consisting of a box and two lines, extending that box and finished by a streak. The bottom and top of the box are showing the first and third quartiles (50% of the data) and the median (band inside the box). The lines extending vertically from the boxes (*whiskers*) indicate variability outside the lower and upper quartiles. Any data not included between the whiskers are plotted as outliers with a circle (Tukey 1977).

To interpret the differences in abundance and species richness of the recorded species in the investigated systems, at first the data had to be tested for normal distribution. This was performed in *R*, using the *Kolmogorov-Smirnov-test* (KS-test). The result of the KS-test showed that the abundance data of forest and oil palm were not normal distributed, so that for further statistical analyses, the non-parametric *Mann Whitney-U-test* had to be applied (Whitley & Ball 2002). Using the package *coin*, version *1.0-23*, in *R*, the variations in epiphyte abundance and species richness per phorophyte between forest and oil palm could be tested for significance (p-value < 0.001 = highly significant, ***; p-value > 0.05 = not significant, n.s.).

A very informative way of giving a first overview of the species abundance distribution in the investigated areas is the method of plotting *rank/abundance plots*, also known as *Whittaker plots* (Whittaker 1965). In these plots the collected species are ranked from most to least abundant on the x axis and their corresponding abundances are displayed on the y axis. Because the abundances in the oil palm plantation differed extremely from those in the forest, the rank/abundance curves could not be visualized clearly when plotting the absolute abundance values. So to make the different abundances of the two systems comparable at first sight, proportional abundances were used in the Whittaker-plot. The abundance of all recorded epiphytic species was designated as 1.0 and the relative abundance of each single species was given as a proportion of the total. The abundances were displayed in a $\log_{10}$ scale on the y axis, so that even species, whose abundances have a high extend, could be easily shown in the same plot (Magurran 2004). On the one hand, these plots give a quick impression of the differences in species composition and on the other hand the shape of the curves is a good indication for the evenness of the investigated systems (Nee *et al.* 1992; Tokeshi 1993). So, very steep plots are expressing communities with a high dominance of one or a few species and shallower slopes are the result of a higher evenness in the community (Magurran 2004). All rank/abundance plots in this work were created in *R*, using the command *unlist* in package *vegan 2.0-9*.

Concerning the epiphyte diversity in this work, we had to distinguish between alpha and beta diversity. While the alpha diversity refers to the diversity within a particular area or ecosystem (*within-habitat diversity)*, the beta diversity provides information about the change in species diversity between these ecosystems (*between-habitat diversity*) and examines the similarity or the dissimilarity in species composition (Whittaker 1972). There are nearly infinite diversity indices (Molinari 1976) to calculate and measure diversity, but we chose the Shannon and the Simpson's index in combination with Pielou's evenness for the examination of the alpha diversity in the two systems. Shannon and Simpson's index both are heterogeneity measures, combining species richness and evenness (Hurlbert 1971). Additionally, the two diversity indices mentioned above are nonparametric indices, because they make no assumption about the underlying species abundance distribution (Magurran 2004). On the contrary, it assumes that the individuals are randomly sampled from an infinite community and that all species are represented in the sample (Pielou 1975). The long-established Shannon index describes the alpha diversity, considering the number of species as well as the abundance (*number of individuals per species*). The Shannon-Index (*H'*) of a population consisting of *N* individuals in *S* different species, of which n_i belong to one species, is

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

Here the quantity p_i is the proportion of individuals found in the *i*th species. The minus sign in the summation is cancelled out by the minus sign in the equation (Shannon & Weaver 1949; Magurran 2004). Values of the Shannon index usually range between 1.5 and 3.5 and seldom rise up to 4 (Margalef 1972). As already mentioned above, the Shannon index takes also the evenness in species abundance into consideration, but it is also possible to calculate a separate evenness measure, represented by Pielou's evenness index:

$$J' = \frac{H'}{H'_{max}} = \frac{H'}{lnS}$$

This index shows that the maximum diversity (H_{max}) can be found when all species have the same number of individuals. The values for Pielou's evenness are ranging between 0 and 1, where 0 is standing for a low and 1 is representing a high evenness (Pielou, 1969). To put it briefly, evenness is a measure for the equability or the inequality of the distribution of the species abundances in a sample.

Another nonparametric index, which is commonly used and very robust, is the Simpson’s Index. This index puts a stronger focus on the abundances of the most common species and is a so called “dominance measure” (Magurran, 2004). This index expresses the probability that two randomly selected individuals of an infinite community belong to the same species. Therefor the probabilities of selecting a species *i* and reselecting that exact species again are multiplied. Afterwards this product will be summed up for all species. The Simpson’s Index *D* is calculated with the formula:

$$D = \qquad p_i^2$$

where p_i represents the proportion of individuals in the *i*th species. For a finite community the formula has to be transformed into:

$$D = \qquad \frac{n_i \; n_i - 1}{N \; N - 1}$$

with n_i standing for the number of individuals in the *i*th species and *N* representing the total number of individuals.

Because of the fact that the scale is counterintuitive, showing a higher diversity, the smaller *D* gets, the Simpson’s Index is most commonly expressed in the form *1 – D* or *1/D*,

$$D1 = 1 - \qquad p_i^2$$

resulting in an increasing *D1* with an increase of diversity. *D1* is 0 when all individuals belong to the same species and it comes closer to 1 the higher the diversity is (Magurran, 2004). All analyses in the context of alpha diversity were performed with the *R*-package *vegan 2.0-9*.

As already mentioned above, the beta diversity provides information about the change in species diversity between different ecosystems (*between-habitat diversity*) and examines the similarity or the dissimilarity in species composition. Therefor typically three variables are combined: *a*, the total number of shared species occurring in both samples; *b*, the number of species only occurring in sample 1; and *c*, the number of species only occurring in sample 2 (Pielou 1984). To describe the beta diversity of pairs of sites, we used the Sørensen Index (Sørensen 1948), also known as the Bray-Curtis dissimilarity, because it is one of the most effective similarity measures (Southwood & Henderson 2000). It is described by the formula:

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

The Bray-Curtis dissimilarity ranges between 0 and 1, where 0 means that the compared sites have all species in common, i.e. they share all species and 1 shows that the sites do not share any species (Bray & Curtis 1957). To calculate the Bray-Curtis dissimilarity within the two systems, we used the *vegdist*-function of the *vegan*-package in *R*. The result was a matrix with the values of the Bray-Curtis dissimilarity for all pairwise beta diversities of the 30 trees per site. For a graphical comparison, all pairwise diversities were visualized by one boxplot for the forest sites and one boxplot for the oil palm plots. With a subsequent analysis of variance (*ANOVA)* the beta diversity between forest and oil palm plots could be tested for a significant difference (p-value < 0.001 = highly significant, ***; p-value > 0.05 = not significant, n.s.).

Another way of showing similarity or dissimilarity of the examined plots is an ordination, which orders objects in a graph, so that similar objects are near each other and dissimilar objects are farther from each other. The ordination is a common method to analyze plant communities in particular (Birks *et al.* 1998). To evaluate the community data of forest and oil palm plantation we chose the ordination with a non-metric multidimensional scaling (*NMDS*). The goal of this NMDS was to place each sampled plot in a two-dimensional space, so that the between-plot distances were preserved as well as possible. Each plot was then assigned coordinates in each of the two dimensions (Borg & Groenen 2005). The result of the ordination was a distance matrix, based on the Bray-Curtis dissimilarity. The information of this distance matrix, i.e. the simmilarity of all sampled plots, could be displayed in a scatterplot, organizing similar plots close to each other and dissimilar plots farther from each other. The NMDS was proceeded in *R*, using the command *meta(MDS)* in the *vegan*-package. By performing function *ordiellipse*, the 95 % confidence ellipses could be plotted around the class centroids of forest and oil palm plantation data points. When the different confidence ellipses do not overlap, the two classes are probably significantly different at level p < 0.05 (Oksanen 2009).

A well suited method to determine, if the number of 30 sampled plots per system was sufficient to deduce the total species richness, is the species accumulation curve. They plot the increasing number of recorded species (*S*) as a function of the sampling effort (*n*) (Colwell & Coddington 1994). In our case *n* is standing for the growing number of sampled plots. With ongoing sampling, new species are added to the inventory and the resulting species accumulation curve is rising. Using the function *specaccum* of the *vegan*-package in *R*, randomizied species accumulation curves can be produced. By adding the sampled plots in a random order to the accumulation curve and repeating this 100 times, the course of the curve can be smoothed. In the resulting plots, the mean value of the 100 permutations is shown as a black line, surrounded by a grey cloud, representing the standard deviation (c.f. Magurran 2004). The course of the species accumulation curve hints to the total species richness. If the curve is rising steadily, still many species can be found with cumulative sampling. If the curve reaches an asymptote, the total species richness is nearly completely revealed.

To provide an estimate of the total richness of an assemblage, which in our case was more important for the forest, the species richness curves can be extrapolated to a fixed number of sites. The extrapolation was proceeded in the statistical estimation software *EstimateS 9.1.0* (Colwell 2013), setting the estimation parameters to a total of 300 sites and 100 random permutations (Colwell *et al.* 2012). The software generates extrapolation curves, based on statistical sampling models, which require an estimator for the extrapolation. For our sample-based incidence data, *EstimateS* uses the estimator *Chao*2:

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

Q_1 is the number of species that occur in one sample only and Q_2 is the number of species that occur in two samples. So for this nonparametric method for the estimation of species richness, only the number of species found in just one sample and the number of species found in exactly two samples have to be known (Colwell & Coddington 1994). The point, where the estimation curve reaches an asymptote, hints to the number of plots, that should have been sampled to capture complete species richness of the two investigated systems.

5 Results

5.1 Abundance, species richness and diversity

In the established 30 plots each in the lowland forest and the oil palm plantations, an overall number of 1935 individuals of 48 epiphytic species and 18 families were recorded. For complete species lists see Appendix 1 (p. 60). Eight species of three families (Clusiaceae, Melastomataceae, Moraceae) were primary hemi-epiphytes whereas the remaining 40 species were listed as holo-epiphytes.

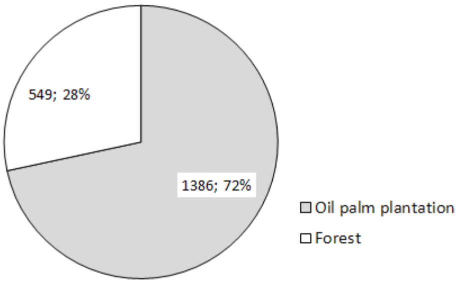

Figure 7: Total number of epiphytic individuals. Absolute and percental distribution of the total of 1935 recorded vascular epiphyte individuals in oil palm plantation and forest.

In the oil palm plantations, we found 1386 individuals of 11 species while the forest plots harboured 549 individuals of 44 species. Figure 7 shows that vascular epiphytes are much more abundant in oil palm plantations than in the forest plots. All in all we found more than twice as many epiphytic individuals on 30 oil palms than on 30 forest trees.

Additionally, a huge number of accidental epiphytes occurred on the oil palm trunks. These accidental species were *Asystasia gangetica*, *Clidemia hirta*, *Elaeis guineensis* and *Hevea brasiliensis*, which were excluded from the statistical analyses, due to the fact, that these species do not belong to the group of true epiphytes. *Asystasia gangetica*, a perennial herb (SEWPaC, 2003) and *Clidemia hirta*, a weak upright shrub (Muniappan, Reddy, & Raman, 2009), are at the same time highly invasive species, particularly in disturbed sites (Tjitrosoedirjo, 2007 and De Poorter, 2007). *Elaeis guineensis* and *Hevea brasiliensis* simply are the introduced and non-indigenous cultivated crops oil palm and rubber. The relatively high abundance of these four species is presented in Table 1.

Table 1: Accidental epiphytes in oil palm plantations. Abundance of the four accidental epiphytic species found on the investigated 30 oil palms.

Species	Family	No. individuals
Asystasia gangetica	Acanthaceae	127
Clidemia hirta	Melastomataceae	187
Elaeis guineensis	Arecaceae	99
Hevea brasiliensis	Euphorbiaceae	7
Total		**420**

The average number of epiphytic individuals and species per phorophyte in the two different systems is shown in Figure 8. The average abundance of epiphytes per tree is significantly higher in the oil palm plantations. With an average number of 46.2 individuals per oil palm and 18.3 individuals per forest tree, the abundance in the plantations is more than twice as high as in the rain forest, even though some outliers with a remarkably higher abundance can be observed in the forest (Fig. 8a). The Mann-Whitney-U-test shows with a p-value less than 0.001 that the two investigated systems differ significantly in their abundances per phorophyte. Looking at the number of epiphytic species per phorophyte (Fig. 8b), it can be said that, with a p-value of 0.28, there is no significant difference between the two systems. In the forest, we found a mean number of 4.9 epiphytic species per tree, while in the plantations on average 5.2 epiphytic species per palm could be found. Here again one outlier of the forest phorophytes is noticeable, carrying a strikingly number of 13 epiphytic species.

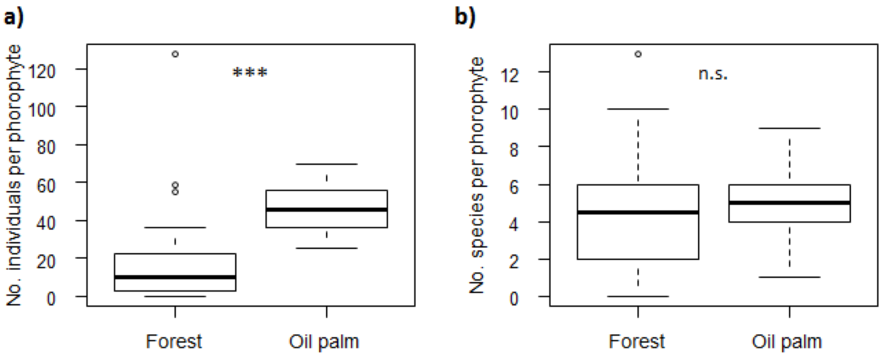

Figure 8: Box-Whisker-Plots. a) Boxplots showing the number of vascular epiphyte individuals per phorophyte in forest and oil palm plantation. The Mann-Whitney-U-test shows a p-value of < 0,001 (***).
b) Number of vascular epiphyte species per phorophyte in forest and oil palm plantation. The Mann-Whitney-U-test shows a p-value of 0.28 (n.s.).

Fig 9a shows that most of the investigated epiphytes on the oil palms occurred in the Johansson zones (JZ) one and two. In these JZ, we found an average number of 24.5, respectively 19.4 individuals per palm. JZ3 shows an essentially lower mean of 2.2 individuals per palm. For the forest trees, it can be seen that there is no such huge range in the number of epiphytic individuals per JZ. The average number of individuals rises from 0.7 in JZ1 to 3 epiphytes in JZ2, 3.6 in JZ3, 5.3 in JZ4 up to 6.3 individuals in JZ5. Comparing the average distribution of individuals across the JZ in forest and oil palm plantation, we find a highly significant difference between the two systems in JZ1 and JZ2 (Mann-Whitney-U-test p-values lower than 0.001). Showing a p-value of 0.14, the average number of epiphytes in JZ3 does not differ significantly.

Looking at the distribution of epiphytic species across the Johansson zones (Fig. 9b), the oil palm boxplots show a similar trend. With average values of 4.2 species in JZ1, 3.3 species in JZ2 and 0.8 in JZ3, the number of epiphytic species in the lower zones is about more than four times higher than in the third JZ.

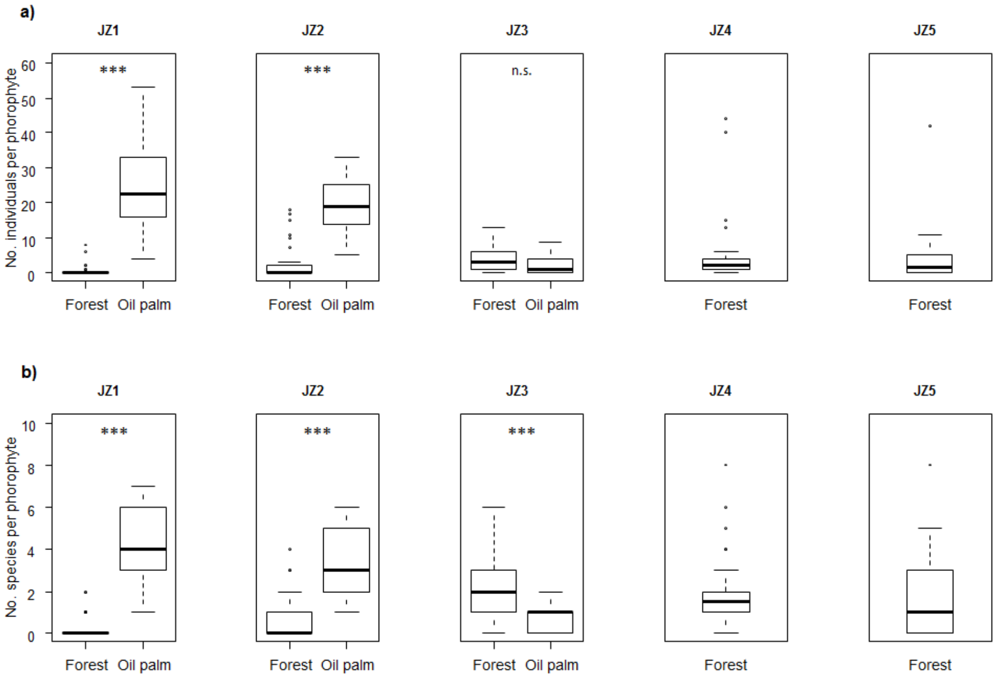

Figure 9: Abundance and number of species per Johansson zone (JZ). Boxplots showing the distribution of vascular epiphyte individuals (a) and species (b) across Johansson zones 1-5 of the investigated 30 forest trees and 30 oil palms. The Mann-Whitney-U-test ranks p-values < 0.001 as highly significant (***) and values > 0.05 as not significant (n.s.). Due to visual clarity, outliers lying outside the scale dimensions are not shown.

The highest number of epiphytic species in the forest can be found in JZ3, JZ4 and JZ5. Here we have a mean of 2, 2.2 and 1.6 species per plot. In contrast to that, in the lower zones averagely only 0.3 and 0.8 epiphytic species per phorophyte could be found. Comparing the two systems, it can be seen that the average number of species differs significantly (p-values lower than 0.001). In JZ1 and JZ2 we have approximately 14 resp. 4 times more species on the oil palms than on the forest trees. In contrast to that, JZ3 of the forest trees shows a two times higher number of species than JZ3 of the oil palms.

To compare the alpha diversity of the two investigated systems, the Shannon- and Simpson-index for all 30 forest trees and 30 oil palms were calculated. Additionally, Pielou's evenness was calculated to show the equitability of the abundances of the recorded epiphytic species within the two systems. For the Shannon-index on plot level, we have in both systems an average value of H' = 1.17 per tree/palm (Fig.10a) and the Simpson-index averages in forest and oil palm plantation at D1 = 0.58 per tree/palm (Fig. 10b). The values for Pielou's evenness differ from J' = 0.85 in the forest plots to 0.72 in the oil palm plots, hinting at a higher evenness in the forest plots (Fig. 10c). On landscape level, the Shannon-index was with H' = 3.02 significantly higher in the forest than in the plantation with H' = 1.63. The values for Pielou's evenness were with J' = 0.8 in the forest and 0.68 in the oil palm plantation equal to the values on plot level.

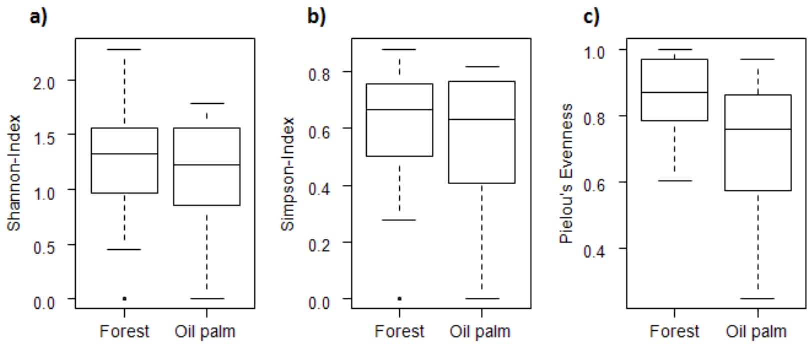

Figure 10: Alpha diversity and evenness. Boxplots showing the Shannon-index (a), Simpson-index (b) and Pielou's evenness (c) for the 30 forest and 30 oil palm plots.

Table 2 is showing the distribution of all recorded epiphytes across their corresponding 18 plant families. A total of 11 species was found in oil palm plantations and on the forest trees 44 epiphytic species occurred. Six of the 18 families could be found in both investigated systems. In addition to that, the families were assembled into the three large groups *Orchidaceae*, *Ferns* and *other Angiosperms*.

Table 2: Recorded epiphytic families. List of all recorded epiphytic families and their number of encountered individuals and species. Shared families are underlined.

Family	**No. individuals**		**No. species**		
	Forest	**Oil palm**	**Forest**	**Oil palm**	**Taxonomic group**
Apocynaceae	35	-	2	-	*other Angiosperms*
Araceae	1	-	1	-	*other Angiosperms*
<u>Aspleniaceae</u>	28	91	2	3	*Ferns*
Blechnaceae	-	41	-	1	*Ferns*
Clusiaceae	1	-	1	-	*other Angiosperms*
<u>Davalliaceae</u>	25	255	2	1	*Ferns*
Gesneriaceae	-	3	-	1	*other Angiosperms*
Lycopodiaceae	7	-	2	-	*Ferns*
Melastomataceae	11	-	4	-	*other Angiosperms*
Moraceae	5	-	3	-	*other Angiosperms*
<u>Oleandraceae</u>	3	677	1	1	*Ferns*
<u>Ophioglossaceae</u>	58	22	1	1	*Ferns*
Orchidaceae	224	-	17	-	*Orchidaceae*
Pandanaceae	1	-	1	-	*other Angiosperms*
Piperaceae	2	-	1	-	*other Angiosperms*
<u>Polypodiaceae</u>	123	161	4	1	*Ferns*
Rubiaceae	2	-	1	-	*other Angiosperms*
<u>Vittariaceae</u>	23	136	1	2	*Ferns*
Total	**549**	**1386**	**44**	**11**	

In Table 3 the seven species are listed that occurred in the forest as well as in the oil palm plantation. All of these shared species belong to the taxonomic group of the ferns. *Asplenium nidus* is the only epiphyte with an equal abundance in both systems. The other ferns are much more abundant on the oil palms, except *Ophioglossum pendulum* which is the only shared epiphyte with a higher number of individuals in the forest than in the plantation. In summary, it can be said that 37 epiphytic species only occurred in the forest, four species exclusively occurred in the oil palm plantation and seven species could be sampled in both of the investigated systems.

Table 3: Shared species of forest and oil palm plantation. List of all epiphytic species and their abundances recorded in both systems, forest as well as oil palm plantation.

Species	**No. individuals**		**Taxonomic group**
	Forest	**Oil palm**	
Asplenium glaucophyllum	1	16	*Ferns*
Asplenium nidus	27	28	*Ferns*
Davallia denticulata	9	255	*Ferns*
Goniophlebium verrucosum	3	161	*Ferns*
Nephrolepis acutifolia	3	677	*Ferns*
Ophioglossum pendulum	58	22	*Ferns*
Vittaria ensiformis	23	94	*Ferns*

Looking at the abundance in total (Fig. 11a), the ferns represent the largest group with around 85 % of the epiphytic individuals. Around 10 % of all recorded individuals belong to the group of the Orchidaceae and the remaining 5 % are numbered among the other Angiosperms. Members of all three groups could be found in the forest. The two dominating groups in this system are with around 50 % of all encountered individuals the ferns and with 40 % the Orchidaceae. The other Angiosperms form the smallest group with the remaining 10 %. In comparison to that, only two groups are represented in the oil palm plantation, where the ferns are the remarkably dominating plant group with 99 % of all epiphytic individuals. In fact, only three plants did not belong to the ferns, namely individuals of the species *Cyrtandra spec.* (cf. Fig. 5e).

Having a look at Fig. 11b, it can be seen that the forest species are evenly distributed among the three taxonomic groups. Almost 40 % of the species are Orchidaceae, 31 % other Angiosperms and the remaining 29 % belong to the ferns. In the oil palm plantation it is found that the fern species are extremely dominating. As mentioned above, the only occurring non-fern species is *Cytrandra spec*. Species of the family Orchidaceae are completely lacking in the plantations.

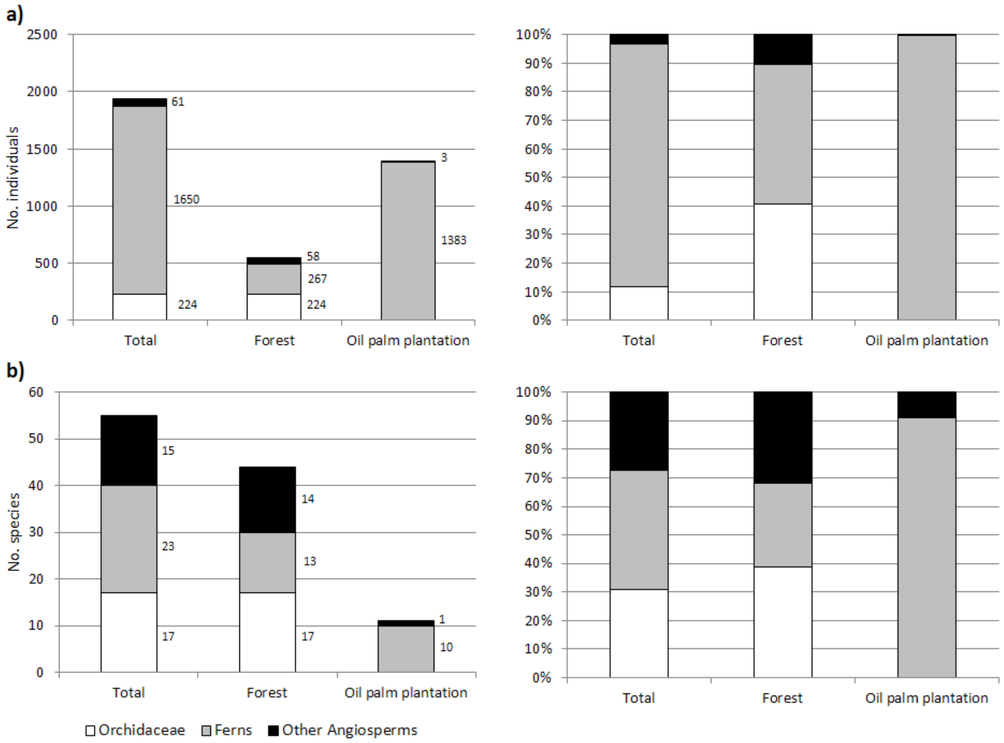

Figure 11: Abundance and species richness. Absolute and percental distribution of vascular epiphyte individuals (a) and species (b) among the taxonomic groups Orchidaceae, Ferns and other Angiosperms.

To visualize the species richness and the species evenness of forest and oil palm plantation, the species are plotted in order from most (rank 1) to least abundant along the x axis in the rank/abundance plots in Figure 12. The corresponding abundances are displayed in absolute values on the y axis.

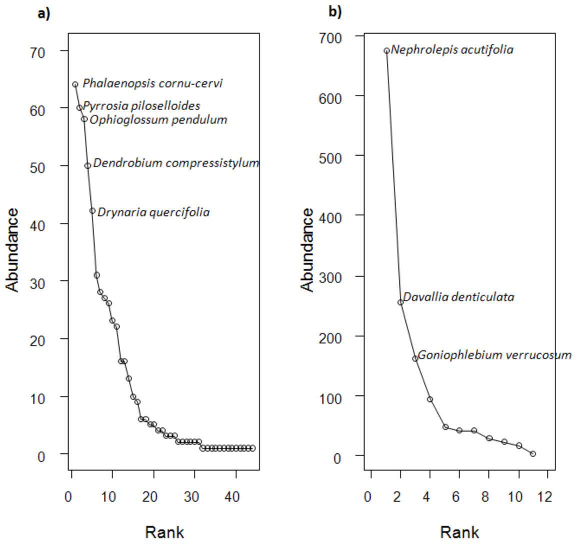

Figure 12: Rank/abundance plots. Species rank (x axis) plotted against its abundance (y axis) for the 44 recorded forest (a) and the 11 recorded epiphytic oil palm species (b). The most abundant species are labeled.

At first glance, it can be seen again that the forest has got much more epiphytic species than the oil palm plantation. In addition to that it can be noticed that the distribution of the abundances of the 44 forest species are much more even than the abundances of the 11 oil palm species. In the forest there is a homogeneous mixture of highly and less abundant species as well as several species represented by single individuals (“singletons”). In contrast to that the oil palm plantation presents a few highly dominant species, e.g. *Nephrolepis acutifolia*, while most of the other species show a relatively low abundance.

To make the different abundances of the two systems more comparable, proportional abundances were used in the rank/abundance plot in Fig. 13. Additionally, to involve the above mentioned taxonomic groups Orchidaceae, Ferns and other Angiosperms, the corresponding symbols got colored. Here too, the x axis ranks each species from most to least abundant, but in difference to Fig. 12, the abundances on the y axis are not displayed in absolute values, but on a $\log_{10}$ scale. The abundance of all 48 epiphytic species, i.e. 1935 individuals, was designated as 1.0 and the relative abundance of each single species is given as a proportion of the total. The shape of the curves is an indication for the evenness of the systems. It can be observed that the plantation plot is much steeper than the forest curve, standing for an epiphyte community with a high dominance of a few highly abundant species. In contrast to that the shallower slope of the forest plot hints to a higher evenness within this system. Within the oil palms, the ferns (green) are the representative group, while in the forest, members of all three taxonomic groups can be found, ranging homogeneously from high to low abundances. Having a look at the three most abundant species in the plantation, it can be said that they also occurred with comparatively low rates in the forest.

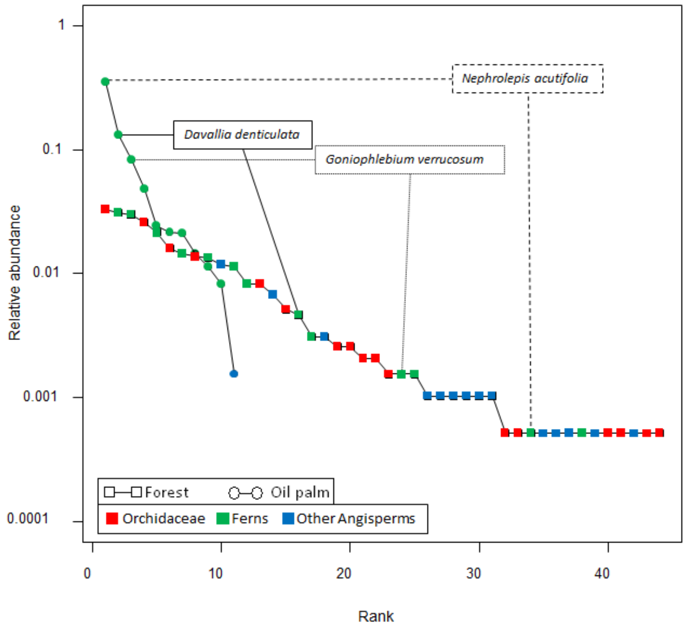

Figure 13: Whittaker plot. The squares show the rank/abundance curve of the forest, the dots the oil palm plantation curve. The y axis ($\log_{10}$ scale) shows the relative abundance of the species while the x axis ranks each species from most to least abundant. The abundance of all 48 collected species is designated as 1.0 and the relative abundance of each single species is given as a proportion of the total. Three of the seven common species in forest and oil palm plantation are labeled. The three taxonomic groups Orchidaceae, Ferns and other Angiosperms are marked in the colours red, green and blue.

To evaluate the difference in the beta-diversity between all 30 plots within each of the two systems, we computed the Bray-Curtis dissimilarity for all possible pairwise plot combinations. The result of the distance matrix is plotted in form of a boxplot in Fig. 14a. The mean value for the Bray-Curtis dissimilarity in the forest is 0.88, while the value in the plantation averages around 0.44. This shows that the species composition in the forest is more various than in the oil palm plantation. Noticeable is the outlier in the forest boxplot with a dissimilarity of 0. This point refers to two trees harboring the exact same species (*Asplenium* nidus). It is clear that the value for the Bray-Curtis dissimilarity has to be 0 in that case, because the two trees share the identical species.

The lower dissimilarity value in the plantation hints to the fact, that the oil palms share more species, while the forest trees do not have that many species in common. The Analysis of Variance (ANOVA) p-value (< 0.001) shows a statistical significant difference between the beta diversity of forest and oil palm plots.

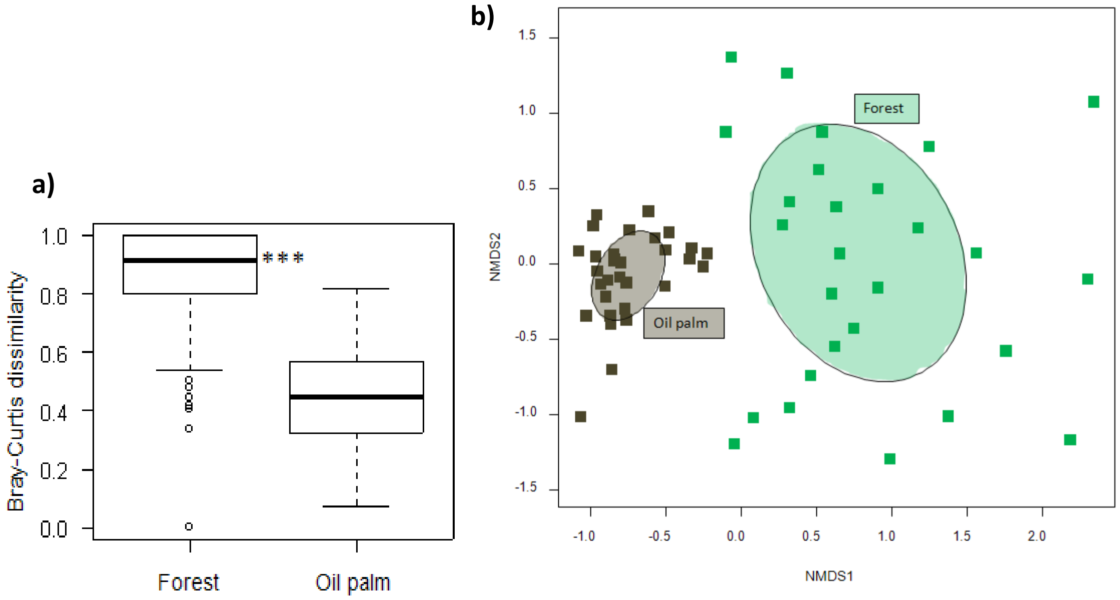

Figure 14: Beta diversity and non-metric multidimensional scaling (NMDS) ordination. a) Boxplots showing the values of the Bray-Curtis dissimilarity for all pairwise combinations of the 30 forest and 30 oil palm plots, p-value of analysis of variance (ANOVA) < 0.001 (***) b) Ordination (two dimensions and 100 random starts in search of stable solution) showing the Bray-Curtis dissimilarity for the oil palm (brown squares) and the forest plots (green squares). Additionally the 95 % confidence ellipses around the class centroids are shown in the corresponding color. The Stress-value of ordination: 0.14.

Another indication for this fact is the ordination in Fig. 14b. It shows that the two groups differ enormously. First it can be noticed that the two groups of points are quite isolated. The oil palm plots stick together in the left side of the plot and the forest plots are widely spread throughout the whole right side of the ordination. In addition to that the oil palm plots are relatively close together, which shows that they do not vary much in their species composition. As already mentioned above, the oil palms share a lot of species, which means that on every single oil palm there are almost represented the same species. In contrast to that, it can be observed that there are relatively high distances between the single forest plots. This shows that there is a high variability in the species composition, i.e. the forest plots do not have a lot of species in common and on almost every single tree there are represented different species.

5.2 Species accumulation curves and species richness estimators

The species accumulation curves in Fig. 15 show the rate at which new species were found in the course of the sampling. The x axis shows the number of sampled sites and the y axis represents the number of recorded species. The plot illustrates the mean and the standard deviation of the two systems' species richness. It can be seen that the two curves differ extremely in their trend. The accumulation curve of the forest is growing with each added sample site, showing that new species are added to the inventory with every new plot. In addition to that a saturation of the curve is just slightly indicated at the end of the plot, i.e. after 30 sampled sites. On the contrary the accumulation curve of the oil palm plantation is characterized by a relatively flat course, reaching saturation after 6-8 sampled sites. This shows that already after the first 6–8 oil palms all 11 epiphytic plantation species have been found and these species just repeated on the other investigated 22-24 oil palms.

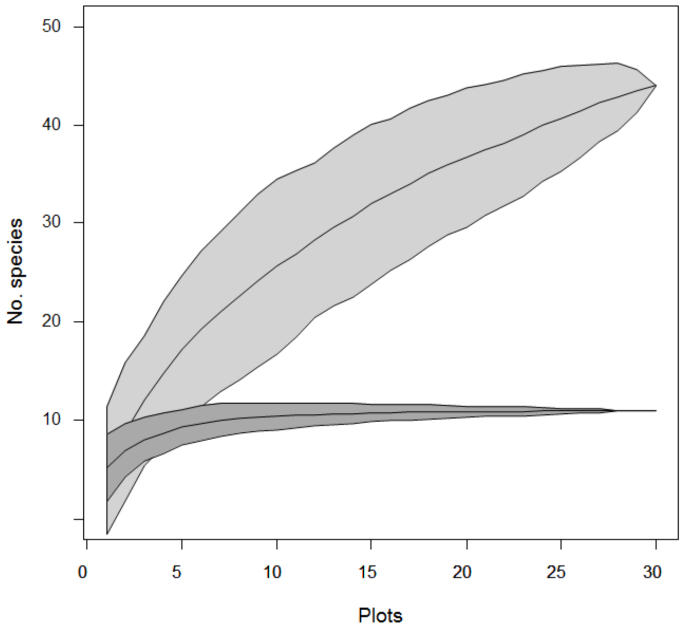

Figure 15: Average species richness. Mean species accumulation curves and their standard deviation from 100 random permutations are shown. Forest (light-grey), oil palm plantation (dark-grey).

To examine if the sampling effort of 30 plots per system was sufficient, we extrapolated the species lists to a total number of 300 plots. The resulting extrapolated accumulation curves are shown in Fig. 16.

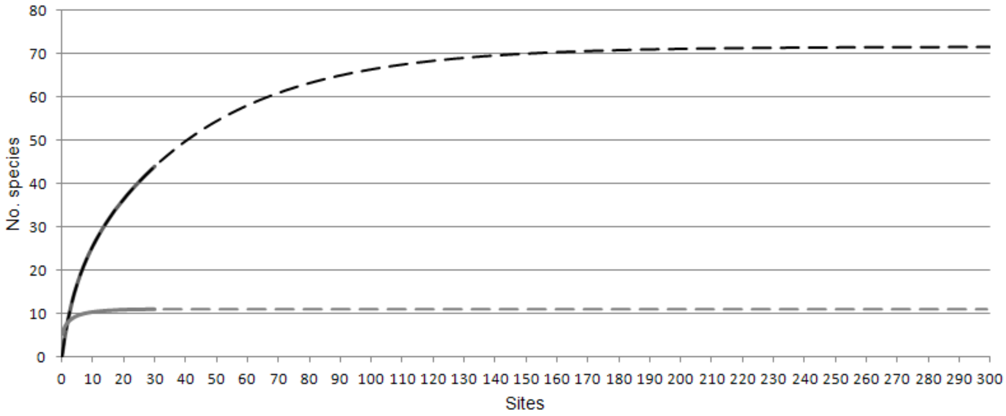

Figure 16: Extrapolation forest plots. Mean species accumulation curves for the 30 forest plots (black line) and the 30 oil palm plots (grey). The dotted line shows the result of an extrapolation (using richness estimator CHAO2) up to 300 sites (100 random permutations) with the statistical biodiversity estimation software EstimateS (Colwell, 2013).

It can be noticed that the curve of the plantation is reaching an asymptote already within the first 30 sampled sites. This shows that 30 investigated oil palms were sufficient to determine the epiphytic species richness of the plantation. In contrast, the curve for the forest is leveling off after approximately 120 sampling sites. This is again an indication that the epiphytic species richness in the lowland rainforest is obviously higher than in the oil palm plantation.

5.3 Microclimate

The climate graphs (Fig. 17) are showing the daily mean values of temperature and relative humidity in 10 minute intervals for the corresponding Johansson zones.

The course of the day shows an obvious difference between night and day in both systems. During the evening and early morning, temperatures are relatively low, ranging around 23-25 °C. With the rising sun, temperatures are increasing as well, reaching their peak of approximately 35 °C between 1 and 3 pm. Having a look at the humidity, a similar trend in the course of day and night can be observed. The highest values of 100 % relative humidity occur in the time from midnight until 8 am. From dawn on, simultaneously with the rising temperature, it becomes dryer in both systems. The values of the humidity reach their minimum exactly at that time, when the temperature reaches its peak. Comprising, it can be said that the difference between minimum and maximum for temperature and humidity in both systems is ca. 11 °C resp. 40 %.

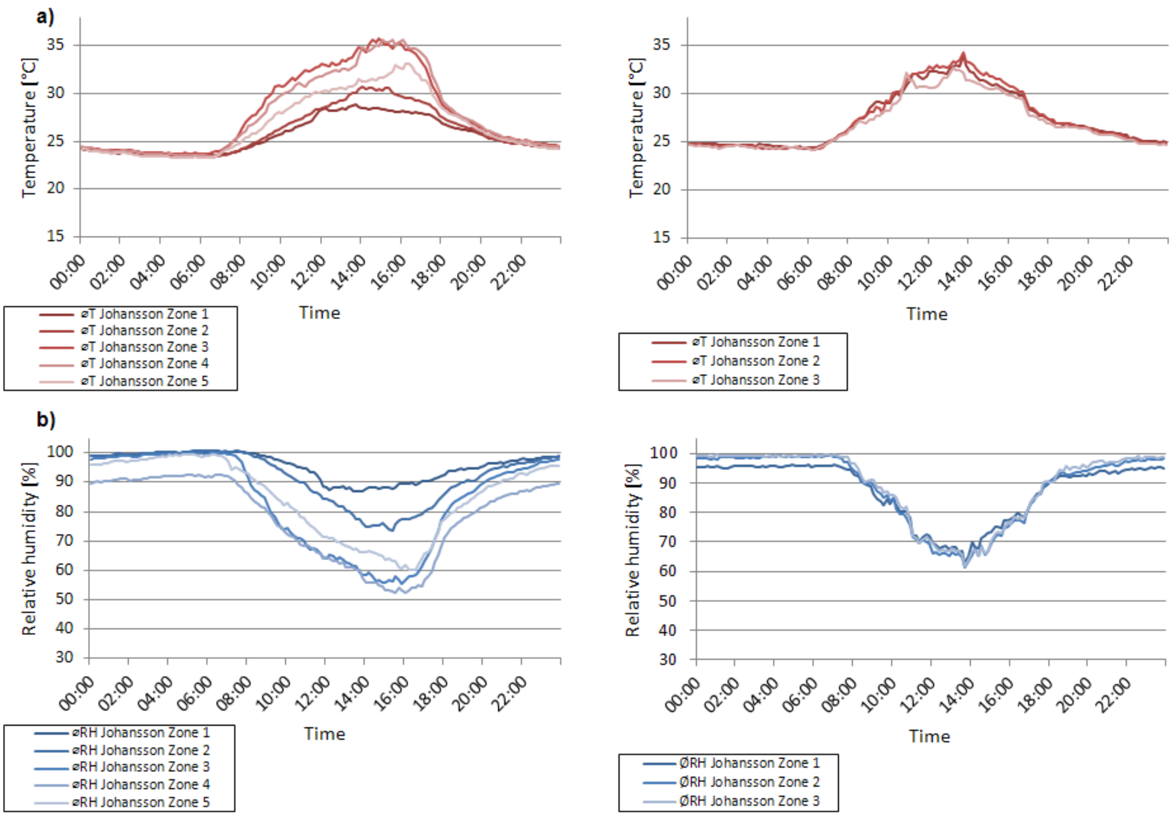

Figure 17: Climate graphs. Mean temperature (a) and mean relative humidity (b) over the day for Johansson zones 1-5 in forest plot PF05 (left) and for Johansson zones 1-3 in oil palm plot OPP19 (right). Data-logging every 10 minutes. Testing time forest: 15.03.2013-04.04.2013, testing time oil palm: 09.04.2013-15.04.2013)

Considering the differences in the Johansson zones, it can be said that the oil palms do not differ much. The curves for temperature and humidity are nearly equal and just show slight variations. The temperature at midday in JZ3 is for instance marginally lower than in the other zones. In addition to that JZ1 seems to be a little dryer, especially in the early-morning hours. Looking at the climate curves of the forest, it can be seen that the microclimate of the five Johansson zones are not as homogenous as the oil palm zones. The lower JZ are cooler throughout the whole day, in particular around midday. The warmest zones in the tested tree are JZ3 and JZ4. The same applies to the relative humidity. The wettest areas are the JZ1 and JZ2, where the humidity does not fall beneath 75 resp. 89 %. The relative humidity of the remaining three zones reaches its minimum at around 55 %.

Comparing the climate data of both systems, it can be observed that higher temperatures are reached in the forest, where the loggers recorded temperatures of over 35 °C in the upper Johansson zones. In the oil palm plantation the 35 °C mark is not reached during the testing period. In addition to that there are also zones in the forest tree that reach a lower humidity than the oil palm. In fact the humidity in the plantation does not fall beneath 60 %, while in the forest the humidity falls down to almost 50 % in zones three and four.

Among the temperature and the relative humidity, the light intensity in the Johansson zones was measured. The curves are presented in Fig. 18. It can be seen that in the forest the lower zones are quite dark and not much sunlight reaches the first nine meters. The light intensity rises in JZ3 and decreases slightly in JZ4 and JZ5. The reference measurement in a clearing near the investigated tree went wrong, so that the corresponding curve has to be considered as not significant. The light intensity in the plantation is all in all lower than in the forest. Admittedly, it is increasing from JZ1 to JZ2 and up to JZ3, but it never reaches the maximum of the forest values. The reference measurement outside of the plantation is another approval for the relatively dark condition in an oil palm plantation.

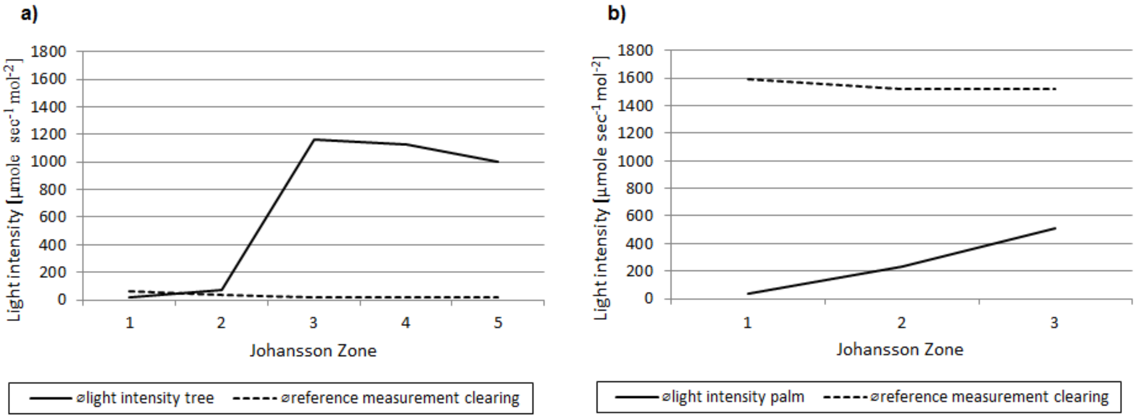

Figure 18: Light intensity. a) Mean light intensity in Johansson zones 1-5 in forest plot PF05 and reference measurement in a clearing nearby. b) Mean light intensity in Johansson zones 1-3 in oil palm plot OPP19 and reference measurement outside the plantation. Presented are the mean values out of three individual measurements for each zone, with a time interval of 20 seconds between each measurement.
Testing day forest: 13.03.2013, testing day oil palm: 09.04.2013. Height of measurement in forest: 1.5 m (JZ1), 9 m (JZ2), 22.8 m (JZ3), 26 m (JZ4), 30 m (JZ5); Height of measurement in oil palm plantation: 0.7 m (JZ1), 2.2 m (JZ2), 3.4 m (JZ3).

In the forest the simple linear regressions show a significant correlation between the epiphyte richness per JZ and the microclimatic factors temperature and light intensity. The relative humidity explains the species richness in the JZ just slightly significant (Fig. 19a). Additionally, the slope of the regression line shows a positive correlation for the temperature and the light intensity. The warmer and brighter it gets, the more species occur in the JZ. The majority of the species grew in the JZ with mean temperatures of 27 °C and higher and with a mean light intensity of 1000-1200 µmole sec^{-1} mole^{-2}. The relative humidity shows a negative correlation, so that more epiphytic species could be observed in the dryer JZ with humidity values between 80 and 87 %. The relatively high values of the coefficient of determination r-squared represent a good fitting model.

In the oil palm plantation a slightly significant correlation exists between species richness per JZ and the temperature (Fig. 19b). The highest number of epiphytic species occurred in the JZ with temperatures above 27.3 °C. The remaining climatic factors do not show any significant correlation. In addition to that, more species could be found in the dryer and darker JZ with a relative humidity of above 88.5 % and a light intensity lower than 300 µmole sec^{-1} mole^{-2}. Three data points are too few for further statistical analyzes, so a regression line was not drawn. The high values for r-squared show a good fitting model, but they derive from the lack of sufficient data points.

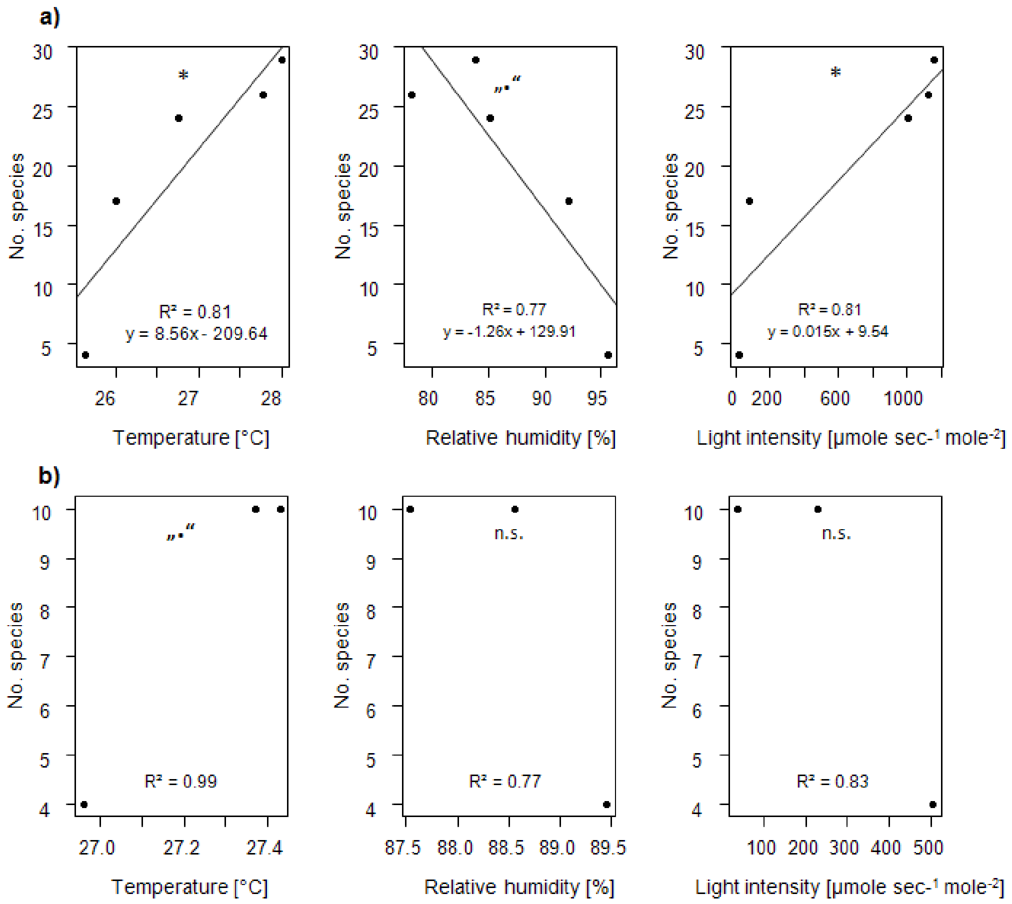

Figure 19: Linear regression of microclimate vs. total no. of species per Johansson zone. Correlation between the mean temperature, mean relative humidity and mean light intensity and the epiphyte richness per Johansson zone (JZ) in forest (a) and oil palm plantation (b). The dots symbolize the number of species in the corresponding JZ. Significance levels: 0 *** 0.001 ** 0.01 * 0.05 . 0.1   1.

6 Discussion

6.1 Change in epiphyte richness, diversity and species composition from forest to oil palm plantation

This study revealed the enormous difference in species richness between the tropical lowland rainforest of Jambi and the transformation system of oil palm plantations. Regarding the landscape level, 44 of the recorded 48 epiphytic species occurred in the sampled rainforest area, whereas the oil palm plantations only harboured 11 species. This is leading to a four times higher overall species richness in the primary forest. In addition to that, only seven species were shared in both systems and only four species occurred exclusively in the plantations. The majority of these shared and exclusive species belonged to the pteridophytes (*ferns*), which will be discussed later. In contrast to the relatively low species richness, the plantation epiphytes are outnumbering the forest epiphytes in their abundances. With 1386 of 1935 recorded vascular epiphytes, we found almost three-fourths of all epiphytic individuals in the plantation. Approximately only one quarter of all recorded individuals was growing in the forest. The lower abundance is also noticeable on lower levels. Per plot, the average abundance of epiphytes is significantly higher in the plantations. With a mean number of 46.2 individuals per oil palm and 18.3 individuals per forest tree, the average abundance in the single plantation plots is more than twice as high. In contrast to that, we observed an average number of approximately 5 epiphytic species per sampled tree/palm, leading to the assumption that forest trees and oil palms do not differ significantly in their number of occurring epiphyte species on plot level. Reducing the dimensions one step further and regarding the abundance on Johansson zone level in the forest, averagely most individuals could be sampled in the higher zones of the tree. The same pattern was shown for the occurrence of epiphyte species, where mean species richness was again highest in JZ3 to JZ5. Comparing these results with the abundances and species richness in the JZ of the oil palms, we observed an extreme decrease of the average number of epiphytic individuals from JZ1 to JZ3. The same decrease, even though a bit smoother, could be observed in the species richness distribution, where averagely less than 1 epiphyte species per JZ3 of the oil palms occurred. This is the exact opposite of the observations made in the forest plots. It is highly probable that this is mainly correlated with the form of the oil palm. The crown area is simply inhospitable, because only the fresh and new leaves of the palm are located there, without providing enough substrate and space for a potential colonization of epiphytes. On the contrary, it comes to an enormous accumulation of organic matter in the dead leaf axils of the stem (Luskin & Potts 2011), which is therefore the exact factor, explaining the high abundances in JZ1 and JZ2 of the oil palms.

Further could be noticed, that in addition to true epiphytes, also accidental epiphytes played an important role in the oil palm plots, as they were represented highly abundant. A total of 420 individuals of the species *Asystasia gangetica*, *Clidemia hirta*, the oil palm itself (*Elaeis guineensis*) and even the rubber tree (*Hevea brasiliensis*), which normally grow on the ground, could be observed on nearly every single sampled oil palm. If we had included them in the statistical analyses, the accidental epiphytes would have represented almost 25 % of all recorded oil palm individuals. As organic litter is accumulating in the dead leaf axils of the oil palms, primarily ground-growing plants are able to benefit from the resulting substrate and conquer the palms, becoming even more dominant in the plantations. Besides our recorded accidental epiphytes, which belonged unexceptional to the group of Angiosperms, similar observations have been made for pteridophyte species, which could use the oil palms themselves as a substrate (Beukema & Noordwijk 2004, Beukema *et al.* 2007). The role of accidental epiphytes in oil palm plantations will be further discussed in chapter 6.2.

An exact evaluation of the results so far is complicated, due to the fact that not many previous studies comparing the epiphytic flora of Southeast Asian oil palm plantations and forests have been published. Only Mojiol *et al.* (2009) tried to acquire data on vascular epiphyte diversity by ground base inventory in a Malaysian forest reserve and could find 15 epiphytic species on a total of 36 host trees (18 standing, 4 dead standing, 14 fallen trees). But as the ground based epiphyte assessment using binoculars is insufficient to gather total epiphyte richness of the rainforest (Gradstein 1992), it is clear that we were able to record 3 times more vascular epiphyte species by climbing the phorophytes. As already mentioned in the introduction, there are many more studies investigating the epiphyte diversity in the neotropics (Freiberg 1996, Barthlott *et al.* 2001, Kreft *et al.* 2004, Köster *et al.* 2009, 2011). Regarding the results of these studies, it can be concluded that the vascular epiphyte species richness in the Bukit Duabelas National Park has to be considered as relatively low, in comparison to the neotropical rainforest. Köster *et al.* (2011) revealed for instance a total of 381 species in 110 sampled plots in a lowland rainforest in Ecuador. Additionally, each phorophyte harboured a mean number of 68 epiphyte species, showing a 13 times higher average species number per phorophyte than the lowland rainforest of Sumatra. Having a look at the extrapolation in Fig. 16, after 110 sampled plots the total species richness of the Bukit Duabelas National Park would range around 65 epiphyte species, which is almost 6 times lower than in the lowland rainforest of Ecuador.

The statement that forest trees and oil palms do not differ in their species richness on plot level (see above) is also supported by the equal mean values for the Shannon- and Sørensen-index on that level (H’ = 1.17, D1 = 0.58). This is a proof that the majority of the individual forest trees and oil palms do not differ in their alpha diversity, even though, all in all, the forest trees possess a significantly higher total number of vascular epiphyte species. The fact that Pielou’s evenness is higher and therefore closer to 1 in the forest (J’ = 0.85) indicates that the individual rainforest trees are much more even than the oil palms (J’ = 0.72), i.e. the abundances of the epiphyte species on the individual trees are much more equally distributed. On landscape level, including all trees and palms into the calculation of the Shannon-index, the alpha diversity differs considerably. With H’ = 3.02 the alpha diversity of the entire lowland rainforest is almost twice as high as the alpha diversity of the entire oil palm plantation (H’ = 1.63), confirming the higher species richness in the rainforest. Pielou’s evenness on landscape level shows again that the abundances among the epiphyte species are distributed more even in the forest (J’ = 0.8) than in the plantation (J’ = 0.68).

The results concerning the alpha diversity go along with the study of Barthlott *et al*. (2001), who observed equal alpha diversities (3.15 in forest, 1.61 in plantation) for a primary montane rainforest and tree plantations (*Cedrela* and *Pinus* species) in the Venezuelan Andes. But in this study again, total epiphyte species richness was higher (178 spp.) than in the lowland forest of the Bukit Duabelas National Park (44 spp.). Total species richness in the investigated tree plantations was slightly higher (13 spp.) than in the oil palm plantations of Jambi (11 spp.).

Important parts of the epiphytic rainforest flora of the Bukit Duabelas National Park belong to the groups of orchids, ferns and other Angiosperms. The number of species is relatively equal distributed among the three groups, with the dominating orchids and a slightly lower dominance of the ferns and the other Angiosperms. In contrast to that, the abundances of these groups are not equally distributed. Orchids and ferns were represented each with approximately 45 % of all forest individuals, whereas the other Angiosperms only represented 10 %. The trend of a dominance of orchids and ferns was also observed in the Malaysian rainforest (Mojiol *et al.* 2009), with the exception that the ferns represented the biggest part of the epiphyte species composition. But as already mentioned, that study was a ground based observation of epiphytes, so that it has to be kept in mind that smaller epiphytes (mostly Angiosperms) can be overlooked more easily, whereas the immense ferns (e.g. *Asplenium* and *Platycerium*) are relatively easy to spot, even in the high zones of the phorophytes. The observed species composition in the Bukit Duabelas National Park conforms to the described species composition in the neotropics. In addition to a high relative contribution to species richness of orchids and ferns, the group of other Angiosperms is more diverse in the neotropics. In contrast to the lowland rainforest of Jambi, also species of families like Araceae, Bromeliaceae, Cactaceae or Gesneriaceae, which were underrepresented or completely absent in our study, play a major role in the neotropical forests (cf. Ibisch *et al.* 1996, Barthlott *et al.* 2001, Kreft *et al.* 2004).

The species composition of the oil palm plantations shows an extremely high dominance of the ferns, with only one species of the other Angiosperms and a complete lack of orchids. Ten of eleven species belong to the ferns and 99 % of all observed epiphytic individuals in the plantations are ferns. The high dominance of fern species with a simultaneous absence of epiphytic orchids in oil palm plantations was also observed by Danielsen & Beukema (2009).

In addition to the dissimilar species composition, the abundances of the individual species in the plantation are extremely uneven. As the rank/abundance curve (Fig. 13) shows, the plantation is characterised by the dominance of a few highly abundant species (e.g. *Nephrolepis acutifolia* and *Davallia denticulata*). On the contrary, the smoother curve of the forest epiphyte community indicates a higher evenness, i.e. the abundances are evenly distributed amongst the 44 forest species and the Bukit Duabelas National Park is characterised by a equal mixture of highly and less abundant species, as well as several species represented by single individuals (*singletons*). In addition to that, the abundances are also evenly distributed among the three groups of orchids, ferns and other Angiosperms, i.e. all groups are represented equally by abundant and less abundant species. The lowest abundance in the plantation is represented by three individuals of *Cyrtandra*, which is extremely dominated by the remaining ten fern species. Additionally, the most abundant plantation species are also occurring with a relatively low abundance in the forest.

Another instrument to evaluate the species composition of the two landscapes is the beta diversity. As described in the introduction the beta diversity provides information about the change in species diversity between different ecosystems (*between-habitat diversity*) and examines the similarity or the dissimilarity in species composition (Whittaker 1972). As the mean values for the Bray-Curtis dissimilarity are significantly higher in the forest plots (0.88), it can be concluded that the species composition is more various than in the oil palm plots (0.44). The species composition on each individual forest tree is therefore more diverse to the other forest trees than the species composition on each oil palm in comparison to the other oil palms. Simply put, on every individual forest tree, there is a different combination of the recorded epiphyte species, i.e. the forest plots do not have many species in common. But on every single oil palm, species composition of the eleven epiphyte species is almost the same and the oil palm plots share nearly all of their species, leading to a relatively low beta diversity. This fact is further proved by the ordination in Fig. 14b. The ordination of our epiphyte data shows an isolation of the two plot groups and additionally a low scattering for the oil palm plots and a wide scattering for the forest plots. On the one hand, this is indicating that the two investigated sites differ in their species composition on landscape level. On the other hand, as the data points of the oil palm plots stick close together, it can be concluded again that they do not vary much among themselves in their epiphyte species composition. On the contrary, the forest data points show relatively high distances among themselves, hinting at a higher variance in the epiphyte species composition.

As the species accumulation curves show (Fig. 15), 30 investigated forest trees were not sufficient to reveal total species richness of the lowland rainforest in Jambi. The forest accumulation curve is growing with ongoing plot sampling, because with every new plot, new epiphyte species are added to the inventory. In contrast to the unrevealed real species richness of the forest, the accumulation curve for the oil palm plantation shows that approximately five sampled oil palms were sufficient to describe total epiphyte species richness in the plantation. After a relatively low investigation effort, all eleven vascular epiphyte species were discovered. The extrapolation of the forest data showed, that approximately 100 examined phorophytes would be necessary to reveal potential total species richness. As the remaining primary forest fragment of the Bukit Duabelas National Park is relatively small, the investigation of more than 30-40 trees seems utopian, because the total number of suitable phorophytes was already nearly exhausted in the course of our study. Nevertheless, as already discussed above, estimated total species richness is still lower than in the neotropics (cf. Köster *et al*. 2011).

Summarizing, it can be said that the hypothesis can be proved, that the transformation of primary lowland rainforest in Sumatra leads to a radical change in vascular epiphyte diversity and species composition. As alpha diversity on plot level is approximately equal in reference and transformation system, on landscape level, species richness is significantly higher in the rainforest, with four times more epiphytic species. In addition to that, species composition in the oil palm plantation is monotonous with a dominance of fern species and an absence of orchids and other Angiosperms. Additionally high rates of accidental epiphytes could be observed. In the forest, epiphyte species are evenly distributed among the orchids, ferns and other Angiosperms. The abundances of all recorded individuals were much more evenly distributed among the epiphyte species of the forest, whereas the oil palm plantation was dominated by few highly abundant species. The forest trees among themselves show a higher dissimilarity, i.e in the forest plots, beta diversity is significantly higher. Oil palms do not differ much among themselves in species composition and are therefore sharing the same few epiphyte species, which hints to a lower beta diversity.

The loss of diversity and species richness due to oil palm expansion was also observed for vertebrate and invertebrate species by Danielsen & Beukema (2009) and will be further discussed in the next chapter.

6.2 Conservation value of oil palm plantations

As this study shows, transformation from tropical lowland rainforest to oil palm plantations leads to a dramatic loss of epiphyte species richness. With eleven vascular epiphyte species, total species richness of the investigated oil palm plantations is four times lower than in the forest. Forest and oil palm plots only share seven species and just four species were observed, which occurred exclusively in the oil palm plantations. Ten out of eleven species are ferns and the majority of the plantation epiphytes could also be recorded in the forest plots or in rubber plantations (cf. Böhnert 2013). The fact that most of the plantation species (e.g. *Asplenium nidus*) are also present in the forest and other plantations shows that they seem to have a wide ecological spectrum and can colonize various habitats (Zhang *et al.* 2010). They can be therefore characterized as generalists with relatively low ecological requirements and a high tolerance for disturbance. In addition to the high abundances of these generalists, the fond stubs remaining on the oil palm trunks act as pots, in which organic litter is accumulating. The resulting substrate provides a new habitat, which is commonly used by a wide range of accidental epiphytes (cf. Danielsen & Beukema 2009). Quite often these accidental epiphytes can be invasive species, for example *Asystasia gangetica* or *Clidemia hirta* (Tjitrosoedirjo 2007). As oil palm plantations are expanding throughout wide areas of the Southeast Asian tropics, these species can possibly use the oil palms to expand their own invasion area. Besides invasive plant species, oil palm monocultures are also creating an opportunity for the invasion of pests, like rats and herbivorus insects or by diseases caused by fungi (Corley & Tinker 2003, Turner & Gillbanks, 2003). The fact that pests and diseases are most commonly controlled by the use of chemicals indicates another possible reason for a decrease of plant and animal diversity in plantations (Foster *et al.* 2011).

As shown above, the oil palm plantations in our study are lacking of forest specialists like orchids or other Angiosperms. Additionally, typical components of the forest vegetation, including large forest trees and lianas are absent in the plantation (Danielsen & Beukema 2009, personal observation). Regarding the beta diversity within the oil palm plantation, the species composition of the oil palms shows a relatively high similarity, i.e. the oil palms share a lot of species. This shows that the oil palm plantation can be seen as a quite monotonous ecosystem. This is also proved by the microclimatic conditions in the plantation, which will be discussed later. Besides the climate, also the “architectural complexity” (Foster *et al.* 2011) is much simpler than in the natural ecosystem of the tropical lowland rainforest, with fewer and more open canopy layers.

In addition to the loss of epiphyte richness and diversity in oil palm plantation, the same alerting changes are shown for numerous vertebrate and invertebrate species. Danielsen & Beukema (2009) concluded that species richness of birds, lizards and mammals was always lower in oil palm plantations than in forest. They also observed a domination of a few highly abundant invertebrate species in the plantation, which is conform to the epiphyte species composition in our study.

To conclude, it can be said that oil palm plantations cannot be considered a substitute for natural tropical forest. Due to their structurally less complexity combined with instable microclimatic conditions and the dominance of a few generalists, specialized forest species are not able to establish in the oil palm plantation and will disappear with ongoing oil palm expansion and rainforest loss.

6.3 Impact of microclimatic conditions on epiphyte diversity and composition

The measured mean values of temperature and relative humidity make clear that the microclimatic conditions in the lowland rainforest and the oil palm plantation differ considerably. While the forest tree shows a wide range of temperature and humidity between the individual Johansson zones, the oil palm does not differ at all. During the day, temperature and humidity are rising and falling simultaneously in the oil palm, without showing the slightest difference between the individual zones. Especially the lower zones of the oil palm are significantly warmer and drier throughout the whole day than the climatic conditions in the forest tree. The hotter and drier climate in the oil palm plantation was already shown for plantations in Malaysia (Luskin & Potts 2011).

In addition to temperature and humidity, the light intensity shows an equal trend. As light intensity differs extremely from zone to zone in the forest, the oil palm is characterised by a relatively low light intensity with the darkest zone at the base of the trunk and the comparatively brightest zone in the canopy. The forest tree shows a dark situation with almost no light intensity in the low zones and a high light intensity, above the shrub layer, between JZ2 and JZ5. All in all it can be observed that the conditions in the plantation are consistently darker than in the higher zones of the forest.

As Foster et al. (2011) figured out, the difference in the microclimatic conditions is strictly correlated with the simplification of the habitat, because the oil palm canopy is lower, more open and simpler than the more complex rainforest canopy layer. This leads at the same time to extremer conditions within the plantation, which makes it more diffcult for forest epiphytes to colonise oil palms. Nevertheless, even though the oil palm canopy is more open, our study showed that light conditions in the plantation are much darker than in the higher zones of the forest. As highest epiphyte diversity is observed in areas with a relatively high light intensity and a high humidity (Gentry & Dodson 1987, Benzing 1990, Barthlott et al. 2001, Kreft et al. 2004), it is clear that the species richness in the comparatively dry and dark oil palm plantation has to be relatively low, as conditions are to harsh for the forest specialists to survive in the plantation.

The correlation between species richness and microclimatic conditions was also examined by linear regressions, showing a significant positive correlation for epiphyte species richness and the microclimatic factors temperature and light intensity. The relative humidity explains the species richness just slightly significant with a negative correlation (Fig. 19). According to the results of this correlation analysis, the epiphyte species richness in our study is highest in the hottest, driest and brightest zones of the forest trees (JZ3 and JZ4). As this result contradicts the above mentioned conditions for high epiphyte diversity, this statement should be considered with caution, because we chose a rather inappropriate phorophyte for the measurement of the climate in the forest. As we had to reach all five Johansson zones of the tree for the attachment of the data loggers, we chose a relatively freestanding tree, which was not surrounded by other trees. As JZ3 and JZ4 of that tree were not shadowed by the canopy of neighbouring trees, the data loggers in these two zones were exposed to higher sunlight and temperatures. This shows that the measured microclimatic conditions should not be seen as characteristic for the whole primary forest of the Bukit Duabelas National Park. The analysis of the correlation of epiphyte richness and microclimate in the plantation was not realisable, due to the lack of sufficient data points.

All in all it can be said that we proved that the conversion of forest areas into oil palm plantations leads to uniform climatic conditions (cf. Luskin & Potts 2011). Additionally we showed that temperatures and humidity are varying in a wider range in the forest. As the conditions in the plantation are too extreme (high temperatures, low humidity), highly sensitive epiphyte species cannot colonise the oil palms and species richness is therefore lower than in the more complex, cooler and wetter forest system. To get significant correlations between microclimatic conditions and epiphyte species richness, further measurements on additional trees over a longer time period should be carried out.

6.4 Conclusion

As part of the subproject B06 of the CRC 990 project, this study was the first to investigate the effects of transformation from tropical lowland rainforest into oil palm plantations for vascular epiphyte diversity in Southeast Asia. As epiphytes are important parts of the tropical flora and play also important roles in ecosystem processes, and the remaining Southeast Asian primary forests are undergoing high rates of deforestation and transformation into monoculture plantations, epiphytes should be of a high interest in future studies. Even though a lot is known about the diversity patterns and the ecology of epiphytes in the neotropics, relatively few is known about the consequences for epiphyte diversity in Southeast Asia.

We proved in our study that the diversity in the primary rainforest is significantly higher than in the transformation system of oil palm plantations. As there are many possible reasons for that loss of species richness, we could show that the extreme microclimatic conditions (relatively hot and dry) can explain the lower species diversity in the oil palm plantation. The enormous differences in the ecosystem complexities lead to a lack of forest specialists, which should be of highest conservation concern, whereas generalists, which should be of low conservation concern, are able to invade and dominate the plantations in high abundances. As this study only investigated the microclimate exemplarily on one forest tree and one oil palm, the influence of the microclimatic conditions should be investigated in further studies on more trees and over a longer time period, to get significantly provable data for further correlation analyses. As this subproject already collected epiphyte data for the tropical lowland forest, oil palm plantations and rubber plantations, further data collection for the transformation system of the agroforestry system jungle rubber would be recommendable, to get an overview of the consequences for epiphyte diversity in all dominating transformation systems in Jambi.

Taken together, it has to be said that oil palm plantations are no substitute for the conservation of vascular epiphyte species of the forest. As expansion of oil palm plantations is going on that rapidly, it is just a question of time until the sensitive forest epiphytes have vanished. Additionally the oil palm monocultures are facilitating the establishment of a few dominant species, which is leading sooner or later to a completely uniform and relatively similar plantation flora and fauna. Therefore, it is essential that scientists and conservation organisations work closely together with the palm oil industry to find a possibility to arrange palm oil production with biodiversity interests. This is complicated today, due to the high levels of demand for palm oil from consumers all over the world. The increasing demand for palm oil leads directly to the clearance of forested land to develop new plantations. Another quite controversial issue is the transformation of primary forest into oil palm plantations to get palm oil for producing carbon-neutral fuels. The result of that deforestation is a total net carbon emission of 25 % and it would take between 75 and 93 years for the carbon emissions saved through use of biofuel to compensate the carbon loss through forest transformation (Danielsen & Beukema, 2009). Additionally forest conservation is complicated by the overwhelmed governments in the producer countries, which need to become better at establishing protected forest areas and provide for steady controls of illegal logging (Fritzherbert *et al*. 2008). Finally it has to be said, that the threats of expanding monoculture plantations and the simultaneous deforestation can only be avoided by establishing a sustainable crop management with a strong focus on the conservation of the remaining primary forests and the associated sensitive biodiversity.

7 Summary

As part of the collaborative research project CRC 990, funded by the *Deutsche Forschungsgemeinschaft* (*DFG*) and organised in close cooperation between the University of Göttingen and the University of Jambi (*UNJA*), the Bogor Agricultural University (*IPB*), the Tadulako University (*UNTAD*) and the Indonesian Institute of Science (*LIPI*), this study investigated the differences in vascular epiphyte diversity between the primary lowland rainforest and the transformation system oil palm plantation in and around the Bukit Duabelas National Park in Jambi, Sumatra, Indonesia. We investigated the epiphyte diversity of the two systems by climbing 30 trees in the primary rainforest and by ground based observation with binoculars of 30 oil palms. In addition to that, data loggers measured temperature, relative humidity and light intensity of one forest tree and one oil palm.

Vascular epiphyte species richness was significantly higher in the rainforest (549 individuals, 44 spp.) than in the oil palm plantation (1386 individuals, 11 spp.). The Shannon- and Simpson-index on plot level showed an equal mean alpha diversity for both systems, whereas on landscape level, the alpha diversity of the forest was significantly higher. The vascular epiphyte species of the forest were equally distributed among the defined groups of orchids, ferns and other Angiosperms. The oil palm plantation was extremely dominated by fern species, with only one occurring species representing the other Angiosperms. Orchids were not represented on any oil palm, but a very high abundance of accidental epiphytes could be observed in the oil palm plantation. The uneven species composition was also proved mathematically with Pielou's evenness. As the value was higher and closer to 1 in the forest, it could be concluded that the species community in the forest was much more even, i.e. the individual abundances were evenly distributed among all forest species. In contrast to that, the lower evenness value for the oil palm plantation indicated the dominance of a few highly abundant species. To investigate the beta diversity within the two systems, we calculated the Bray-Curtis dissimilarity. The higher value for the forest plots indicated higher beta diversity in this system. This means that the single forest plots differ significantly in their species composition, i.e. they do not have that many species in common. As the relatively low dissimilarity value for the plantation shows, the individual oil palms share a lot of species among themselves. An ordination of all plot data points revealed the same dissimilarity patterns. The oil palm data points were closer together as they did not differ much in their species composition, whereas the forest plots were spreading over a wide range, indicating a higher dissimilarity and few shared species. Species accumulation curves showed that 30 forest plots were insufficient to reveal total epiphyte species richness of the forest, whereas already after five oil palms all eleven oil palm epiphyte species were explored. An extrapolation of the sampled plots showed an estimated total species richness for the forest of approximately 70 species. The measurement of the microclimate characterized the oil palm as equally dry, hot and dark in all three Johansson zones, while the zones of the forest tree differed among themselves and were mainly cooler, wetter and brighter than the oil palm.

As an important result, this study showed that oil palm plantations are no substitute for the conservation of vascular epiphyte species. Future projects should therefore investigate how

epiphyte diversity is changing from primary forest to the other dominating transformation systems rubber plantation and jungle rubber.

8 Zusammenfassung

Als Teil des durch die Deutsche Forschungsgemeinschaft (*DFG*) geförderten transdisziplinären Kooperationsprojektes SFB 990 zwischen der Universität Göttingen, der Universität Jambi (*UNJA*), der Landwirtschaftlichen Universität Bogor (*IPB*), der Tadulako Universität (*UNTAD*) und dem Indonesischen Institut der Wissenschaften (*LIPI*), untersuchte die vorliegende Studie die Unterschiede in der Diversität vaskulärer Epiphyten zwischen dem Primärregenwald und dem Transformationssystem Ölpalmenplantage in und um den Bukit Duabelas National Park in Jambi, Sumatra, Indonesien. Wir ermittelten die Epiphytendiversität der beiden Systeme durch Beklettern von 30 Bäumen im Primärregenwald und durch die Beobachtung von 30 Ölpalmen mittels Fernglas vom Boden aus. Zusätzlich wurden noch für je einen Baum und eine Palme die Klimaparameter Temperatur, relative Luftfeuchte und Lichtintensität mit Hilfe von Datenloggern aufgezeichnet.

Der Artenreichtum der vaskulären Epiphyten war deutlich höher im Regenwald (549 Individuen, 44 Arten) als in der Plantage (1386 Individuen, 11 Arten). Der Shannon- und der Simpson-Index zeigten auf Plot-Level eine gleiche durchschnittliche Alpha-Diversität für beide Systeme, während sie auf Landschafts-Level deutlich höher für den Wald war. Die Epiphytenarten waren im Wald gleichmäßig verteilt auf die vorher definierten Großgruppen der Orchideen, Farne und sonstigen Angiospermen. Die Ölpalmen waren deutlich dominiert von Farnarten, mit nur einer auftretenden Art, die die sonstigen Angiospermen repräsentierte. Orchideen fehlten gänzlich auf den Ölpalmen. Im Gegensatz hierzu konnte eine große Anzahl zufälliger Epiphyten ausgemacht werden. Die ungleiche Verteilung der Artenzusammensetzung wurde mathematisch nachgewiesen durch die Ermittlung von Pielou’s Evenness. Da der Wert für den Wald höher, d.h. näher bei dem Wert 1 lag, konnte angenommen werden, das die Artenzusammensetzung im Wald wesentlich gleichverteilter war, d.h. die einzelnen Abundanzen waren gleichmäßig auf alle Wald-Arten verteilt. Im Gegensatz dazu, bewies der geringere Wert in den Ölpalmenplantagen, die Dominanz einiger weniger hoch abundanter Arten. Um die Beta-Diversität innerhalb der beiden Systeme zu untersuchen, berechneten wir den Bray-Curtis Koeffizienten. Der höhere Wert für die Waldplots deutet auf eine höhere Beta-Diversität in dem System hin. Das heisst, die einzelnen Waldplots unterscheiden sich erheblich untereinander in ihrer Artzusammensetzung und haben nicht viele Arten gemeinsam. Wie der relativ niedrige Wert für die Ölpalmen zeigt, zeichnen diese sich durch viele gemeinsame Arten aus. Die Ordination der Datenpunkte zeigt ein gleiches Muster für die Beta-Diversität. Da die Datenpunkte der Ölpalmenplots in der Ordination näher beieinander lagen, kann davon ausgegangen werden, dass sie sich hinsichtlich der Artenzusammensetzung weniger unterscheiden als die weit gestreuten Datenpunkte der Waldplots. Die Artenakkumulationskurven deuteten darauf hin, dass eine Anzahl von 30 untersuchten Plots nicht ausreichend war, um den Gesamtartenreichtum des Waldes aufzudecken, während bereits fünf Ölpalmen reichten, um alle vaskulären Epiphytenarten zu entdecken. Die Extrapolation deutete auf einen zu erwartenden Gesamtartenreichtum von ca. 70 Arten hin. Die Messung des Mikroklimas zeigte, dass die Zustände in allen drei Johansson Zonen der Ölpalme insgesamt wesentlich trockener, wärmer und dunkler waren, während die Zonen des Waldbaumes sich stark untereinander unterschieden und insgesamt betrachtet deutlich kühler, feuchter und heller waren als die Ölpalme.

Als wichtiges Ergebnis dieser Studie bleibt festzuhalten, dass Ölpalmenplantagen kein geeignetes Mittel für eine Erhaltung der vaskulären Epiphytendiversität sind. Zukünftige Projekte sollten daher untersuchen, wie es sich mit dem Wandel der Epiphytendiversität von Primärwald zu den anderen dominierenden Transformationssystemen Kautschukplantage und „Jungle Rubber“ verhält.

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10 Appendix

Appendix 1: Total species list of recorded epiphytes

No.	Family	Genus	Species	Author	Rainforest	Oil palm plantation
1	Apocynaceae	*Dischidia*	*cf. imbricata*	Blume (Steud.)	22	-
2	Apocynaceae	*Hoya*	*carnosa*	(L.f.) R.Br.	13	-
3	Araceae	*Rhaphidophora*	*spec.*		1	-
4	Aspleniaceae	*Asplenium*	*glaucophyllum*	Alderw.	1	16
5	Aspleniaceae	*Asplenium*	*longissimum*	Blume	-	47
6	Aspleniaceae	*Asplenium*	*nidus*	L.	27	28
7	Blechnaceae	*Stenochlaena*	*palustris*	(Burm. f.) Bedd.	-	41
8	Clusiaceae	*Clusia*	*spec. 1*		1	-
9	Davalliaceae	*Davallia*	*denticulata*	(Burm. f.) Mett. ex Kuhn	9	255
10	Davalliaceae	*Davallia*	*triphylla*	Hook.	16	-
11	Gesneriaceae	*Cyrtandra*	*spec.*		-	3
12	Lycopodiaceae	*Huperzia*	*cf. carinata*	(Desv. ex Poir.) Trevis.	6	-
13	Lycopodiaceae	*Huperzia*	*phlegmarioides*	Rothm.	1	-
14	Melastomataceae	*Genus 1*	*spec.*		6	-
15	Melastomataceae	*Genus 2*	*spec.*		1	-
16	Melastomataceae	*Genus 3*	*spec.*		2	-
17	Melastomataceae	*Genus 4*	*spec.*		2	-
18	Moraceae	*Ficus*	*spec. 1*		2	-
19	Moraceae	*Ficus*	*spec. 2*		2	-
20	Moraceae	*Ficus*	*spec. 4*		1	-
21	Oleandraceae	*Nephrolepis*	*acutifolia*	(Desv.) H. Christ	3	677
22	Ophioglossaceae	*Ophioglossum*	*pendulum*	L.	58	22
23	Orchidaceae	*Acriopsis*	*densiflora*	Lindl.	1	-
24	Orchidaceae	*Acriopsis*	*liliifolia*	(J.König) Seidenf.	1	-
25	Orchidaceae	*Bulbophyllum*	*spec. 1*		5	-
26	Orchidaceae	*Bulbophyllum*	*spec. 2*		3	-
27	Orchidaceae	*Bulbophyllum*	*spec. 3*		26	-
28	Orchidaceae	*Bulbophyllum*	*spec. 4*		4	-
29	Orchidaceae	*Dendrobium*	*compressistylum*	J.J.Sm.	50	-
30	Orchidaceae	*Dendrobium*	*crumenatum*	Sw.	31	-
31	Orchidaceae	*Dendrobium*	*indragiriense*	Schltr.	16	-
32	Orchidaceae	*Dendrobium*	*spec. 1*		10	-
33	Orchidaceae	*Grammatophyllum*	*speciosum*	Blume	5	-
34	Orchidaceae	*Luisia*	*spec.*		4	-
35	Orchidaceae	*Genus 4*	*spec.*		1	-
36	Orchidaceae	*Genus 8*	*spec.*		1	-
37	Orchidaceae	*Phalaenopsis*	*cornu-cervi*	(Breda) Blume & Rchb.f.	64	-
38	Orchidaceae	*Pteroceras*	*spec.*		1	-
39	Orchidaceae	*Trichotosia*	*cf. ferox*	Blume	1	-
40	Pandanaceae	*Freycinetia*	*cf. sumatrana*	Hemsl.	1	-
41	Piperaceae	*Peperomia*	*spec.*		2	-
42	Polypodiaceae	*Drynaria*	*quercifolia*	(L.) J. Sm.	42	-
43	Polypodiaceae	*Goniophlebium*	*verrucosum*	J.Sm.	3	161
44	Polypodiaceae	*Pyrrosia*	*angustata*	(Sw.) Ching	18	-
45	Polypodiaceae	*Pyrrosia*	*piloselloides*	(L.) M.G. Price	60	-
46	Rubiaceae	*Hydnophytum*	*cf. formicarum*	Jack	2	-

47	Vittariaceae	*Vittaria*	*elongata*	Sw.	-	42
48	Vittariaceae	*Vittaria*	*ensiformis*	Sw.	23	94

Appendix 2: Total species list of phorophytes

Area	Plot-no.	Family	Species	Bark roughness	height [m]	DBH [cm]	Start of canopy [m]	GPS south	GPS east
Forest TNBD Permatang Kabau	PF01	Dipterocarpaceae	*Shorea spec.*	heavy	35	122,55	26	S 01° 56,571'	E 102° 34,867'
Forest TNBD Permatang Kabau	PF02	indet	*indet.*	medium	50	100,17	27	S 01° 56,502'	E 102° 34,868'
Forest TNBD Permatang Kabau	PF03	Burseraceae	*Santiria cf. laevigata*	medium	35	71,52	20	S 01° 56,383'	E 102° 34,955'
Forest TNBD Permatang Kabau	PF04	Olacaceae	*Ochanostachys cf. amentacea*	smooth	32	51,69	32	S 01° 56,496'	E 102° 34,913'
Forest TNBD Permatang Kabau	PF05	Malvaceae	*Malvaceae spec.*	medium	42	74,1	18	S 01° 56,432'	E 102° 34,842'
Forest TNBD Permatang Kabau	PF06	Olacaceae	*Ochanostachys cf. amentacea*	medium	36	84,26	20	S 01° 56,464'	E 102° 34,929'
Forest TNBD Permatang Kabau	PF07	Lauraceae	*Litsea spec.*	heavy	35	57,14	22	S 01° 56,494'	E 102° 34,842'
Forest TNBD Permatang Kabau	PF08	indet	*Dacryodes incurvata*	medium	40	75,69	18	S 01° 56,585'	E 102° 34,921'
Forest TNBD Permatang Kabau	PF09	indet	*Dillenia spec.*	smooth	35	74,99	21	S 01° 56,603'	E 102° 34,897'
Forest TNBD Permatang Kabau	PF10	indet	*indet.*	heavy	18	65,86	33	S 01° 56,594'	E 102° 34,869'
Forest TNBD Permatang Kabau	PF11	indet	*Dacryodes cf. nervosa*	heavy	30	55,32	10	S 01° 56,540'	E 102° 34,900'
Forest TNBD Permatang Kabau	PF12	indet	*Annonaceae spec.*	medium	32	44,44	13	S 01° 56,503'	E 102° 34,900'
Forest TNBD Permatang Kabau	PF13	indet	*Calophyllum molle*	medium	33	40,58	19	S 01° 56,477'	E 102° 34,910'
Forest TNBD Permatang Kabau	PF14	indet	*indet.*	heavy	41	92,85	19	S 01° 56,443'	E 102° 34,980'
Forest TNBD Permatang Kabau	PF15	indet	*indet.*	heavy	50	105,84	25	S 01° 56,549'	E 102° 34,883'
Forest TNBD Permatang Kabau	PF16	indet	*Palaquium spec.*	smooth	50		24	S 01° 56,574'	E 102° 34,851'
Forest TNBD Permatang Kabau	PF17	indet	*Myristicaceae spec.*	medium	40	66,91	24	S 01° 56,592'	E 102° 34,958'
Forest TNBD Permatang Kabau	PF18	indet	*Lauraceae spec.*	smooth	35	49,34	20	S 01° 56,555'	E 102° 34,917'
Forest TNBD Permatang Kabau	PF19	indet	*indet.*	smooth	50	93,58	24	S 01° 56,554'	E 102° 34,956'
Forest TNBD Permatang Kabau	PF20	indet	*indet.*	heavy	38	51,69	18	S 01° 56,562'	E 102° 34,994'
Forest TNBD Permatang Kabau	PF21	Euphorbiaceae	*Hydnocarpus cf. kunstleri*	smooth	25	41,76	15	S 01° 56,558'	E 102° 34,977'
Forest TNBD Permatang Kabau	PF22	indet	*indet.*	medium	40	80,15	25	S 01° 56,579'	E 102° 34,993'
Forest TNBD Permatang Kabau	PF23	indet	*indet.*	medium	30	44,31	17	S 01° 56,541'	E 102° 34,985'
Forest TNBD Permatang Kabau	PF24	indet	*Aglaia eximia*	smooth	33	55,86	13	S 01° 56,443'	E 102° 34,898'
Forest TNBD Permatang Kabau	PF25	indet	*indet.*	smooth	32	53,86	16	S 01° 56,622'	E 102° 34,894'
Forest TNBD Dusun Baru	PF26	indet	*indet.*	smooth	55	90,94	25	S 01° 59,709'	E 102° 45,140'
Forest TNBD Dusun Baru	PF27	indet	*indet.*	medium	40	86,68	18	S 01° 59,673'	E 102° 45,082'
Forest TNBD Dusun Baru	PF28	indet	*indet.*	smooth	40	77,38	21	S 01° 58,901'	E 102° 45,049'
Forest TNBD Dusun Baru	PF29	indet	*indet.*	smooth	45	62,45	19	S 01° 58,930'	E 102° 45,037'

Forest TNBD Dusun Baru	PF30	indet	*indet.*	smooth	50	88,59	25	S 01° 58,893'	E 102° 45,016'
OPP Permatang Kabau	OPP01	Arecaceae	*Elaeis guineensis*	heavy	8	65,03	3,4	S 01° 57,253'	E 102° 35,697'
OPP Permatang Kabau	OPP02	Arecaceae	*Elaeis guineensis*	heavy	8	61,12	3,4	S 01° 57,225'	E 102° 35,683'
OPP Permatang Kabau	OPP03	Arecaceae	*Elaeis guineensis*	heavy	10	72,57	5,3	S 01° 57,268'	E 102° 35,668'
OPP Permatang Kabau	OPP04	Arecaceae	*Elaeis guineensis*	heavy	9	67	4,5	S 01° 57,222'	E 102° 35,651'
OPP Permatang Kabau	OPP05	Arecaceae	*Elaeis guineensis*	heavy	9	67,96	3,4	S 01° 57,333'	E 102° 35,695'
OPP Permatang Kabau	OPP06	Arecaceae	*Elaeis guineensis*	heavy	8	77,35	3	S 01° 57,333'	E 102° 35,723'
OPP Permatang Kabau	OPP07	Arecaceae	*Elaeis guineensis*	heavy	10	58,45	5	S 01° 58,255'	E 102° 34,796'
OPP Permatang Kabau	OPP08	Arecaceae	*Elaeis guineensis*	heavy	11	84,99	8	S 01° 58,285'	E 102° 34,804'
OPP Permatang Kabau	OPP09	Arecaceae	*Elaeis guineensis*	heavy	11	79,74	6,5	S 01° 58,315'	E 102° 34,808'
OPP Permatang Kabau	OPP10	Arecaceae	*Elaeis guineensis*	heavy	10	86,74	6	S 01° 58,353'	E 102° 34,803'
OPP Permatang Kabau	OPP11	Arecaceae	*Elaeis guineensis*	heavy	11	62,01	7	S 01° 58,392'	E 102° 34,778'
OPP Permatang Kabau	OPP12	Arecaceae	*Elaeis guineensis*	heavy	12	58,95	7,7	S 01° 58,384'	E 102° 34,823'
OPP Permatang Kabau	OPP13	Arecaceae	*Elaeis guineensis*	heavy	12	65,44	8	S 01° 58,344'	E 102° 34,835'
OPP Permatang Kabau	OPP14	Arecaceae	*Elaeis guineensis*	heavy	8	60,64	4,8	S 01° 58,297	E 102° 34,831'
OPP Permatang Kabau	OPP15	Arecaceae	*Elaeis guineensis*	heavy	10	79,58	5	S 01° 58,260'	E 102° 34,828'
OPP Lubuk Kepayang	OPP16	Arecaceae	*Elaeis guineensis*	heavy	6	73,53	3	S 02° 04,534'	E 102° 47,509'
OPP Lubuk Kepayang	OPP17	Arecaceae	*Elaeis guineensis*	heavy	7	80,88	3,7	S 02° 04,510'	E 102° 47,524'
OPP Lubuk Kepayang	OPP18	Arecaceae	*Elaeis guineensis*	heavy	7	82,82	3,3	S 02° 04,526'	E 102° 47,550'
OPP Lubuk Kepayang	OPP19	Arecaceae	*Elaeis guineensis*	heavy	7	80,5	3,3	S 02° 04,554'	E 102° 47,540'
OPP Lubuk Kepayang	OPP20	Arecaceae	*Elaeis guineensis*	heavy	9	66,97	4,5	S 02° 04,243'	E 102° 47,555'
OPP Lubuk Kepayang	OPP21	Arecaceae	*Elaeis guineensis*	heavy	8	59,08	4	S 02° 04,247'	E 102° 47,584'
OPP Lubuk Kepayang	OPP22	Arecaceae	*Elaeis guineensis*	heavy	11	78,43	5,5	S 02° 04,269'	E 102° 47,571'
OPP Lubuk Kepayang	OPP23	Arecaceae	*Elaeis guineensis*	heavy	10	75,69	4,5	S 02° 04,271'	E 102° 47,660'
OPP Lubuk Kepayang	OPP24	Arecaceae	*Elaeis guineensis*	heavy	12	81,77	5,4	S 02° 04,261'	E 102° 47,639'
OPP Lubuk Kepayang	OPP25	Arecaceae	*Elaeis guineensis*	heavy	12	70,28	6	S 02° 04,296'	E 102° 47,638'
OPP Lubuk Kepayang	OPP26	Arecaceae	*Elaeis guineensis*	heavy	13,5	82,82	6,6	S 02° 04,296'	E 102° 47,579'
OPP Lubuk Kepayang	OPP27	Arecaceae	*Elaeis guineensis*	heavy	8	81,55	3,5	S 02° 04,254'	E 102° 47,523'
OPP Lubuk Kepayang	OPP28	Arecaceae	*Elaeis guineensis*	heavy	15	79,67	3,5	S 02° 04,266'	E 102° 47,496'
OPP Lubuk Kepayang	OPP29	Arecaceae	*Elaeis guineensis*	heavy	9	77,06	3,6	S 02° 04,240'	E 102° 47,482'
OPP Lubuk Kepayang	OPP30	Arecaceae	*Elaeis guineensis*	heavy	8	80,02	3,5	S 02° 04,284'	E 102° 47,523'

Persönliche Erklärung

Hiermit erkläre ich, dass ich die vorliegende Masterarbeit zum Thema „Diversität vaskulärer Epiphyten im Tieflandregenwald und in Ölpalmenplantagen auf Sumatra (Indonesien)" selbständig und nur unter Verwendung der angegebenen Hilfsmittel verfasst habe. Die Stellen der Masterarbeit, die anderen Quellen im Wortlaut oder dem Sinn nach entnommen wurden, sind durch Angaben der Herkunft kenntlich gemacht.

(Datum, Unterschrift)