



Effects of land-use change on vascular epiphyte diversity in Sumatra (Indonesia)



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ARTICLE INFO

Article history:

Received 15 September 2015

Received in revised form 3 August 2016

Accepted 8 August 2016

Available online xxxx

Keywords:

Agroforest
Jungle rubber
Oil palm
Epiphytes
Southeast Asia
Tropical rainforest

ABSTRACT

Land-use change is the main driver of biodiversity loss in the tropics worldwide. Lowland rainforest regions in Southeast Asia are experiencing particularly high rates of large-scale conversion of forests and agroforests into monocultural tree plantations including oil palm and rubber with devastating effects on forest-dependent species. Canopy-dwelling organisms such as epiphytes are expected to be particularly susceptible to changes in land use, vegetation structure, and microclimate but the consequences of these changes are only poorly known for this plant group in Southeast Asia. We investigated the diversity of vascular epiphytes in four major land-use systems in Jambi Province (Sumatra, Indonesia). Epiphyte communities were sampled in 120 20 × 20 m plots in Bukit Duabelas National Park (lowland rainforest) and in surrounding jungle rubber agroforests as well as in rubber and oil palm plantations owned by smallholders. At plot level, lowland rainforest, jungle rubber, and oil palm were statistically indistinguishable in terms of richness, diversity, and evenness but had significantly higher values than rubber. Oil palm plantations had the highest epiphyte abundance, but lowest total species number of all systems. Furthermore, oil palm had distinct, fern-dominated epiphyte communities that differed significantly from the other systems. In conclusion, the value of monocultural tree plantations of oil palms and rubber trees for epiphyte conservation is very low. Jungle rubber, an extensively managed yet vanishing system, represents a refuge for epiphytes and could play a vital role in conserving epiphyte diversity, especially of ferns and orchids. Non-orchid angiosperms, however, mainly occurred in forest and are thus most threatened by forest conversion.

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1. Introduction

Tropical rainforests are of paramount importance for conserving the world's biodiversity (Gibson et al., 2011) and provide crucial ecosystem services including climate regulation and carbon storage and sequestration (Bonan, 2008; Dixon et al., 1994). Rising global demands for tropical agricultural products put tropical forests under enormous pressure from deforestation and conversion into agricultural land (Laurance et al., 2014). Furthermore, there is an on-going trend of intensification within existing agricultural areas in many tropical regions; e.g. a conversion of diverse agroforestry systems into monocultural cash crop plantations (Perfecto and Vandermeer, 2008; Tschardt et al., 2011).

Land-use change and intensification are particularly dramatic in Indonesia (Koh et al., 2004), which has experienced the largest increase in deforestation worldwide and currently loses 2 million ha yr⁻¹ of forest cover (Hansen et al., 2013). Increasing deforestation rates are mainly due to the country's role as the world-leading palm oil and rubber producer (Koh and Wilcove, 2008) and an expansion of lands for mining or large-scale plantations of fast-growing trees (Abood et al., 2015). At the same time, Indonesia is one of the most biodiversity-rich countries (Barthlott et al., 2005; Koh and Ghazoul, 2008), a globally outstanding biodiversity hotspot (Myers et al., 2000), and still containing the greatest portion of Southeast Asia's remaining forests (Koh and Wilcove, 2007; Sodhi et al., 2004). The Indonesian island of Sumatra is an epicenter of the recent oil-palm and rubber expansion (Miettinen et al., 2011), which was responsible for 2.9 million hectares loss of Sumatra's forests between 2000 and 2012 (Margono et al., 2014). Following large-scale logging between 1970 and 2000, much previous lowland rainforest areas have been converted to jungle rubber agroforests and increasingly to large-scale monocultures of oil palm (*Elaeis guineensis* Jacq.), rubber (*Hevea brasiliensis* (Willd.) Müll. Arg.),

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and *Acacia* spp. plantations for pulp production (Beukema et al., 2007). Magnitude and scale of agricultural expansion in Southeast Asia are leading to conflicts between economic interests, the demand for food and other natural resources, and nature conservation. Oil palm, for instance, is one of the world's most rapidly increasing crops (Fitzherbert et al., 2008) and recent studies have shown that the conversion from lowland rainforest to oil palm plantation leads to losses in species richness, density, and biomass (Foster et al., 2011; Drescher et al., 2016), but also to a serious loss in ecosystem functionality (Barnes et al., 2014) that might hamper economic development and human well-being in the long-run (Dislich et al., early online).

Vascular epiphytes are an important element of tropical rainforests, provide various ecological functions including habitat, food, and shelter for a great number of animal species (Ellwood and Foster, 2004; Méndez-Castro and Rao, 2014; Nadkarni and Matelson, 1989), and contribute to the regulation of water and nutrient cycles (Díaz et al., 2010; Nadkarni et al., 2004). Their host-tree dependency makes epiphytes particularly vulnerable to deforestation and changes in forest structure generally leading to a loss in epiphyte diversity (Köster et al., 2009). The conversion from rainforest into agroforestry systems or tree monocultures, however, provides a potential habitat for epiphytes, and some plantation systems have been shown to harbor a substantial portion of the forest epiphyte community (e.g. Haro-Carrión et al., 2009; Hietz, 2005).

Forest conversion is usually accompanied by changes in canopy cover, radiation, temperature, and humidity (Luskin and Potts, 2011; Drescher et al., 2016), factors that are key factors for epiphytes (Petter et al., 2016). In contrast to terrestrial species, epiphytes lack the access to soil water and are expected to be more sensitive towards changes in temperature and humidity (Benzing, 1990). Therefore, the conversion of forest into tree crop monocultures is expected to cause changes in epiphyte diversity and community composition. There is a comparatively rich literature on epiphyte–arthropod associations from Southeast Asia (e.g. Clausen, 1998; Fayle et al., 2005, 2010), but few studies investigate how epiphytes are affected by land-use change. For instance, Beukema et al. (2007) found lower diversity of epiphytic pteridophytes in Sumatran rubber agroforests than in rainforests. Prescott et al. (2015) showed that the common practice of epiphyte removal in oil palm plantations does not affect yields in Borneo.

We investigated the effects of land-use change and intensification on vascular epiphyte diversity in Sumatran lowland rainforest and three regionally important agricultural systems: jungle rubber agroforests, rubber plantations, and oil palm plantations. Plot-based species inventories were carried out in Jambi Province (Sumatra, Indonesia). We hypothesized that (1) epiphyte diversity is higher in forest than in agricultural systems; (2) rainforest and jungle rubber comprise epiphyte communities that are composed of species restricted to one system whereas epiphyte communities in monocultural plantations consist of more widely distributed habitat generalists; (3) changes in epiphyte diversity are linked to changes and differences in microclimatic conditions and host tree characteristics.

2. Material and methods

2.1. Study sites

Fieldwork was conducted from March to April 2013 and from August to September 2014 in the project region of the EForTS project (Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems (Sumatra, Indonesia); www.uni-goettingen.de/EForTS) in the lowlands of Jambi Province in central Sumatra (Indonesia) (cf. Drescher et al. (2016) for a detailed description of the project and the study area). The study region was located 50–90 km southwest of Jambi City. Jambi City has a mean annual temperature of 27.4 °C and receives c. 2235 mm of precipitation per year with two peak rainy seasons around March and December (Drescher et al.,

2016). We studied the epiphyte flora in old-growth forests inside Bukit Duabelas National Park (BDNP) and in adjacent jungle rubber, rubber plantations and oil palm plantations. BDNP was established in 2000 and covers about 60,500 ha (Kusuma and Hendrian, 2011). The natural vegetation of BDNP is dipterocarp-dominated lowland rainforest (Laumonier, 1997). The topography of the park ranges from 50 to 438 m a.s.l., but our plots were all located <100 m a.s.l. BDNP is affected by different kinds and intensities of human activities including shifting cultivation by indigenous people (Orang Rimba) (Sager, 2008), selective logging, and illegal plantations. BDNP thus classifies as primary degraded forest sensu Margono et al. (2014): primary forest with partial canopy loss and altered forest composition and structure due to selective logging or other human disturbances (hereinafter referred to as 'forest'). Jungle rubber is an extensively managed smallholder agroforestry system of rubber trees planted in degraded old-growth or secondary forests (Gouyon et al., 1993; Wibawa et al., 2005). Jungle rubber agroforestry has been established in Sumatra since the early 20th century (Joshi et al., 2002). The rubber and oil palm plantations studied were 7–16 years (rubber) and 8–15 years old (oil palm), monocultures owned by smallholders.

2.2. Epiphyte sampling and identification

We established a total of 120 plots with 30 plots in each of the four land-use systems. Each plot measured 20 × 20 m and contained one central host tree which was examined for the presence and abundance of vascular epiphytes following the protocol of Gradstein et al. (2003). Additionally, all epiphytes were recorded within the first 2 m of all other trees with a diameter at breast height (DBH, measured at 1.30 m above ground) ≥ 10 cm within the plot (Gradstein et al., 2003). Epiphytes were defined as non-parasitic plants germinating and growing on trees (Zotz, 2013). Accidental epiphytes (Benzing, 1990; Ibsch, 1996), i.e. terrestrial species occasionally growing epiphytically, were recorded for completeness but excluded from statistical analyses. Plots were randomly placed in the field with a minimum distance of 50 m from each other. Host trees in forest and jungle rubber required additional attributes to guarantee climbing safety. Therefore, only trees with a minimum DBH of ≥40 cm were chosen. Trees in forest and jungle rubber were climbed with single-rope climbing techniques modified after Perry (1978). In jungle rubber, only native host tree species were investigated. Due to the low stature of trees in rubber and oil palm plantations, epiphytes were surveyed with binoculars and cameras (Flores-Palacios and García-Franco, 2001). For all central host trees, we recorded DBH and bark texture (smooth, medium, rough, oil palm). Epiphytes were distinguished as morphospecies in the field and if possible three herbarium specimens per morphospecies were collected for later identification at Herbarium Bogoriense (BZ), and the herbarium of the Southeast Asian Regional Center for Tropical Biology (SEAMEO BIOTROP; BIOT) where specimens were deposited (collection numbers Tim Böhnert TB01–TB93 and Arne Wenzel A01–A96–). The species and higher-level taxa names follow The Plant List (2013) and The Angiosperm Phylogeny Group (2009). To analyze differences in the floristic composition between land-use systems, epiphyte species were grouped into 'orchids' (family Orchidaceae), 'ferns' (monilophytes and lycophytes) and 'other angiosperms' (flowering plants excluding Orchidaceae; Barthlott et al., 2001).

2.3. Microclimatic analyses

To examine the vertical variation in stand microclimatic conditions across land-use systems, we installed two data loggers (iButton®, Hydrochron temperature/relative humidity logger) in one tree per land-use system. One data logger was placed near the trunk base and one in the outer tree crown (forest: 1.5 and 32 m, jungle rubber: 1.4 and 26.5 m, rubber: 1.7 and 10.5 m, oil palm: 0.7 m and 3.4 m). In case of oil palms, the upper logger was installed among the leaf bases

near the meristem. Temperature (°C) and relative humidity (%) measurements were recorded in parallel at tree base and crown over a period from 15 March–4 April 2013 in forest, 9 April–15 April 2013 in oil palm and rubber plantations, and from 15 August–24 September 2014 in jungle rubber. From these measurements, we calculated the range in mean diurnal variations in temperature and humidity between trunk base and crown. As it was logistically not possible to take parallel measurements at tree crown and base at the same time in all four land-use systems, we used reference climate data from four meteorological stations per land-use system: air temperature (°C) and relative humidity (%) were measured hourly from May/June 2013 until October 2014 using Galltec Mela® thermo-hygrometers placed at a height of 2 m above ground. Data were stored in an UIT LogTrans 16-GPRS data logger. For each land-use system, mean daily averages of air temperature and humidity from the reference meteorological stations were calculated and shown in curves. The mean diurnal ranges between climatic conditions at tree base and crown were plotted in relation to the climate curves from the meteorological stations from each land-use system.

2.4. Statistical analyses

To estimate and compare the total species number per system, we calculated species accumulation curves for each system with Kindt's exact accumulator method (Ugland et al., 2003) and Chao2 richness estimator values (Magurran, 2004). Species and individual numbers, inverse Simpson's diversity index (1/D) and Pielou's evenness (Magurran, 2004) were used to compare epiphyte communities at the plot level. To detect differences in epiphyte diversity between the different land-use systems, we used analyses of variance (ANOVA) and subsequent simultaneous tests for general linear hypotheses and Tukey's all-pairwise comparisons of means (Hothorn et al., 2008; Herberich et al., 2010). Differences in epiphyte colonization of host trees with different bark textures were analyzed with Kruskal-Wallis rank sum tests and multiple comparison tests after Kruskal-Wallis. Further, we used simple linear regression models to assess the relationship between epiphyte species richness and abundance and phorophyte basal area in each land-use system. The floristic composition of the plots in the four systems was analyzed with abundance based non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity, a widely used and efficient way to compute between-sample dissimilarities (Clarke et al., 2006; McCune et al., 2002). Plots with less than two individuals were excluded. Based on ordination results, differences between land-use systems were tested using analysis of similarities (ANOSIM) and the Bray-Curtis distance metric (Warton et al., 2012). All statistical analyses were conducted in the statistic software R version 3.0.2 (R Core Team, 2013) using the packages *vegan* version 2.2-1 (Oksanen et al., 2013), *multcomp* version 1.3-7 (Hothorn et al., 2008), *pgirmess* version 1.6.4 (Giraudoux, 2016), *sandwich* version 2.3-2 (Zeileis, 2004, 2006), and *RColorBrewer* (Neuwirth, 2014).

3. Results

3.1. Species richness and abundance

In the 120 plots, we recorded a total of 3913 individuals of vascular epiphytes from 78 species and 15 families (21 families including accidental epiphytes; Table 1). Accidental epiphytes including some non-native species were abundant in oil palm plantations where they accounted for 26% of all individuals recorded. In contrast, accidental epiphytes were absent in forest, jungle rubber and rubber plantations.

The total number of epiphyte individuals in jungle rubber and oil palm plantations surpassed the other systems by far (49% of all individuals were recorded in jungle rubber and 34% in oil palm, Table 2). Jungle rubber had a total of 45 species, the highest overall richness of all investigated systems. Oil palm plantations in turn had the lowest overall richness (9 species, 6 families, Table 2). Rubber plantations had

slightly higher total species numbers (11 species, 6 families) than oil palm plantations but lowest total individual count (88). Jungle rubber surpassed forest (43 species) in terms of species numbers, but family diversity was higher in forest (14 families) than in jungle rubber (9 families).

The majority of epiphyte species in forest and jungle rubber were exclusively recorded in these particular systems, while most species in the plantations were also found in the other land-use systems (Fig. 1). 63% of the species recorded in forest and 67% of the species in jungle rubber were exclusively found in the respective system. Most species recorded in the plantations, on the other hand, were also found in forest and jungle rubber. Species restricted to plantations were *Myrmecophila sinuosa* (Hook.) Nakai ex H. Itô in rubber and *Asplenium longissimum* Blume and *Cyrtandra oblongifolia* (Blume) C.B. Clarke in oil palm plantations. Only three species (*Asplenium nidus* L., *Davallia denticulata* (Burm. f.) Mett. ex Kuhn and *Vittaria elongata* Sw.) were encountered in all four systems.

Species-accumulation curves indicated that the species sampling of 30 plots per system approached an asymptote for rubber and oil palm plantations (Fig. 2). However, continued sampling is expected to result into higher overall species richness in forest and jungle rubber as their species accumulation curves have not yet reached an asymptote. According to Chao species richness estimators, 100% of the estimated species in oil palm plantations were recorded in our survey. In the other land-use systems, estimated species numbers exceeded our observations: in forest, 63% of 67.9 estimated species were recorded, in jungle rubber 58% of 76.9 estimated species, and in rubber plantation 65% of 16.8 estimated species. Continued sampling would therefore likely lead to higher species numbers in forest, jungle rubber and rubber, but not in oil palm plantations.

At plot level, the four land-use systems differed significantly in terms of species richness, abundance, diversity, and evenness (Fig. 3). In all four aspects, rubber plantations had significantly lower values than any other system. This was partly driven by the fact that epiphytes were completely absent in 16 of the 30 sampled rubber plots. Forest, jungle rubber, and oil palm plots were statistically indistinguishable from each other in terms of richness, diversity and evenness. Oil palm plots had on average the highest epiphyte abundance, but some outliers in forest and especially jungle rubber reached much higher epiphyte abundance (Fig. 3b). The low total richness of epiphytes in oil palm plantations in combination with relatively high plot-level richness (Fig. 3a) and diversity (Fig. 3c), indicates relatively high alpha but very low levels of beta diversity (meaning that mostly the same species occurred in each plot).

3.2. Floristic composition

The epiphyte communities of each land-use system were dominated by a different set of species which were often absent or rare in other systems (Table 1). In oil palm plantations, for example, 81% of all recorded epiphyte individuals belonged to only three dominant fern species: *Nephrolepis biserrata* (Sw.) Schott, *Davallia denticulata* and *Goniophlebium percussum* (Cav.) Wagner & Grether. The most abundant species in forest (*Phalaenopsis cornu-cervi* (Breda) Blume & Rchb.f.) and jungle rubber (*Antrophyum callifolium* Blume) in turn were absent in the plantations and even species that occurred in more than two land-use systems often varied in their importance: *Asplenium nidus* was the most abundant species in rubber plantations and was also among the most common species in forest and jungle rubber, but in oil palm plantations it was less abundant. Here, the most abundant species was *Nephrolepis biserrata*, a species that is comparatively rare in forest and jungle rubber and absent in rubber plantations.

The composition of epiphyte communities at higher taxonomic level varied strongly between the different land-use systems. The monocultural plantations were clearly dominated by ferns both in terms of individual and species numbers. Orchids and other angiosperms with a few exceptions were restricted to lowland rainforest and jungle

Table 1

Individual numbers of epiphytes and accidental epiphytes in the four land-use systems: F - forest, J - jungle rubber, R - rubber plantations, O - oil palm plantations, total - total number of individuals per species. Epiphyte species are sorted after plant group (ferns, orchids, other angiosperms) and family. Naturalized alien species are marked by * based on the [Global Invasive Species Database \(2016\)](#).

Family	Species	Author	F	J	R	O	Total	
Ferns								
Aspleniaceae	<i>Asplenium glaucophyllum</i>	Alderw.	1	–	–	16	17	
	<i>Asplenium longissimum</i>	Blume	–	–	–	46	46	
	<i>Asplenium nidus</i>	L.	27	183	27	28	265	
Davalliaceae	<i>Davallia denticulata</i>	(Burm. f.) Mett. ex Kuhn	9	106	5	255	375	
	<i>Davallia triphylla</i>	Hook.	16	3	–	–	19	
	<i>Humata heterophylla</i>	(Sm.) Desv.	–	1	–	–	1	
	<i>Humata repens</i>	(L. f.) J. Small ex Diels	–	2	–	–	2	
Lycopodiaceae	<i>Huperzia cf. carinata</i>	(Desv. ex Poir.) Trevis.	6	–	–	–	6	
	<i>Huperzia phlegmarioides</i>	Rothm.	1	–	–	–	1	
	<i>Huperzia</i> sp. 1		–	60	–	–	60	
Nephrolepidaceae	<i>Nephrolepis biserrata</i>	(Sw.) Schott	3	23	–	677	703	
Polypodiaceae	<i>Aglaomorpha speciosa</i>	(Blume) M.C. Roos	–	3	–	–	3	
	<i>Drynaria quercifolia</i>	(L.) J. Sm.	42	125	10	–	177	
	<i>Goniophlebium percussum</i>	(Cav.) Wagner & Grether	3	1	–	161	165	
	<i>Microsorium punctatum</i>	(L.) Copel.	–	30	–	–	30	
	<i>Myrmecophila sinuosa</i>	(Hook.) T. Nakai ex H. Itô	–	–	12	–	12	
	<i>Phymatosorus scolopendria</i> *	(Burm. f.) Pic. Serm.	–	5	–	–	5	
	<i>Platyserium coronarium</i>	(Mull.) Desv.	–	2	9	–	11	
	<i>Polypodiaceae</i> sp. 1		–	1	–	–	1	
	<i>Pyrrosia adnascens</i>	(Burm. f.) C.V. Morton	–	–	4	–	4	
	<i>Pyrrosia angustata</i>	(Sw.) Ching	18	3	2	–	23	
	<i>Pyrrosia lanceolata</i>	(L.) Farw.	–	7	–	–	7	
	<i>Pyrrosia piloselloides</i>	(L.) M.G. Price	60	23	10	–	93	
	Vittariaceae	<i>Antrophyum callifolium</i>	Blume	–	540	–	–	540
		<i>Monogramma</i> sp. 1		–	12	–	–	12
		<i>Vittaria elongata</i>	Sw.	58	54	1	64	177
<i>Vittaria ensiformis</i>		Sw.	23	220	–	94	337	
Orchids								
Orchidaceae	<i>Acriopsis densiflora</i>	Lindl.	1	26	–	–	27	
	<i>Acriopsis liliifolia</i>	(J. König) Seidenf.	1	6	–	–	7	
	<i>Bulbophyllum</i> sp. 1		5	–	–	–	5	
	<i>Bulbophyllum</i> sp. 2		3	–	–	–	3	
	<i>Bulbophyllum</i> sp. 3		26	–	–	–	26	
	<i>Bulbophyllum</i> sp. 4		4	–	–	–	4	
	<i>Bulbophyllum</i> sp. 5		–	1	–	–	1	
	<i>Bulbophyllum</i> sp. 6		–	23	–	–	23	
	<i>Bulbophyllum</i> sp. 7		–	3	–	–	3	
	<i>Bulbophyllum</i> sp. 9		–	51	–	–	51	
	<i>Cleisostoma subulatum</i>	Blume	–	21	–	–	21	
	<i>Dendrobium aloifolium</i>	(Blume) Rchb.f.	–	9	–	–	9	
	<i>Dendrobium compressistylum</i>	J.J. Sm.	50	–	–	–	50	
	<i>Dendrobium crumenatum</i>	Sw.	31	23	7	–	61	
	<i>Dendrobium indragiriense</i>	Schltr.	16	5	–	–	21	
	<i>Dendrobium leonis</i>	(Lindl.) Rchb.f.	–	330	–	–	330	
	<i>Dendrobium</i> sp. 1		10	–	–	–	10	
	<i>Dendrobium</i> sp. 2		–	1	–	–	1	
	<i>Dendrobium</i> sp. 3		–	1	–	–	1	
	<i>Eria</i> sp. 1		–	1	–	–	1	
	<i>Grammatophyllum speciosum</i>	Blume	5	–	–	–	5	
	<i>Liparis</i> sp. 1		–	1	–	–	1	
	<i>Luisia</i> sp. 1		4	–	–	–	4	
	Orchidaceae sp. 4		1	–	–	–	1	
	Orchidaceae sp. 8		1	–	–	–	1	
	Orchidaceae sp. 9		–	1	–	–	1	
	Orchidaceae sp. 10		–	1	–	–	1	
	<i>Phalaenopsis cornu-cervi</i>	(Breda) Blume & Rchb.f.	64	–	–	–	64	
	<i>Pomatocalpa diffusum</i>	Breda	–	16	–	–	16	
	<i>Pomatocalpa</i> sp. 1		–	2	–	–	2	
	<i>Pteroceras</i> sp. 1		1	–	–	–	1	
	<i>Thelasis</i> sp. 1		–	1	–	–	1	
	<i>Trichotosia cf. ferox</i>	Blume	1	–	–	–	1	
	Other angiosperms							
	Apocynaceae	<i>Dischidia imbricata</i>	(Blume) Steud.	22	–	1	–	23
		<i>Hoya cf. revoluta</i>	(L.f.) R. Br.	13	–	–	–	13
Araceae	<i>Philodendron</i> sp. 1		1	–	–	–	1	
Clusiaceae	<i>Clusia</i> sp. 1		1	–	–	–	1	
Gesneriaceae	<i>Cyrtandra oblongifolia</i>	(Blume) C.B. Clarke	–	–	–	3	3	
Melastomataceae	Melastomataceae sp. 1		6	–	–	–	6	
	Melastomataceae sp. 2		1	–	–	–	1	
	Melastomataceae sp. 3		2	–	–	–	2	

(continued on next page)

Table 1 (continued)

Family	Species	Author	F	J	R	O	Total
	Melastomataceae sp. 4		2	–	–	–	2
	Melastomataceae sp. 5		–	1	–	–	1
	Melastomataceae sp. 6		–	1	–	–	1
Moraceae	<i>Ficus deltoidea</i>	Jack	–	2	–	–	2
	<i>Ficus</i> sp. 1		2	–	–	–	2
	<i>Ficus</i> sp. 2		2	–	–	–	2
	<i>Ficus</i> sp. 4		1	–	–	–	1
	<i>Ficus</i> sp. 5		–	2	–	–	2
Piperaceae	<i>Peperomia</i> sp. 1		2	–	–	–	2
Rubiaceae	<i>Hydnophytum</i> cf. <i>formicarum</i>	Jack	2	–	–	–	2
			548	1933	88	1344	3913
Accidental epiphytes							
Acanthaceae	<i>Asystasia gangetica</i> *	(L.) T. Anderson	–	–	–	128	128
Arecaceae	<i>Elaeis guineensis</i> *	Jacq.	–	–	–	99	99
Blechnaceae	<i>Stenochlaena palustris</i>	(Burm. f.) Bedd.	–	–	–	41	41
Euphorbiaceae	<i>Hevea brasiliensis</i> *	(Willd.) Müll. Arg.	–	–	–	7	7
Melastomataceae	<i>Clidemia hirta</i> *	(L.) D. Don	–	–	–	187	187
						462	462

rubber (Table 2). The only angiosperms found in the plantations were the widespread *Dendrobium crumenatum* Sw. (Orchidaceae) and *Dischidia imbricata* (Blume) Steud. (Apocynaceae) in rubber and *Cyrtandra oblongifolia* (Gesneriaceae) in oil palm plantations. Lowland forest was the only system where all three epiphyte groups were almost evenly represented at species level (Table 2). Jungle rubber was dominated by ferns and orchids while other angiosperms were represented by only four species (*Ficus deltoidea* Jack (Moraceae), *Ficus* sp. 5 (Moraceae) and two unidentified Melastomataceae species). *Phalaenopsis cornu-cervi* and *Dendrobium compressistylum* J.J. Sm., which were abundant in forest, were not observed in jungle rubber. In all four systems, ferns were the most abundant group. While jungle rubber also harbored many orchids, this family was represented by only one species with 7 individuals in rubber plantations and completely absent in oil palm plantations. The number of other angiosperms was much higher in rainforest (10%) than in the other systems (around 1%).

NMDS ordination and analyses of similarity revealed significant differences in the floristic composition between the four systems (Fig. 4, ANOSIM: $R = 0.55$, $p = 0.001$, NMDS stress value = 0.179, see also Supplementary Table 2). The floristic composition of forest, jungle rubber and partly also rubber plantations showed similarities based on the degree of overlap in confidence areas. Epiphyte communities in oil palm plantations, on the other hand, were clearly distinct from the other systems. Jungle rubber plots with very high individual numbers (outliers in Fig. 3b) appeared outside the jungle rubber confidence area but within the forest confidence area indicating a higher floristic similarity to forest plots than to other jungle rubber plots.

3.3. Host tree characteristics

We found significant differences between epiphyte diversity and abundance on host trees with different bark textures (abundance/bark: Kruskal-Wallis chi-squared = 24.207, $df = 3$, p -value = 2.261e–05;

species richness/bark: Kruskal-Wallis chi-squared = 50.23, $df = 3$, p -value = 7.135e–11). Host trees with a smooth bark had significantly less epiphyte species (Supplementary Fig. 1a) and individuals (Supplementary Fig. 1b) than trees with a medium bark and oil palms. Oil palms with their irregular surface were colonized by significantly more epiphyte individuals than trees with smooth or medium bark textures. Host trees with a rough bark had intermediate values and were indistinguishable from other bark texture classes. Epiphyte richness and abundance were positively correlated with the basal area of the central host tree in rubber and abundance with the basal area in jungle rubber (Supplementary Table 3).

3.4. Microclimate

Long-term microclimatic measurements showed strong differences between the studied land-use systems, both in the absolute values and in the diurnal variation. Monocultural plantations were on average warmer and drier and showed stronger differences between day and night in air temperature and relative humidity. Forest had lower temperatures (mean diurnal temperature below 28 °C) and humidity did not fall below 88% indicating cooler and more humid microclimatic conditions compared to the other systems (Fig. 5a,b). Highest mean diurnal temperature (>30 °C) and lowest mean humidity (<70%) occurred in rubber plantations (Fig. 5e,f). Similar differences were observed between the base and the canopy crown, which showed that forest and jungle rubber had a wider range in both air temperature and humidity than the plantations (Fig. 5). At night, mean minimum and maximum temperature/humidity did not differ markedly among the different tree zones. In all land-use systems, temperature reached a minimum around 6:00 a.m. and humidity

Table 2

Total number of species and individuals of vascular epiphytes in four land-use systems divided into three taxonomic groups: ferns, orchids, other angiosperms (others).

	System	Ferns	Orchids	Others	Total
Species	Forest	13	17	13	43
	Jungle rubber	21	20	4	45
	Rubber	9	1	1	11
	Oil palm	8	0	1	9
	Individuals	Forest	267	224	57
	Jungle rubber	1404	523	6	1933
	Rubber	80	7	1	88
	Oil palm	1341	0	3	1344

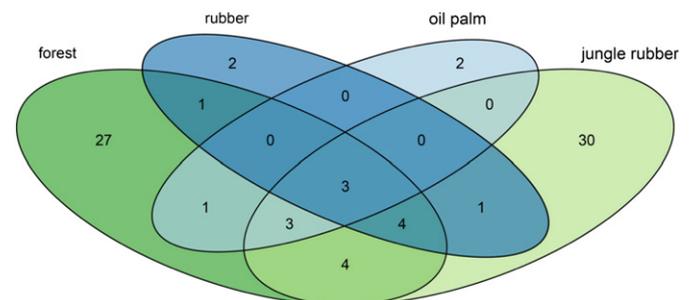


Fig. 1. Venn diagram showing numbers of epiphyte species shared and unique in the four land-use systems.

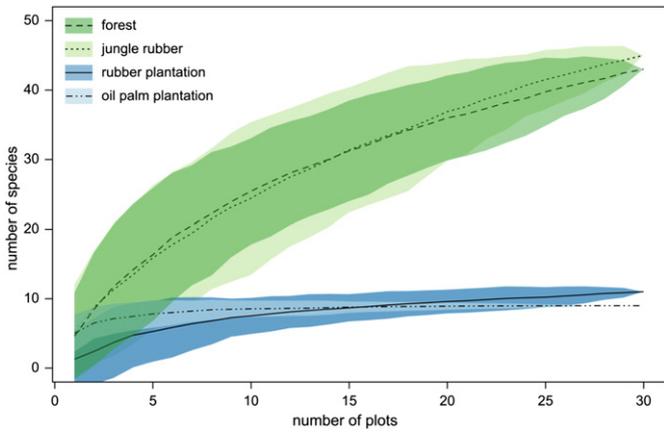


Fig. 2. Species-accumulation curves for vascular epiphytes in the four observed land-use systems. Mean values (lines) and standard deviations (polygons) from 100 permutations of 30 plots per system are shown.

peaked around 8:00–9:00 a.m. During the day, minimum and maximum temperatures/humidity in different zones of the same tree became more separate from each other with up to 4.5 °C and 25% humidity difference in rainforest. Jungle rubber canopies shared the wide range in microclimatic conditions at daytime with forest, but had higher average and maximum temperatures as well as lower humidity (Fig. 5c,d). Oil palm showed the smallest contrast in microclimate between floor and crown and was the only system where the variation in relative humidity between the tree zones was higher at night than during the day (Fig. 5h).

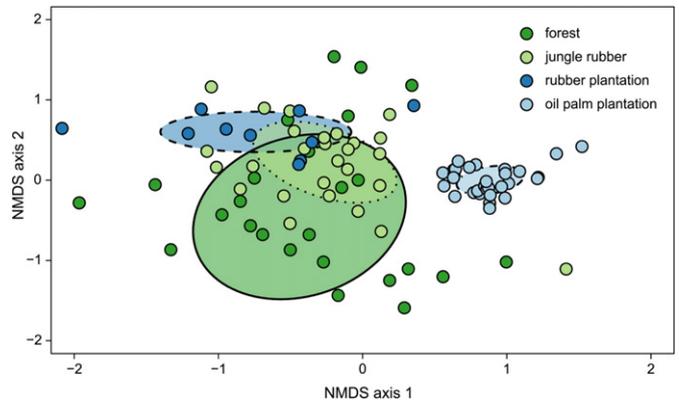


Fig. 4. Floristic composition of study plots. NMDS ordination based on Bray-Curtis dissimilarity of species numbers between plots ($n = 30$ per land-use system). Plots with less than two individuals were excluded (4 forest, 3 jungle rubber, 20 rubber & 1 oil palm plot). Ellipses show core part of the corresponding system. Analysis of Similarity (ANOSIM) indicates a separation between the systems with overlapping elements ($R = 0.55$) and a significance level of $p = 0.001$. Stress-value: 0.179.

4. Discussion

We detected major differences in epiphyte abundance, diversity, and composition among the four land-use systems and these effects were strongly dependent on the spatial scale considered. At the plot level, rubber plantations had significantly lower epiphyte abundance and diversity compared to the other systems. However, total epiphyte diversity was much higher in rainforest and jungle rubber than in rubber and

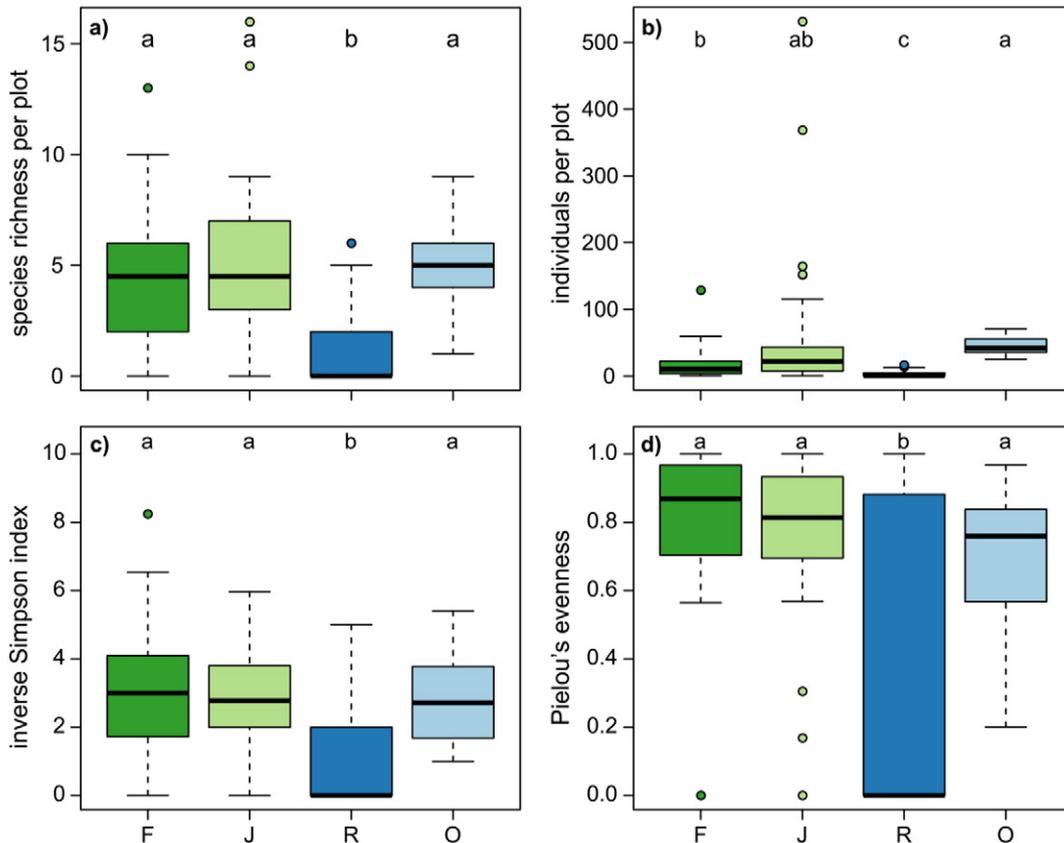


Fig. 3. Plot-level epiphyte species richness (a), abundance (b), diversity (c) and evenness (d) in four different land-use systems (F - forest, J - jungle rubber, R - rubber plantations, O - oil palm plantations, $n = 30$ plots per system). Boxes indicate second and third quartile, whiskers the upper and lower quartile, bold vertical line shows median and dots outlier. Letters indicate significant differences between systems (ANOVA results/Tukey's all pairwise comparisons of means, $p < 0.05$).

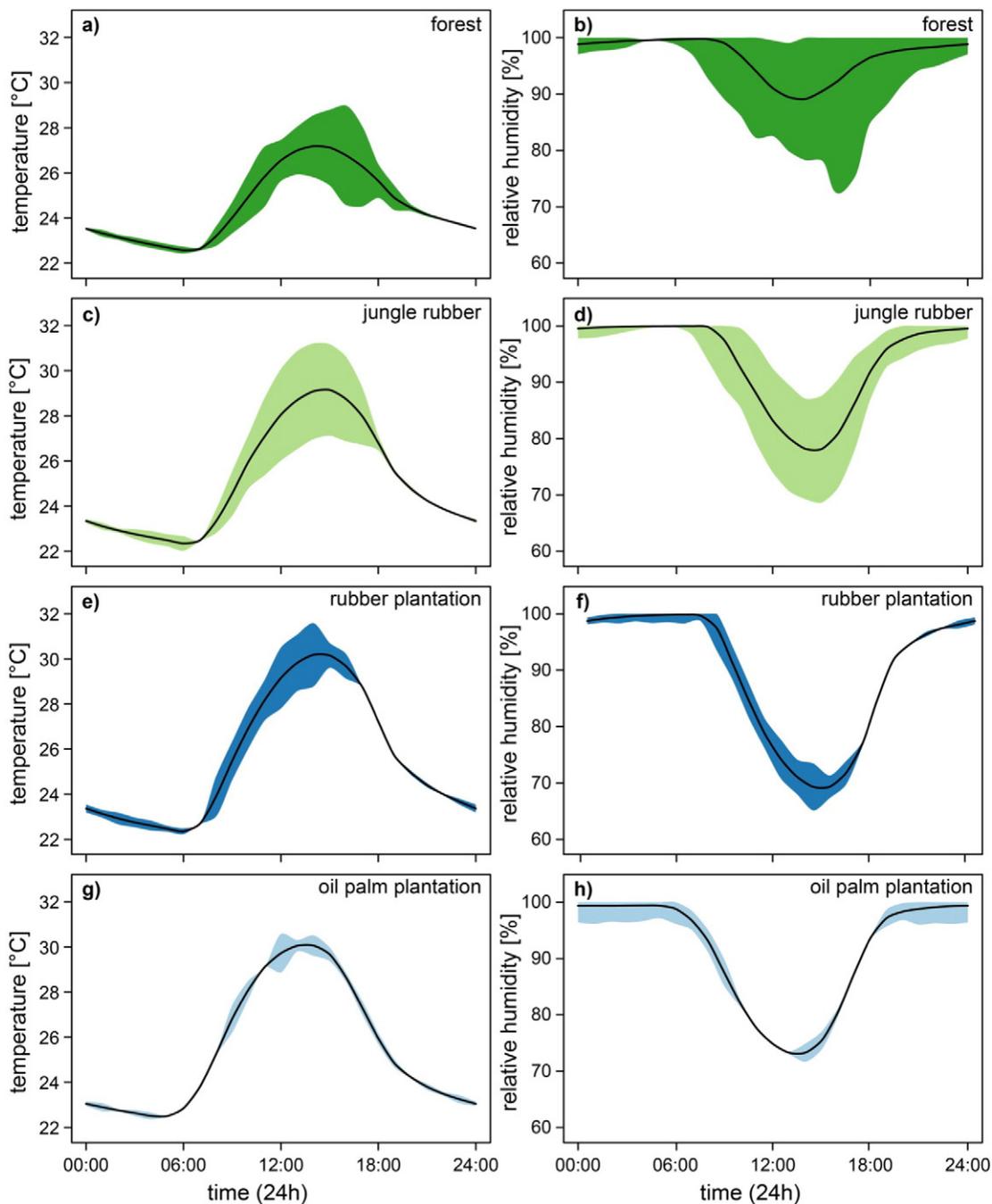


Fig. 5. Average diurnal microclimatic conditions of temperature (°C) and relative humidity (%) measured hourly in meteorological stations from May/June 2013 until October 2014 in four land-use systems (black curves). Colored areas represent differences between parallel measurements at tree base and crown (forest: 1.5 m and 32 m, jungle rubber: 1.4 m and 26.5 m, rubber: 1.7 m and 10.5 m, oil palm: 0.7 m and 3.4 m) measured over a period from 15 March–4 April 2013 in forest, 9 April–15 April 2013 in oil palm and rubber plantations, and from 15 August–24 September 2014 in jungle rubber. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

oil palm plantations. We suggest that three main factors are responsible for the lower epiphyte diversity in plantations: a less favorable and more homogenous microclimate, the age and characteristics of the host trees, and the removal of epiphytes by plantation workers.

4.1. Microclimatic influence

Our climatic measurements show that rubber and oil palm plantations are hotter and less humid than rainforest and jungle rubber. This is in line with a comparison of rainforests and oil palm plantations in Malaysia (Luskin and Potts, 2011). Our measurements at the tree base and in the crown further revealed that rainforest and jungle rubber

show a wider range in microclimatic conditions. Less benign climatic conditions are well known to reduce epiphyte diversity in disturbed forests (Barthlott et al., 2001; Krömer and Gradstein, 2003). Water shortage is generally a strong constraint for epiphytes as they do not have access to soil water (Zotz and Hietz, 2001). Therefore, a more humid microclimate in rainforest and jungle rubber, especially in the lower canopy, provides more suitable conditions for epiphytic growth compared to hotter and drier conditions in the plantations. A greater within-stand variability in microclimatic conditions in turn may provide a larger ecological niche space for a greater number of specialized epiphyte species: dark and humid conditions near the tree base and light and dry conditions in the exposed crown. In plantations, differences in

microclimate between tree base and crown were small, and this may allow only epiphyte species with particular adaptation to grow there (Petter et al., 2016). Long-term measurements of below-canopy air temperature and humidity in the same study area confirm the generally cooler and more humid climate in forest, followed by jungle rubber and then the two monocultures (Drescher et al., 2016). The same study showed that the climatic conditions correspond nicely with higher canopy openness in the plantations.

4.2. Host tree characteristics

Host tree age and co-varying aspects like tree size and structural complexity are important factors structuring epiphyte communities (Zotz and Vollrath, 2003). For instance, in oil palm plantations in the study region, epiphyte diversity increases with oil palm age (Krobbach, 2014). The rubber and oil palm plantations in our study were of intermediate age and thus much younger than the trees in forest and jungle rubber. Consequently, epiphytes had more time for colonization and for developing diverse communities (Taylor and Burns, 2015). Rubber and oil palm plantations are generally replanted after about 25–30 years (Corley and Tinker, 2003) so the plantation management prevents the age-related increase of epiphyte species richness.

Host tree size (represented by basal area) showed significant correlations with epiphyte richness and abundance in rubber plantations. However, results from a case study in the region suggest that old rubber trees in jungle rubber still had lower epiphyte diversity than co-occurring native trees (Beeretz, 2015), which might indicate that rubber trees are generally less suitable host trees regardless of size or age. Possible explanations for the low abundance and diversity of epiphytes in rubber plantations might include the smooth bark (Fig. S1) and drought-deciduous habit of rubber trees. The unusual surface of oil palm stems clearly affect epiphytes: leaf bases of cut oil palm leaves usually stay attached to the trunk for about 20 years where they slowly decay and accumulate organic substrate until they eventually fall down and leave the naked palm trunk (Corley and Tinker, 2003). These decaying leaf bases provide a flowerpot-like habitat that is filled with organic matter and provides nutrients and stores water. These in principle suitable but rather unusual conditions in the canopy of Southeast Asian lowland forests promote dense epiphytic vegetation consisting of a mixture of few dominant epiphytic fern species and terrestrial weeds growing as accidental epiphytes.

4.3. Epiphyte diversity

Surprisingly, jungle rubber even slightly exceeded forest in terms of total epiphyte species richness and number of recorded individuals. At plot level, these differences were less pronounced or absent. One possible explanation could be that forest plots were restricted to accessible parts of BDNP, while jungle rubber sites were widely spread over the landscape. With a more even spatial sampling, the total number of forest species might equal or even surpass jungle rubber. Moreover, richness and abundance in jungle rubber were highly variable. Some host trees in jungle rubber had dense and diverse epiphyte cover (outliers in Fig. 3) while others were almost free of epiphytes. This high variability partly reflects the history of the particular jungle rubber plot. Jungle rubber might originate from degraded old-growth forests enriched with rubber trees or from clear-cut areas where rubber trees grow together with native early successional trees (Gouyon et al., 1993). The former type often harbors tall remnant forest trees which are much older than the rubber trees and are thus able to maintain high epiphyte abundance and diversity (compare Köster et al., 2009; Krömer et al., 2005). The second type of jungle rubber rather resembles secondary forest in terms of age and structure, which are typically less diverse in epiphytes (see e.g. Köster et al., 2009, 2011).

In our study, the epiphyte flora of oil palm plantations consisted of only 9 species. Other studies in Southeast Asian oil palm plantations reported 25 (Nadarajah and Nawawi, 1993) or even 58 (Prescott et al., 2015) species of vascular epiphytes, but mainly because also climbers or accidental epiphyte species were included.

Epiphyte research in Southeast Asia is still in its infancy compared to other tropical regions, and this hampers rigorous comparisons. With a total of 78 species of vascular epiphytes, epiphyte diversity in our study area is rather low compared to the Neo- and Afrotropics. This holds true for individual trees (e.g. >80 species in the Neotropics (Kreft et al., 2004; Krömer et al., 2005) and at plot level (e.g. mean of 67.8 species per plot from the lowlands of Ecuador (Köster et al., 2011)). Comparable study sites in the Neotropics can have >300 species (Köster et al., 2009, 2013; Kreft et al., 2004), and also African sites appear to be richer with c. 100–170 species (Biedinger and Fischer, 1996; Eggeling, 1947; Johansson, 1974; Rembold, 2011). Although species richness estimators suggest that continuing sampling would result into more species in forest, jungle rubber and rubber, we tentatively conclude that the regional species pool of epiphytes in our study region is of moderate size.

4.4. Epiphyte removal by farm workers

An additional reason for the low epiphyte diversity in plantations might be the occasional removal and spraying of epiphytes by farm workers who commonly assume that epiphytes reduce yields by parasitizing on the trees (pers. communication with farm workers). This assumption is widely held, and epiphyte removal is also suggested in pertinent management manuals (see references in Prescott et al., 2015). The risk of epiphytes to harm trees is minor unless the epiphyte cover become so dense that it competes with the tree for light or that trees have to invest more into wood for structural support. A study by Prescott et al. (2015) on the effect of epiphyte coverage and removal on oil palm yield in plantations in Sabah confirmed that epiphytes have no effect on yield. The complex structure of oil palm stems hampers complete epiphyte removal. Mainly larger individuals might be affected by this practice which can be removed by pulling on their fronds while parts of their rhizomes might stay behind. Rubber trees, in contrast, are sparsely colonized by epiphytes anyway so that the removal drastically impacts the epiphyte community.

4.5. Conclusion and conservation implications

Conversion of rainforest into tree monocultures leads to a loss of epiphyte diversity and changes in floristic composition. The loss in diversity was strongly scale-dependent, not easily detectable at the plot level, and most pronounced at landscape scale. In oil palm plantations, a high local abundance and diversity of epiphytes was contrasted with very low total species richness and a floristic composition that was clearly distinct from forest communities. Rubber plantations were characterized by low epiphyte abundance and diversity at all spatial scales, but were more similar to forest than to oil palm plantations. The conservation value of oil palm and rubber plantations is thus very low. Jungle rubber agroforests were surprisingly diverse and thus represent a species-rich refuge for forest epiphytes, especially for ferns and orchids, while other angiosperms tended to be underrepresented. Traditional jungle rubber agroforests are presently in a rapid process of conversion into rubber and oil palm monocultures so that they most likely share the fate with the few remaining forest remnants and will vanish soon without appropriate incentives for local farmers.

Maintaining epiphyte diversity in future plantation landscapes in the tropics will require an effective conservation of the remaining forest reserves as well as an enrichment of plantations with native forest trees that have the chance to grow tall and become epiphyte-laden host trees. Farmers' interests to make tree monocultures more epiphyte-friendly appear to be very low at present. In fact, some management manuals

even propagate epiphyte removal, although it is clear that epiphytes do not harm oil palms or rubber trees. The removal of epiphytes has to be seen critically as in an intact ecosystem epiphytes interact closely with a variety of other organisms, biogeochemical cycles, and provide ecosystem functions and services. The oil palm industry now broadens its focus to Africa and South America which will cause dramatic changes in those areas as well, making the expansion of tree monocultures to one of the most urgent conservation challenges for the future.

Author contributions

Fieldwork was carried out by T.B., A.W., C.A., and L.B. S.S.T. supported preparation, identification, and deposition of herbarium specimens. K.R. and H.K. designed this study. T.B., A.W., C.A., K.R., and H.K. analyzed data. T.B., K.R., and H.K. wrote the manuscript and all authors contributed to revisions.

Acknowledgment

This paper is dedicated to Professor Wilhelm Barthlott on the occasion of his 70th birthday. We are grateful to the landowners and the staff of Bukit Duabelas National Park and the owners of the EFForTS core plots for granting us access to their land. We thank Dr. Bambang Hariyadi, the staff of the BIOTROP herbarium, the Herbarium Bogoriense and the Botanical Garden Bogor (orchid house) to provide work facilities and useful advice during plant identification. We acknowledge the Ministry of Research, Technology and Higher Education (RISTEKDIKTI) for research permission in Indonesia. This study was financed by the German Research Foundation (DFG) in the framework of the Collaborative Research Centre 990 EFForTS (<http://www.uni-goettingen.de/crc990>). H.K. acknowledges core support from the DFG and the University of Göttingen in the context of the Free Floater program. Travel funds were kindly provided by the German Academic Exchange Service (C.A., A.W., and L.B.) and the Heinrich Böll Foundation (T.B.).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.08.008>.

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