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Diversity and dynamics of vascular epiphytes and arthropods in oil palm plantations in Sumatra (Indonesia)

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Diversity and dynamics of vascular epiphytes and arthropods in oil palm plantations in Sumatra (Indonesia)

Judith Krobbach

Abstract

Aim The expansion of oil palm (*Elaeis guineensis*) plantations has become a major threat to tropical Southeast Asia's unique biodiversity. This study aims to analyze and quantify biodiversity patterns and their drivers for epiphytic vascular plants and arthropods in oil palm plantations, focusing in particular on the role of plantation age. Understanding ecological processes in oil palm plantations is crucial for developing conservation strategies.

Location Jambi Province, Sumatra (Indonesia): Oil palm plantations in Bukit Makmur (unit 5 of Sungai Bahar, 2°1'56.6''S 103°23'15.7'' E, 24.2 m a.s.l.), Marga Mulya (unit 2 of Sungai Bahar, 1°57'21.1'' S 103°26'43.6'' E, 20.9 m a.s.l.) and Permatang Kabau (1°56'47.2'' S 102°35'10.2'' E, 77.4 m a.s.l.).

Methods A chronosequence of each (0-6 yrs), middle (10-15 yrs) and old (20-30 yrs) plantations (one each) was surveyed in each location. Six oil palms were surveyed in each plantation (n = 54). Epiphytic plants, oil palm-dwelling arthropods and habitat characteristics were surveyed at the oil palm level and in 0.5 x 0.m m² plots (n = 120) attached to oil palm trunks at heights of 0 m, 2.5 m and 5 m, if available. Arthropods were collected from epiphytic plants with a net and extracted from organic matter in oil palm leaf axils with Winkler's traps.

Results Eighteen epiphyte species found in total. Epiphyte diversity and abundance increased with age class, a strong predictor, but did not show a vertical distribution. The epiphyte community was mainly composed by six stress-tolerant pteridophyte species, headed by *Vittaria ensiformis*, made up 71.14% of epiphyte individuals on old plantations. Orchids were absent. Species composition varied little between oil palms. 31 accidental epiphyte species were recorded, dominated by *Elaeis guineensis* and two invasive species (*Clidemia hirta* and *Asystasia gangetica).* Species richness and abundance decreased with plantation age and trunk height and depended on the availability of organic matter. Fourteen epiphyte-dwelling arthropod taxa and seventeen taxa in organic matter were recorded, including twelve overlapping taxa. Epiphyte cover partly explained the diversity and abundance of epiphyte-dwelling arthropods, which also differed across the locations. Diversity of arthropods in organic matter decreased with age.

Main conclusions Epiphyte diversity is dramatically low in the oil palm plantations investigated. The community of epiphytic plants undergoes a succession, influenced by changes in substrate availability on oil palm trunks with palm age. The lack of vertical epiphyte stratification is likely caused by the absence of a vertical microclimatic gradient. The expansion of oil palm plantations endangers forest-specialized epiphytes, which were entirely lacking from the plantations investigated. Location and plant cover were drivers for arthropod abundance and diversity in part, but major determinants of arthropod diversity patterns need to be investigated further. Natural forests in proximity to plantations likely enhance arthropod diversity within plantations. To manage oil-palm plantations for higher arthropod biodiversity, epiphytes should not be removed.

Keywords

Biodiversity, oil palm plantations, *Elaeis guineensis*, epiphytes, arthropods, Sumatra, age gradient.

1 Introduction

1.1 Southeast Asia – a biodiversity hotspot

The humid tropics in Southeast Asia harbor a globally unique biodiversity including many endemics, but species are endangered by habitat loss (Koh & Wilcove 2007; Sodhi et al. 2004). 11% of the world's remaining rainforests are in Southeast Asia (Koh & Wilcove 2007). These forests are one of the most species-rich ecosystems on earth but they have also experienced the highest relative rate of deforestation of any tropical region (Sodhi et al. 2010; Sodhi et al. 2004). Four of the global biodiversity hotspots, Sundaland, Philipines, Wallaceae and Indo-Burma, are at least partly within Southeast Asia (Myers *et al.* 2000). Sundaland includes peninsular Malaysia and the islands Sumatra, Java and Borneo. In 2000, the remaining primary vegetation of Sundaland covered only 7.8% of its original extent (Myers *et al.* 2000). This hotspot has 25,000 plant species including 15,000 endemics. These endemics make up 5% of the global plant species. Furthermore, 1,800 vertebrate species including 701 endemics are found there (Myers *et al.* 2000).

Speciation has been favored in this region by a complex geographic setting, with many isolated island archipelagos (Richter 2001). Tectonic shifts, volcanic activity and fluctuating sea-levels caused colonization, isolation and speciation events that resulted in globally outstanding high species richness and endemism (Sodhi *et al.* 2004). It is all the more astonishing that, compared with other tropical regions, Southeast-Asia's biodiversity is poorly studied (Laumonier *et al.* 2010).

Agricultural conversion of forests, logging, anthropogenic fire and overexploitation of wildlife are the major threats to Southeast Asia's biodiversity (Wilcove *et al.* 2013). The expansion of oil palm is a particularly major driver of forest loss in Southeast Asia (Wilcove *et al.* 2013).

1. 2 Epiphytes and arthropods in tropical rainforests

Epiphytes and arthropods both are abundant and functionally important organism groups in tropical regions (Basset *et al.* 2012; Fayle et al. 2011; Richter 2001). For this reason, they were chosen as model groups for the investigation of biodiversity in oil palm plantations.

Tropical rainforests have a complex canopy structure, causing a vertical gradient of microclimate with lowest temperatures and highest relative humidity at the ground (Johansson 1974). Light intensity decreases from the top of the trees to the ground.

Rainforests are characterized by an enormous diversity of trees, epiphytes and lianas (Richter 2001). Epiphytes are plants that germinate and root non-parasitically on other plants, named phorophytes (Zotz 2013; Benzing 1990). Holo-epiphytes do not have any contact to the forest floor during their entire life cycle. Hemi-epiphytes have a vascular connection to the ground in the early (primary hemi-epiphyte) or late stage (secondary hemi-epiphyte) of their life. Hemi-epiphytes represent 8% of all epiphyte species (Nieder, Prosperí & Michaloud 2001). Vascular epiphytes, including primary hemi-epiphytes, represent 9% of the vascular plant diversity (Zotz 2013). 27,614 species in 913 general in 73 families are known in epiphytes. Alone 68% of epiphyte species are represented by orchids, which contribute almost 19,000 species in 543 genera. Ferns and fern-allies include approximately 2,700 epiphytic species, half of them in Polypodiaceae. Typical terrestrial species that rarely grow epiphytically are called accidental epiphytes (Zotz 2013; Benzing 1990).

The canopy is a habitat with extreme ecological conditions. Epiphytes show diverse adaptions for coping with a vertical flow of water and nutrients (Benzing 1990). Water balance strategies such as CAM photosynthesis, poikilohydry, xeromorphic structures or absorptive organs and tissues are documented. Nutrients are accessed from canopy soils, animal excrements or by mycorrhizas or carnivory. Litter-basket epiphytes gain nutrients from falling leaves from their phorophytes. Ants might play a great role in epiphyte nutrition as they carry large amounts of organic matter into the canopy. Ant-nest gardens or ant-fed ant-house epiphytes represent highly specialized adaptions to the life in the canopy (Rico-Gray & Oliveira 2007).

Over the years, the form and size of the canopy and the bark structure of the phorophytes change (Johansson 1974) and canopy soil may accumulate under the epiphytes (Benzing 1990). Epiphyte succession is faster than succession of ground vegetation due to the restricted life span of phorophytes (Benzing 1990). The naked bark is usually first settled by non-vascular plants (lichens, bryophytes, mosses) that provide a substrate for stress-tolerant ferns and later for more vulnerable ferns and angiosperms that are humiphilous (Benzing 1990). Holo-epiphytes show a vertical distribution along the forest strata (Nieder *et al.* 2001).

Epiphytes a highly specialized growth form for living in the canopy, and there are many host-specific epiphytes (Benzing 1990). Hence, epiphytes are in particular vulnerable to deforestation. Vascular epiphytes showed a decline in species richness along a gradient of disturbance in forests and secondary vegetation (Barthlott *et al.* 2001). Furthermore, epiphyte species with a small geographic range are in particular threatened by human-induced habitat changes (Köster *et al.* 2013). A low ecological plasticity makes species vulnerable to (micro-) habitat changes (Köster *et al.* 2013).

Epiphyte diversity, composition and distribution indicate human disturbance (Haro-Carrión *et al.* 2009). Understanding epiphyte patterns and dynamics in oil palm plantations might help to develop protection strategies.

Epiphytes provide an important structure in rainforest canopies (Ellwood & Foster 2004). Bird's nest ferns are islands of diversity in the canopy (Fayle *et al.* 2005). Their interior is inhabited by ants, termites, cockroaches, centipedes and many other invertebrates (Fayle *et al.* 2005; Ellwood & Foster 2004). Stuntz et al. (2002) found a very distinct taxonomically and ecologically arthropod fauna in three different epiphyte species on *Annona glabra* trees in a moist lowland forest in Panama. On the same tree species, ant abundance is positively correlated with the load of non-myrmocophilic epiphytes (Stuntz *et al.* 2003). A noticeable number of ant-epiphyte interactions are found in tropical rainforests (Rico-Gray & Oliveira 2007). That includes ant-nest gardens or ant-housing epiphytes in the canopy (see also Kaufmann & Maschwitz 2006; Benzing 1990).

Arthropods are the dominant group within the tropical fauna (Basset *et al.* 2012). The tropics harbor estimated 6.1 million arthropod species (Hamilton et al. 2011) and forest canopies hold a high abundance and biomass of them (Dial *et al.* 2006). Arthropods provide important ecosystem services such as pollination, decomposition or preying on pests (cp. Turner & Foster 2009). In particular the ants are one of the most ecologically important taxon in the tropics (Hölldobler & Wilson 1990). They have important ecological functions such as pollination, soil turnover and seed dispersal (Alonso & Agosti 2000 in Fayle *et al.* 2010). Similarly to epiphytes, vertical ecological gradients in the canopy structure, light intensity and microclimate primary cause a vertical gradient in arthropod abundance and biomass (Dial *et al.* 2006). Successional stages of arthropod orders in the floor litter were observed in tropical rainforests in China (Yu & Yang 2007). The arthropod community was found to change along an gradient of forest disturbance in a study in Malaysia (Floren & Linsenmair 2001). Disturbed forests were characterized by a less complex ant community, but high abundances in Coleoptera and non-formicine Hymenoptera.

1.2 Oil palm plantations and their impact on biodiversity

Cultivation history and current role of oil palm

The expansion of oil palm is a major cause of forest loss in Southeast Asia. Alone in the last decade, the area of oil palm plantations had increased by 87% (Wilcove *et al.* 2013), following an increasing global demand for palm oil (Koh & Wilcove 2007). Oil palm products are widely used as food, cosmetics, lubricants and biofuel (Santosa 2008). Currently, palm oil is the cheapest of all vegetable oils and contributes 30% to the global oil production (Carter *et al.* 2007). In 2012, 32.81 million ha were harvested for oil palm fruits globally (FAOSTAT 2013). More than 80% of the global palm oil is produced in Indonesia and Malaysia (Koh & Wilcove 2007). Both countries are not only rich in biodiversity but also have a high endemism rate; e.g. approximately 60% of Indonesia's vascular plants are endemic (Koh & Wilcove 2007). A high proportion of endemics enhances the risk of global extinctions in a regional biota faced by habitat loss (Sodhi *et al.* 2010).

Oil palms belong to the Arecaceae and contain two species. *Elaies oelifera* (Kunth) Cortés 1897 is native to tropical Central and South America. Previously, it is not commercial cultivated and the obtained oil is only used locally (Santosa 2008; Corley & Tinker 2003). Native to West Africa, *Elaeis guineensis* Jacq. 1763 is currently the world's most rapidly growing crop (Corley & Tinker 2003; Fitzherbert et al. 2008). Natural habitats are riverine forests and freshwater swamps in tropical lowland (Harlan 1976; Corley & Tinker 2003).

Humans probably started to use wild oil palm fruits several thousand years ago (Corley & Tinker 2003) and local palm oil gloves established around villages in West Africa. Closely linked with the Industrial Revolution, the demand for palm oil in the northern countries rose. It was wanted for the manufacturing of soap, candles, margarine, cooking fat, lubricants for machinery and industrial processes (Dike 1956 in Aghalino 2000 and Corley & Tinker 2003). Additional, kernel husks were used as animal food (Santosa 2008). Until the time of World War II, an early plantation industry was established in West African colonies and Belgian Congo. Nigeria was the greatest palm oil producer until the 1960s (Santosa 2008), but due to political changes, governmental mismanagement and unrests in West Africa, there was a shift of main cultivation areas to South-east Asia (Corley & Tinker 2003).

The first four oil palms have been introduced to Indonesia in 1848 and planted in the botanical gardens in Bogor, Java (Bickmore 1869 in Jelsma et al. 2009) in the Dutch East Indies. The progeny of these first oil palms were distributed widely in Southeast Asia and were transferred to Sumatra in 1875. Large plantations of this stock, named 'Deli palm', were first established in 1911 in Sumatra and in 1917 in Malaysia by the Dutchmen. With the start of a New Order in Indonesian politics in 1967, the oil palm industry expanded exponentially until today (Jelsma *et al.* 2009; Figure 1).

Oil palm life cycle in a plantation

There are three different cultivation systems of oil palms (*Elaeis guineensis*) in Indonesia: private large-scale plantations, nucleus estate smallholders and independent smallholders (Obidzinski & Andriani 2012). Irrespective of the cultivation system, oil palms are usually planted as monocultures. Wild oil palms can live up to 200 years, but in plantations, the economic life span is about 20 to 30 years (Armstrong 1999).

After germination, the seedling forms a wide stem base (Corley & Tinker 2003). After three years, the internodes begin to elongate. Growth in height is determined by the single apical meristem, which is surrounded by 30 to 50 leaves arranged in a spiral. First fruits can be harvested after four to five years (comment by Bapak Solekin, Permatang Kabau). Old and dry leaves break off or are cut off by plantation owners at the rachis. A small part of the leaf base remains attached to the trunk, which is said to be rough. Over the years, organic matter accumulates in the leaf axils (Luskin & Potts 2011). After several years, leaf bases drop off, starting from the middle of the trunk. Old oil palms have leaf bases only directly beneath the crown. The naked trunk is smooth but has scars from the leaf bases (Corley & Tinker 2003).

Oil palm plantations have a low, relatively open and simple canopy structure compared to rainforests (Koh, Levang & Ghazoul 2009). The microclimate (temperature and relative humidity) shows small vertical variation but greater daily fluctuations (Altenhövel 2013; Koh et al. 2009). Young oil palm plantations are hotter and show more deviation from forest conditions than old plantations (Luskin & Potts 2011).

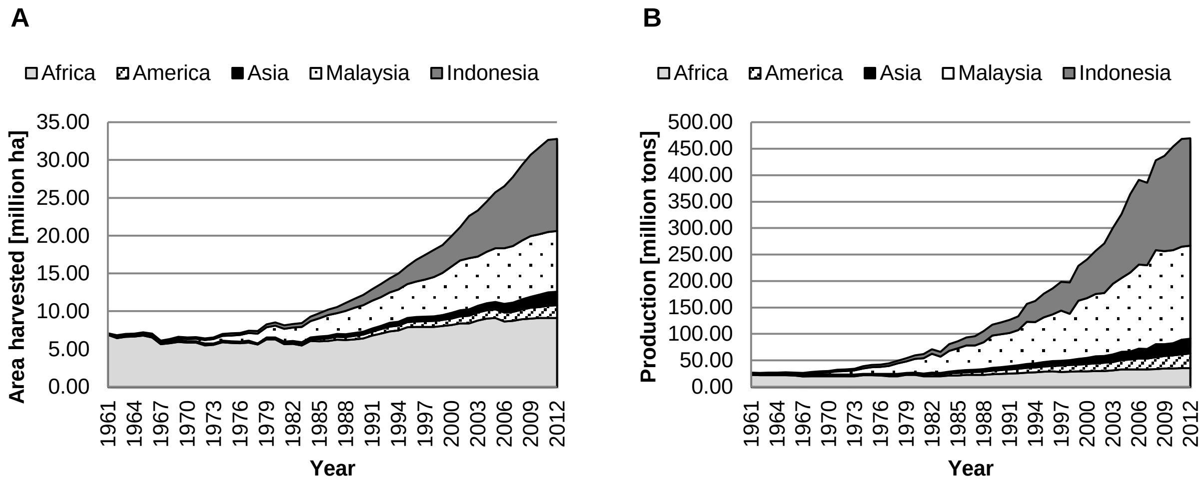

Figure 1: Oil palm agriculture worldwide from 1961 to 2012. A: Global area harvested for oil palm fruits per year. B: Global oil palm fruit production per year. Countries in *Africa*: Angola, Benin, Burundi, Cameroon, Central African Republic, Congo, Côte d'Ivoire, D. R. Congo, Equatorial Guinea, Gabon, Gambia, Ghana, Guinea-Bissau, Guinea, Liberia, Madagascar, Nigeria, Sao Tome and Principe, Senegal, Sierra Leone, Togo, Tanzania; in *America*: Brazil, Colombia, Costa Rica, Dominican Republic, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Paraguay, Peru, Suriname, Venezuela; in *Asia*: China (mainland), Papua New Guinea, Philippines, Solomon Islands, Thailand. Data source: FAOSTAT (2013).

Figure 2: Oil palm agriculture in Jambi Province, Sumatra. A: Large areas of rainforests have been logged for establishing new oil palm plantations (see background); along the road to Permatang Kabau. B: Harvested oil palm fruits in a plantation; Bukit Makmur. C: Trucks that transport oil palm fruits to mills for further processing; Bukit Makmur. D: *Setothosea asigna*, a species of nettle catepillars (Limacodidae, *'ulat api'*) that are common oil palm pests; Bukit Makmur (bm.m).

Current state of knowledge

Oil palm agriculture has become the greatest immediate threat to Southeast Asian's biodiversity (Wilcove & Koh 2010). The most prominent example is the dramatic decline in populations of orangutan (*Pongo* spp.), which are now close to extinction in the wild (Nantha & Tisdell 2009). In many instances, oil palm companies have been involved in illegal logging and land grabbing, often accompanied by the violation of human rights of indigenous people (Colchester 2011). In addition, the transformation of lowland tropical rainforest to oil palm plantations emits an estimated net amount of 163 tons/ha stored carbon to the atmosphere and therefore contributes to global warming (Danielsen *et al.* 2009).

Nevertheless, less than 1% of all scientific publication about oil palms address biodiversity and species conservation, although the number of scientific publications concerning effects of the transformation of rainforest to oil palm plantations on biodiversity has risen in the last years (Turner *et al.* 2008). Such research has mainly been carried out in Malaysia (e.g. Lucey & Hill 2012; Azhar et al. 2011; Fayle et al. 2010; Turner & Foster 2009; Koh 2008; Fayle et al. 2005; Nadarajah & Nawawi 1993). Most studies have focused on birds, mammals or particular arthropod taxa – in particular ants, beetles and butterflies (see Foster et al. 2011). Nearly all studies emphasized a loss of either species richness or abundance of forest species (Foster *et al.* 2011).

Few studies have examined epiphyte communities in oil palm plantations. Nadarajah & Nawawi (1993) identified 29 epiphyte species including non-vascular plants in oil palm plantations in Malaysia. Altenhövel (2013) found 11 species of vascular epiphytes in oil palm plantations compared to 44 species in a nearby tropical lowland rainforest in Sumatra. Epiphyte communities have not been investigated in more detail – comparing plantations of different ages.

The only study that considered the whole arthropod community in oil palm plantations found different patterns for different orders and in different microhabitats (Turner & Foster 2009). There have been other studies on single arthropod taxa, but no other study has compared different arthropod taxa. No research has been carried out on epiphyte-dwelling arthropods on oil palms beside taxa inhabiting bird's nest ferns (Fayle et al. 2010; Turner & Foster 2009; Fayle et al. 2005).

Succession of species in oil palm plantations is also poorly understood (Foster *et al.* 2011). In the only study so far, Luskin & Potts (2011) compared epiphyte abundance and density (species richness per m^2) between young and old plantations. They found that epiphyte abundance was doubled in old plantations, but density showed the opposite pattern. They found that ferns were overall dominant in abundance, but their density decreased in old palm plantations. In contrast, the abundance of grasses increased with age. However, they did not distinguish epiphytes and accidental epiphytes, which might be important in understanding succession patterns. Dynamics of epiphyte species richness along an age gradient have also not yet been investigated.

The replacement of rainforest by oil palm plantations clearly has an overall negative impact on biodiversity (Fitzherbert *et al.* 2008). However, little is known about the detailed effects of the transformation of rainforests into oil palm plantations on biodiversity (Foster *et al.* 2011). Understanding the different responses of different taxa and guilds to oil palm expansion is crucial for developing sustainable management strategies for conserving species and ecosystem functioning (Turner *et al.* 2008).

1.3 Aim of the study

To understand the causes and consequences of the transformation of rainforest into agricultural landscapes jungle rubber, rubber and oil palm plantations, a long-term Collaborative Research Centre (CRC 990) was established at the University of Göttingen in cooperation with the Bogor Agricultural University (IPB) and the University of Jambi (UNJA) in 2012. The CRC is named "Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems (Sumatra, Indonesia)" (EFForTS) and is divided into three project groups investigating different aspects of the transformation of rainforest: A – environmental processes, B – biota and ecosystem services, and C – human dimensions. Each project group includes several subprojects. This master's project is a part of the subproject B06 "Taxonomic, phylogenetic, functional, and biogeographical diversity of vascular plants in rainforest transformation systems on Sumatra (Indonesia)" carried out by the Free Floater Research Group in Biodiversity, Macroecology and Conservation Biogeography in the Faculty of Forest Sciences and Forest Ecology at the University of Göttingen.

This thesis aims to quantify and analyze the diversity and dynamics of vascular epiphytes and arthropods in oil palm plantations. Terrestrial plants that grow on oil palm trunks (accidental epiphytes) are also examined. Arthropods are studied in two microhabitats of oil palm trunks: on epiphytes (including accidental ones) and in organic matter in oil palm leaf axils. Habitat characteristics of oil palms are quantified in order to identify drivers of richness and abundance of species and higher-ranked taxa. Particular attention is paid to succession along an age gradient, which is achieved by studying a chronosequence of multiple plantations of different age classes (space-for-time substitution; see Picket 1989).

This study is the first to focus on succession of epiphytes separately from accidental epiphytes. It is also the first to provide data on the abundance, diversity and composition of arthropod taxa on both epiphytes and in organic matter.

Organic matter that accumulates in leaf axils of oil palm trunks creates a special habitat and provides a substrate that might be suitable for terrestrial plants. This leads to the hypothesis that **(H1) accidental epiphytes compose a part of the plant community on oil palm trunks.**

Habitat characteristics of oil palms such as leaf base cover and the amount of organic matter in leaf axils change with age. This leads to the hypothesis that **(H2) abundance, diversity and composition of epiphytes and accidental epiphytes change with plantation age.** Epiphytes are expected to be more abundant in old plantations than in younger ones. However, I expect that only a few dominant species are adapted to the extreme habitat conditions of the tree-like naked trunks of old oil palms. Accidental epiphytes are expected to be most abundant and species rich on rough younger oil palm trunks, and to be absent from old oil palms. Diversity and dynamics are expected to depending primary on age and not to differ between locations.

Plant cover provides a food resource for arthropods and structures their habitat. The greater the amount of plant cover the greater the food supply and number of hiding places from predators for herbivorous arthropods. Again, the more herbivorous arthropods, the more prey for predatory arthropods. **(H3) arthropod diversity and abundance in the epiphyte microhabitat are positively related to plant cover of oil palm trunks.**

Organic matter accumulates in the leaf axils of oil palm trunks slowly over years. Probably, the arthropod community undergoes a succession along decomposition stages of organic matter. I hypothesize that **(H4) arthropod diversity, abundance and composition in the organic matter microhabitat change with plantation age.** A decline in species richness but not in abundance is expected, as there might be a competition between different taxa.

On each oil palm trunk, there is an age gradient from old leaf bases at the trunk base to young leaf bases at the top. This leads to the hypothesis that **(H5) abundance, diversity and composition of epiphytes and accidental epiphytes change along the height gradient of oil palm trunks, with similar more detailed patterns as expected in relation to H2.**

Oil palm plantations are intensively managed monocultures. Oil palm-dwelling organisms are exposed to more extreme conditions than organisms in rainforests (see above). For this reason oil palms are expected to provide low-quality habitat for epiphytes. This leads to the hypothesis that **(H6) oil palm plantations harbor a low diversity of forest-specialized epiphytes.** This would mean that oil palm plantations are not suitable for conserving forest-specialized epiphyte species.

2 Methods

2.1 Study area

Field work in the CRC 990 project takes place in Jambi Province, Sumatra. This Indonesian island has an area of 475,000 km² and is the fifth largest island in the world (Laumonier 1997). Sumatra is the largest island of the Sunda Archipelago Arc, which also includes Java and islands of Nusa Tenggara. This volcanic arc was formed between 15 and 3 years BP by tectonic shifting of the Indo-Australian, Eurasian and Pacific plates. Until today, the whole region shows volcanic activity. Sumatra is 6° North and 6° S. The climate is tropical, with high and frequent rainfall and warm temperatures throughout the whole year. Mean monthly temperatures vary from 25 °C to 27 °C, showing daily thermic amplitude of 7 to 27 °C in the lowlands. Sumatra is characterized by five main ecological zones. The west coast zone is placed along the sea and merges into a mountain zone. To the east, this mountain zone turns into a small piedmont zone followed by a large peneplain zone in the east. The eastern coast is built by swamp lowlands (Murdiyarso *et al.* 2002). Sumatra is part of the Malesian biogeographic region. The native flora of Sumatra show great similarity to peninsular Malaysia and also Borneo (Laumonier 1997). The natural vegetation is widely characterized by Dipterocarp forests. However, Sumatra lost enormous parts of its rainforests due to intensive land use. In the period of 1990-2010, the total area of primary forests lost was 7.54 million ha (35.7%) and another 2.31 million ha (11%) of forest area were degraded (Margono *et al.* 2012). Jambi Province lost 40% of its primary forests. In 2005, oil palm plantations already covered 6.1 million ha of Sumatra (Fritzherbert et al. 2008).

Jambi Province is located in central Sumatra south of the equator and has an area of 49,578 km^2 (Murdiyarso *et al.* 2002). The climate is tropical. Annual rainfall ranges between 2100 and 3000 mm with 7-9 wet months (> 200 mm rainfall) and 2 dry months with 100 mm rainfall (Oldeman; Las 1979 in Murdiyarso et al. 2002). Rainfall usually peaks in November and December. The potential vegetation is tropical lowland Dipterocarp-dominated rainforest. These lowland forests are among the most diverse and complex ecosystems on Earth (Whitten *et al.* 2000).

Originally, the land was used by indigenous tribes of the Orang Rimba (“People of the jungle”) and Suku Anak Dalam (“Traditional children from inside” [the forest]). These people lived in the rainforests as hunters and gatherer and traded forests products, in particular pepper and other spices, with villages along the rivers (Murdiyarso *et al.* 2002). Rubber (*Hevea brasiliensis*) was introduced to Sumatra in the second half of the 19^{th} century from Brazil and became the dominant land-use type in the lowlands of Jambi Province in the beginning of the 20^{th} century (Gouyon et al. 1993 in Murdiyarso *et al.* 2002). In this context, large areas of rainforests were logged over and replaced by agroforests.

With the start of a New Order in Indonesian politics in 1967, Sumatra's oil palm industry expanded exponentially (Jelsma *et al.* 2009). At the same time starting in the 1970s, many roads were constructed in Jambi Province. That greatly facilitated the export of primary products, such as lumber, estate crops and mineral resources (Miyamoto 2006). In 1988, the Indonesian government started to support the private sector of the oil palm agriculture by providing jobs and land for transmigrates from areas with high populations such as Java to the less populated outer islands of Sumatra and Kalimantan (PIR-Trans projects) (Jelsma *et al.* 2009). In the 1980s, the dominant vegetation type was still lowland tropical forest, but in the beginning of the 1990s, it was replaced by agricultural area and settlements (Murdiyarso *et al.* 2002). (Stolle *et al.* 2003) showed that most fires in 1992/1993 in Jambi Province appeared where transmigration projects of the government were settled. Today almost all lowland rainforests are replaced by agricultural landscapes, mainly oil palm plantations, rubber plantations and jungle rubber.

The CRC project installed 32 core pots of 50 m x 50 m 8 each located in lowland rainforests, jungle rubber, rubber and oil palm plantations across the Bukit Duabelas and Harapan landscape. All oil palm plantations in the CRC plots are about 15 years old. As this study requires oil palm plantations of different age classes, research took place on plantations outside the project's core plots (please note: In this work, the term 'plot' is used in a different way than generally used in the CRC project).

This study was carried out at three different locations in Jambi Province (Figure 3):

- **Bukit Makmur (bm)**, unit 5 of Sungai Bahar, 2°1'56.6''S 103°23'15.7'' E, 24.2 m above sea level. This village is located ca. 60 km SSW south-westwards of Jambi City in a hilly area ('bukit' is translated as 'hill') in proximity from Harapan Rainforest. The village is surrounded by large oil palm monocultures. Shrubs or trees between plantations are rare. The grounds are strongly eroded.
- **Marga Mulya (mm)**, unit 2 of Sungai Bahar, 1°57'21.1'' S 103°26'43.6'' E, 20.9 m above sea level. In this location, which is < 50 km SSW of Jambi City and > 5 km from Bukit

Makmur, some of the oldest oil palm plantations in Jambi Province can be found. The area is flat and strongly eroded. Shrubs or trees between plantations are rare. Oil palm plantations are the dominant land-use type.

- **Permatang Kabau (pk)**, 1°56’47.2’’ S 102°35’10.2’’ E, 77.4 m above sea level. This village is located ca. 120 km SWW of Jambi City in the neighborhood to Bukit Duabelas National Park (Taman Nasional Bukit Duabelas), which has an area of 65,000 ha and is home of the indigenous tribe Orang Rimba or Suku Anak Dalam (Steinebach 2008). Permatang Kabau is located in a mosaic landscape consistent of oil palm plantations, rubber plantations and jungle rubber. Mixed-used plantations of oil palms and rubber are existent, too. Also, secondary vegetation and wetlands are present.

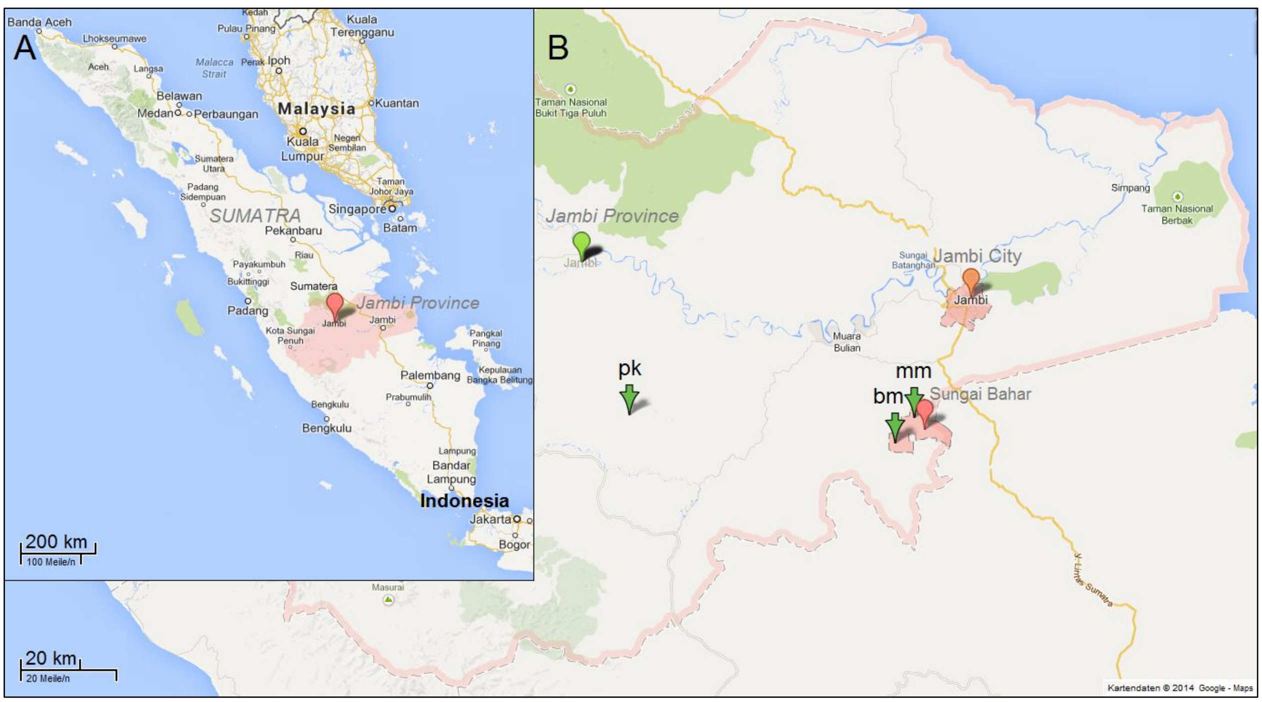

Figure 3: Maps of the study area. A: Jambi Province (red marked) is placed in central Sumatra South of the equator. B: In Jambi Province (red border), this study took place at three different locations (green arrows): Bukit Makmur (bm), Marga Mulya (mm) and Permatang Kabau (pk). Source: Google Maps - © 2014 Google, modified by the author.

At each location, three plantations with the age class **young (y)**, **middle (m)** and **old (o)** were chosen, which resulted in nine investigate plantations, shortened named [location code].[age class code]. First criterion was the fit in clear distinguishable age classes, which were set according to availability: 0-6 years for young, 10-15 years for middle and > 20 years for old. Second, plantations of the age class old should harbor oil palms that start to drop of their leaf bases. Table 1 gives detailed information about planting years, ages at the time of field work and plantation owners. All plantations but 'bm.o' were owned by smallholders. Interviews with smallholders revealed that all of them took part at the transmigration project of the government (see above) and originally came from Java. Small-holder participate in the so-called 'inti-plasma system' and deliver their harvested oil palm fruits to large oil palm mills ("plasma"), where the fruits are processed. In the following, each oil palm plantation which was surveyed in this study is briefly described (for photographs, see Figure 4). Further information about the management of the oil palm plantations is given in Appendix 2.

- **bm.y**: This plantation was planted in 2008 on a flat place within a hilly area and is surrounded by a trench system filled with water. At strong rainfall, 'bm.y' is flooded. The plantation is located in between other oil palm plantations of different age. The owner forgot to use herbicides until now which has resulted in a dense ground vegetation (Figure 4, A), also including some wetland species.
- **mm.y**: This plantation was initially planted in 2008 within older oil palm plantations and possesses a large irrigation system. Water trenches are installed in between each oil palm row and also around the plantation. There is dense ground vegetation with several species commonly found in the wetlands. At the same time when field work was done there, fertilizer was spread.
- **pk.y**: First plantings for this plantation started in 2007, but the main part was planted in 2009. Oil palms planted in 2007 had a trunk height of 3-4 m, whereas the trunk of the ones planted in 2009 was 1.5-2 m high. Only palms planted in 2009 were included here. The ground vegetation was rare on species and apparently dominated by *Clidemia hirta*. The plantation is surrounded by oil palm plantations and by a combined plantation of oil palms and rubber trees at one side including some shrubberies.
- **bm.m**: Planted in 2000 on a slope, large parts of the ground surface are not covered by vegetation but built up by sandy soil caused by erosion. The plantation is surrounded by other oil palm plantations, but no shrubberies. Some nettle caterpillars of the Lepidoptera family Limacodidae were observed on this plantation ('*ulat api*' in Bahasa Indonesia). These caterpillars are known as a common oil palm pest as they feed on oil palm (and also coconut) leaves (Foster *et al.* 2011; Kimura 1978).
- **mm.m**: This plantation, planted in 1998 and surrounded by other oil palm plantations, has a sandy and dry soil and poor ground vegetation.

- **pk.m**: This oil palm plantation was initially planted in 2001. Further, palms were planted two years later and also very young oil palms are present. To include only oil palms fitting to the age class “middle”, palms < 3 m trunk height were excluded from choice. ‘pk.m’ is surrounded by a creek. At the beginning of the field work at ‘pk’, this plantation was knee-high flooded for several days. The ground vegetation is dense in some parts, but in other parts mud covers the ground. In the neighborhood, there is a mixed oil palm and rubber plantation as well as a jungle rubber plantation and also some shrubs and high trees which were actively used by a group of monkeys.
- **bm.o**: Strictly speaking, ‘bm.o’ does not describe a whole plantation, but a part of a very large plantation system planted in 1992. This is why the area indication is in brackets in Table 1. This plantation is the only one in this study owned by a company and not by smallholders. It is located on a slope. The ground is fully covered by vegetation.
- **mm.o**: This 30 year old plantation was the oldest one surveyed. It was planted in 1883 and is surrounded by other old oil palm plantations and little shrubbery. Several large hemi-epiphytes and also a *Lycopodium spec.* were observed on palms but not included into the inventory.
- **pk.o**: This plantation was planted in 1991 and merges at two sides with other plantation of similar age. The other sides are bordered by a trench filled with water. The ground vegetation next to the trench is very dense and > 1 m high and mainly built by terrestrial pteridophytes. On the other side of that trench, there are dense shrubs, where monkeys were observed.

Table 1: Information on the investigated oil palm plantations. If owners named > 1 planting year, the initial planting was done in the first year. In the following years, oil palms which did not grow well were replaced by new ones. Most oil palms were planted in the earliest planting year on each plantation. Only on 'pk.y', the major part was not planted in 2007 but in 2009. Bold numbers indicate main planting year or main age of surveyed oil palms. 'Hamparan' (translated: 'block') labels a part of a large plantation.

Plantation.ID	Location	Age class	Planting year	Age [yrs]	Area [m^2]	Owner
bm.y	Bukit Makmur	young	**2008**; 2010; 2011	2; 3; **5**	5,808	Muhammed Jumi
mm.y	Marga Mulya	young	2008 - 2012	2-5	4,412	Bapak Sugiyanto
pk.y	Permatang Kabau	young	2007/**2009**; 2012	1; **4/6**	2,683	Bapak Solekin
bm.m	Bukit Makmur	middle	2000	13	4,221	Bapak Rusmanto
mm.m	Marga Mulya	middle	1998	15	9,249	Indang Budiarjo
pk.m	Permatang Kabau	middle	2001; 2003	12; 10	3,812	Bapak Solekin
bm.o	Bukit Makmur	old	1992	21	(11,617)	(Hamparan 3.RT.24)
mm.o	Marga Mulya	old	1983	30	11,093	Idang Budiarjo
pk.o	Permatang Kabau	old	1991	22	>20,387	Bapak Solekin

Figure 4: Photographs of the investigated oil palm plantations. Data were collected on 9 oil palm plantations in Jambi Province, Sumatra. Locations from top to bottom: Bukit Makmur (bm), Marga Mulya (mm), Permatang Kabau (pk); Age classes from left to right: young (y), middle (m), old (o) (look at plantation.ID).

2.2 Data collection

2.2.1 Study design - overview

Data were collected in three locations in Jambi Province, Sumatra: Bukit Makmur (bm), Marga Mulya (mm) and Permatang Kabau (pk) at the beginning of the dry season in March and April 2014. In each location, three plantations of the age class young (y), middle (m) and old (o) were chosen. The exact plantation age chosen depended on availability and varied from 1-6 years in young, 10-15 years in middle and 20-30 years in old plantations (Table 1). Thus, research took place on a total of **9 oil palm plantations** (Figure 4). On each plantation 6 oil palms were randomly selected resulting in 18 oil palms per location and also 18 palms per age class (replication). In total, **54 oil palms** were randomly chosen (Figure 5, A), based on three criteria:

- Oil palms of age class ‘young’ had to have a trunk height to meristem of ≥ 0.5 m to facilitate the establishment of plots (see below).
- Oil palms of the age class ‘middle’ already had to have lost ≥ 25% of their leaf bases.
- Target palms were not allowed to be in the direct neighborhood to another target palm.

On each oil palm vertical plots of 0.5 m x 0.5 were established at different heights at the trunk at intervals of 2.5 m starting at 0 m (bottom line of the plot) (Figure 5, B-C). The number of plots per oil palm depended on trunk height. In total, **120 plots** were established in trunk heights of 0, 2.5 and 5 m. They covered a total trunk surface of 30 m². As the number of plots per oil palm varied depending on trunk height, the number of plots also varied between locations and age classes. On young plantation, one plot / oil palm was established. On plantations of the age class m, three plots / oil palm were established on ‘bm.m’ and mm.m, but two plots / oil palm in ‘pk.m’. Old plantations always had three plots / oil palm. Hence, the sample size for the locations was n = 42 plots in ‘bm’, n = 42 in ‘mm’ and n=36 in ‘pk’. For age classes, the sample size was n = 18 plots for ‘y’, n = 48 for ‘m’ and n= 54 for ‘o’. For trunk heights, the sample size was n = 54 plots at 0 m, n = 30 plots at 2.5 m and n = 30 plots at 5 m. Plots for the sampling of epiphytic plants were always attached to the eastern side of the oil palm trunks. Arthropod sampling took place in plots at the southern side of the oil palm trunks.

This study design creates four nested spatial factors: Location, plantation, oil palm and plot. Data were sampled at the oil palm and plot level. Interviews performed with plantation owners refer to plantation level.

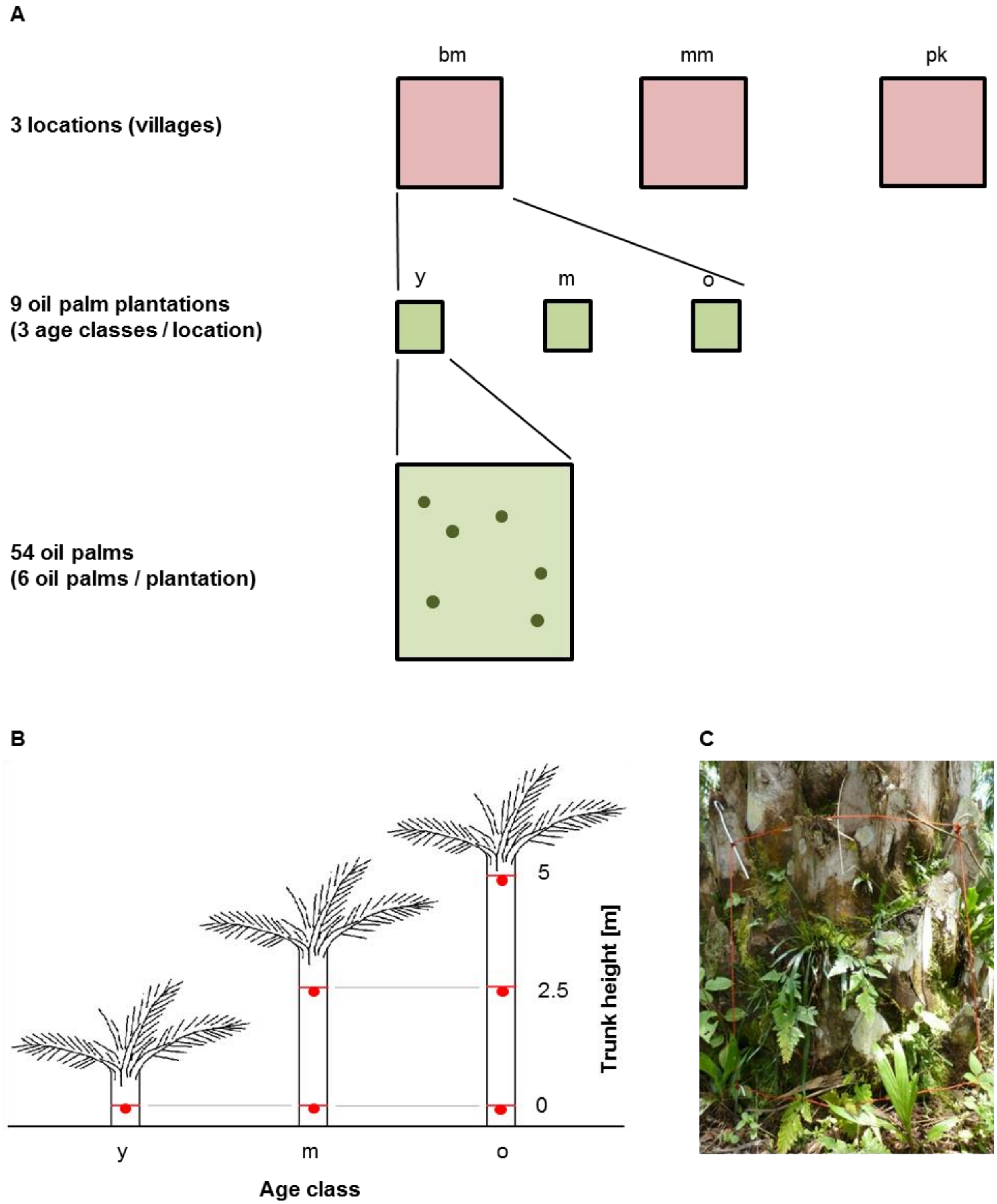

Figure 5: Study design. A: Schematic representation of the hierarchical spatially-nested study design. B: Position of the 0.x m x 0.5 m plots at the oil palm trunks. The number of plots depended on trunk height and thus differed between age classes and also locations. At two plantations ('mm' and 'bm'), oil palms of the age class 'middle' were higher than 5 m, thus three plots could be installed. C: Photograph for an example 0.5 m x 0.5 m plot. Abbreviations in 'location': bm = Bukit Makmur, mm = Marga Mulya, pk = Permatang Kabau; in 'age class': y = young, m = middle, o = old.

2.2.2 Habitat characteristics of oil palm plantations

Plantation level Plantation owners were asked in standardized interviews about the age and management of the oil plantations. They were asked about the use of herbicides and pesticides, removal of epiphytes from the oil palm trunks, about pests and when they harvest the fruits (full question catalogue in Appendix 1). In case of plantation 'bm.o', owned by a large company, the village chief of Bukit Makmur gave us the permission to collect data there. In this case, the interview was performed with him and not with the plantation owner. The interviews were hold in Bahasa Indonesia, supported by an Indonesian field assistant. Answers are documented in Appendix 2.

Oil palm level A set of data as shown below was collected for every oil palm. Additionally, all oil palms were documented by photographs taken from the northern, eastern, southern and western side of the trunk.

- Planting distance [m]: Distance to the next oil palm. Always, the next oil palm with the smallest distance was chosen.
- Trunk height to meristem [m]: Distance between the ground and apical meristem.
- Trunk height to lowest leaf [m]: Old leaves get removed but leaf bases remain at the trunk. Measured is the distance from the ground to the lowest living leaf.
- DBH [m]: Diameter at breast height (c. 1.4 m). In the case of smaller oil palms, DBH was measured directly under the lowest leaves.
- Staying leaves: In most cases same with leaves alive.
- Hanging leaves: In most cases same with leaves dead.
- Leaf base cover [%]: Proportion of trunk surface covered by leaf base in case of old oil palms, where leaf bases already dropped off. Estimated by looking at the photographs.
- Plant cover [%]: Proportion of trunk surface covered by vascular plants. Estimated by looking at the photographs.

Plot level Three variables were measured at the plot level always at the eastern side of the oil palm trunks (coinciding with plots for plant sampling):

- Organic matter (g): In each plant plot, a sample of the whole content of organic matter in one leaf axil was taken. Always, the leaf axil most to the right-up corner of the plot was chosen. The mass of the organic matter was measured on site by a hanging scale but it turned out that the resolution of the scale was not high enough. Thus, the samples were stored in plastic bags (for some days to weeks) and wet weight was measured again on a special accuracy weighing machine in the CRC laboratory at UNJA. After drying in an oven for 2 days at 80 °C, the samples were measured again with the same special accuracy weighing machine. In Appendix 3 the wet weight is plotted against the dry weight. This scatterplot shows that there is a high variance of $R^2 = 0.78$ which could be explained by water loss during storage in plastic bags. After all, only measurements of dry weight of organic matter (g) will be used, as these are the only reliable ones.

- Leaf base cover (%): Proportion of plot area covered by leaf bases.
- Epiphyte cover (%): Proportion of plot area covered by plants.

2.2.3 Epiphyte sampling

Data on epiphytic vascular plants were collected at the oil palm level and at the plot level. In detail, the sampling was performed as following:

Oil palm level The whole trunk of all selected oil palms was visually scanned and each vascular plant species observed was noted down. Higher parts of the trunk were inspected by using a ladder and/or binoculars (Steiner Safari, 10 x 26). This method results in presence-absence data, which give information about the presence (1) or absence (0) of each species over all 54 sampled oil palms.

Plot level Plots for plant sampling were located always at the eastern side of the oil palm trunks. Their exact location and size (0.5 m x 0.5 m) was marked with a removable set of cords and tent pegs (for details in plot establishment on the trunks see Figure 5, B and C). Every plot was documented by a photograph. All epiphyte individuals that rooted within the plot were noted down and specified, using field names. Further measurements about plant traits were taken:

- Plant size: length of longest frond for pteridophytes and length of longest shoot for spermatophytes)
- Sterile or fertile: fertile, if flowers, fruits or sori were observed
- Substrate used by the plant: organic matter which accumulated in leaf axil, leaf base or naked trunk, if leaf bases already dropped off

This method generated abundance data, which include the number of individuals of each plant species per plot (n = 120 plots). Presence-absence data can be calculated easily from abundance data by replacing each value > 0 by “1”.

For every plant species, one or more individuals were documented by photographs and collected as herbarium specimens. Herbarium specimens were dried and pressed in the field and transported to the Southeast Asian Regional Centre for Tropical Biology (BIOTROP) in Bogor, Java, for preliminary storage. Also, a photo herbarium was setup.

Plant species were pre-identified in the field using the photo guide for tropical ferns of Wee (2005) and a project intern photo guide to ‘Common wayside plants of Sumatra’ by Dr. Katja Rembold. Species names verified and completed at BIOTROP and Herbarium Bogoriense (LIPI) in Bogor, Java. Plant names were controlled for accepted names and attached to families by using The Plant List (2013).

Plant species were assigned to **epiphytes (*Epi*)** and **accidental epiphytes (*Acc*)** and analyzed separately. Epiphytes were further sub-classified in holo- and hemi-epiphytes (for a definition see Chapter 1.2). Accidental epiphytes are defined as ’terrestrial species that rarely grow epiphytically without necessarily completing their life cycle there’ (Zotz 2013, p. 2). In accordance with (Zotz 2013), no classification in facultative and obligate epiphytes was done. In order to classify plants as epiphytes or accidental epiphytes, a rapid assessment of the terrestrial vegetation was performed. Every species found in 3 m circumference of each oil palm trunk was recorded (unpublished data). Epiphytic species that were never observed at the ground were classified as epiphytes. Epiphytic species that also occurred at least in one individual abundant terrestrial where classified as accidental epiphytes. As the category ‘accidental epiphytes’ describes plants which accidentally grow on trees, it includes several ‘regular’ growth forms. Accidental epiphytes were subcategorized according to their growth forms herbs, shrubs, trees and climbers (see Cornelissen et al. 2003), but in some cases it was not possible to distinguish shrubs and trees. (Holo- and hemi-) epiphytes are defined as described in Chapter 1.2.

2.2.4 Arthropod sampling

This study considers the microhabitats constituted by the epiphytes and the organic matter of oil palm trunks, respectively. These two microhabitats were sampled for arthropods independently. However, both samplings took place within the same plots (for details see Chapter 2.2.1). The sampling on epiphytes was always carried out first in order to not disturb arthropod activity. Due to restricted time, the sampling was performed independently of day time.

Arthropods on epiphytes (*Art.E*) Arthropods on epiphytes were collected at the plot level from all epiphytic plants on oil palm trunks, including both epiphytes and accidental epiphytes. In total, 90 plots were sampled. The rest of the plots had no plant cover. Arthropods were caught with a net, which was made from a mosquito netting (stitch density = 1.5 mm). The circular opening, stabilized by a wire, had a diameter of 0.42 m and covered an area of 0.139 m^2. The net was pulled over the plants growing within a plot and the plants were cut and put into the net. After closing and shaking the net, arthropods were removed from the net with forceps and transferred to one Eppendorf cup filled with ethanol (60%) per plot. The taxon (usually at order level) was noted down for every individual. This method resulted in abundance data at the plot level.

Arthropods in organic matter (*Art.O*) Organic matter accumulated in oil palm leaf axil was found on 48 of 54 oil palms. The full amount of organic matter in one leaf axil from each plot was collected and stored in cotton bags. In the evenings, samples of organic matter were put into Winkler's traps to extract the arthropods from organic matter. This time and cost efficient method is widely used in ecological and functional studies of soil macro-invertebrate communities and was invented by Emil Moczarski in 1907 (Krell *et al.* 2005). Each Winkler's trap was made of a cotton tube, closed and hung up at the upper end and ending in a bottle filled with ethanol (60%) at the lower end. Inside that tube, a net made of shower puff materials (stitch density = 6 mm, but elastic) and filled with a sample of organic matter was hung up. For oil palms tall enough to be sampled with multiple plots, the organic matter collected in all plots of that oil palm were mixed in one Winkler's trap as the number of traps available was limited. Run-time of the Winkler's traps was four days. Mechanisms of Winkler extraction are first, random movement of arthropods and second, movement out of the organic matter caused by the change of the microclimate (Krell *et al.* 2005). In doing so, they are likely to move out of the net and fall into the bottle. Arthropods caught in the bottle were transferred to Eppendorf cups filled with ethanol (60%), with a separate cup for each mixed-sample. The organic matter was separately stored in closed plastic bags. The organic matter was dried in the oven in the CRC 990 laboratory at UNJA for 2 days at 80 °C. As the same difficulty in measuring wet weight occurred as described in Chapter 2.2.2 (see scatterplot in Appendix 3), only the measurements for dry weight are used. This method produces measurements of numbers of individuals or taxa per dry weight of organic matter. Measurements were standardized to a dry weight of 50 g per oil palm.

Arthropod individuals were identified to order level under a binocular microscope at UNJA. For insects, a key to orders in 'Insects of Australia' (CSIRO 1991) was used. Because of the dominance of Formicidae (ants) in Hymenoptera, this order was further subdivided to the taxa 'Hymenoptera excl. Formicidae' and 'Formicidae'. Diplopoda (class), Symphyla (class) and Acari (subclass) were not identified to order level due to missing identification guides.

2.3 Statistical analyses

A Microsoft Access Database (Version 2010) was setup in order to link the different data sets. Statistical analyses and graphics were mainly done in R, version 2.15.2. Some graphics were done in Microsoft Excel 2010.

2.3.1 Habitat characteristics of oil palm plantations

To facility the interpretation of patterns in abundance and diversity of epiphytic plants and arthropods on the oil palms, for this reason, habitat variables were evaluated first.

Interviews with plantation owners about plantation management and characteristics were translated from Bahasa Indonesia to English. Main results are briefly described. Full answers can be looked up in Appendix 2.

At the oil palm level, the mean and standard deviation was calculated for each variable measured. Descriptive statistics of 'plant cover',' leaf base cover' and 'organic matter' were visualized in Box-Whisker-plots (short: boxplots). Comparisons of means for significant differences were performed with a max-t-test following (Herberich *et al.* 2010) in R using a significance level of $p < 0.05$ as described in Chapter 2.3.2. Further, the impact of 'leaf base cover' and 'organic matter' on 'plant cover' was examined for linear relationships using scatterplots and linear regressions.

2.3.2 Abundance and diversity of species and higher-ranked taxa

Abundance of a taxon is a quantitative measurement of the numbers of individuals per taxon. Species richness, defined as 'number of species of a given taxon in the chosen assemblage' (Magurran 2004, p. 72), is here used as a quantitative measurement of *alpha*-diversity. Species richness can be described by numerical species richness (number of species per number of individuals) or by species density (number of species per collection area or unit) (Magurran 2004). The collected data provide a measurement of species density, in fact species richness per oil palm or species richness per plot.

Analyzes for epiphytes (*Epi*) and accidental epiphytes (*Acc*) were always performed both at the oil palm and plot level. Arthropods on epiphytes (*Art.E*) were analyzed at the plot level only, whereas arthropods in organic matter (*Art.O*) were analyzed at the oil palm level only. The number of individuals and taxa of *Art.O* were standardized to the number of individuals and taxa per 50 g organic matter (dry weight) per oil palm.

Patterns in abundance and richness of species and higher-ranked taxa were compared between different locations, age classes both at the oil palm level and additionally between trunk heights at the plot level.

Means and standard deviations were calculated for number of individuals and species, and higher-ranked taxa. Also, numbers of individuals and species or taxa were summarized in boxplots.

Numbers of individuals and species and higher-ranked taxa were tested for significant differences between subcategories in the variables location, age class and trunk height. Given the presence of heteroscedasticity in the data and an unbalanced design, the max-t-test is a robust test to compare multiple means for significant differences (Herberich *et al.* 2010). The max-t-test was implemented in R following Herberich *et al.* (2010) to control for differences in means at a significance level of $p < 0.05$.

The number of species found also depends on the sampling effort and it is problematic to compare species richness between study sites, if sampling effort was not equal (Magurran 2004). The same applies to number of higher-ranked taxa. Sampling effort usually is measured by the number of samples or individuals or area surveyed. In this study, the sampling effort (number of plots) varied between different locations, age classes, trunk heights and also plantations. To control for that, species accumulation curves (SAC) were used. In SACs, the cumulative number of species observed is plotted against the sampling effort (Colwell & Coddington 1994 in Magurran 2004). The samples are added in a randomized order and that process is repeated several times. SACs show the mean and standard deviation of all processed curves. Thus, SACs give information about the rate at which new species were found and if the sampling effort was high enough to find all species of the study area. If the curve achieves saturation, it is expected that all species of the area were found (Magurran 2004). SACs were calculated at 100 permutations for *Epi* and *Acc* both at the plot and oil palm level with the specaccum()command in the R package vegan, version 2.0-9 (Oksanen *et al.* 2013). Taxon accumulation curves (TACs) were calculated analogous to SACs for *Art.E* at the plot level and for *Art.O* at the oil palm level.

In this study, age is described by the categorical variable ‘age class’. As changes in diversity are in particular expected along an age gradient, the number of individuals and species or taxa was additionally explored along a continuous age gradient. Therefore, the ‘main age’ of investigated oil palms in each plantation was identified. For young plantations, plantation owners reported more than one planting year. These plantations were ordered by ‘trunk height to meristem’, which can be seen as a measurement of age. Boxplots showing the abundance and diversity of the investigated organism groups are shown in Appendix 6.

2.3.3 Community composition

The number of common species and of species restricted to one location or age class was calculated for *Epi* and *Acc*. For arthropods, I searched for overlapping taxa between *Art.E* and *Art.O*.

Rank abundance curves (RACs) were useful to identify, if a community was dominated by one or several species or if species showed similar abundances (Magurran 2004). Species were ranked by their abundance and plotted in descending order. Based on abundance data, the community composition of each investigated organism group was described in RACs. RACs for *Epi*, *Acc* and *Art.E* were generated at the plot level and those for *Art.O* (standardized) at the oil pal level. It was worked on relative abundances. That enabled group comparisons at different sampling effort. RACs include all observed arthropod taxa, but not all species found in epiphytes and accidental epiphytes. Species that are not represented in RACs were only found outside the plot and are not listed in abundance data.

Further, a NMDS (non-metric multidimensional scaling) (Leyer & Wesche 2007) was done for epiphytes based on presence absence data at the oil palm level. This ordination produces a distance matrix based on the Bray-Curtis dissimilarity. It was used to visualize the similarity or dissimilarity between oil palms with respect to epiphyte species. The NMDS was done in the R package vegan (version 2.15.3) with the command metaMD().

The substrate used by epiphytes and the proportion of fertile epiphyte individuals separated by age class were shown in bar plots. Also, the size of epiphytes and the body length of arthropods will be compared between age classes. These investigations will give information about species about the ecology of species on oil palm plantations.

2.3.4 Determinants of abundance and diversity

Factors (predictors) that might determine abundance and diversity of epiphyte species and arthropod taxa (response variables) on oil palms (Table 2) were tested in linear models and linear mixed-effect models.

Linear models (LMs) identify linear relationships between a response variable and one or multiple predictor variables (see Crawley 2007). LMs that directly refer to the hypotheses were performed for oil palm and plot level data. Additionally, LMs for further variables tested are shown in Appendix 7.

Table 2: Response variables and predictors that were tested in linear models and linear mixed-effect models. For each response variable, single and multiple predictors were tested. Organism groups: epiphytes (*Epi*), accidental epiphytes (*Acc*), arthropods on epiphytes (*Art.E*) and arthropods in organic matter (*Art.O*; standardized to number of individuals or taxa per 50 g organic matter (dry weight)). [1] Variable was also tested when $\log_e$-transformed. [2] Only tested for *Art.O*. [3] Only tested for *Art.E*. 'Main age' and 'trunk height to meristem' were tested as another variant to describe age.

Level	response variable	predictors
oil palm	- no. species (*Epi*)[1] - no. species (*Acc*)[1] - no. individuals (*Art.O*)[1] - no. taxa (*Art.O*)[1]	- location - age class - main age - trunk height to meristem - plant cover - leaf base cover - no. species (*Epi*)[1, 2] - no species (*Acc*)[1, 2]
plot	- no. individuals (*Epi*)[1] - no. species (*Epi*)[1] - no. individuals (*Acc*)[1] - no. species (*Acc*)1 - no. individuals (*Art.E*)[1] - no. taxa (*Art.E*)[1]	- location - age class - main age - trunk height to meristem - trunk height (refers to the position of the plot) - plant cover - leaf base cover - organic matter (in one leaf axil, dry weight) - no. individuals (*Epi*)[1, 3] - no. species (*Epi*)[1, 3] - no. individuals (*Acc*)[1, 3] - no. species (*Acc*)[1, 3]

Linear mixed-effect models (LMEs) were applied that are appropriate for data from hierarchically, spatially-nested study designs, as we have in this study. LMEs were performed to explain the number of individuals (*Epi*, *Acc*, *Art.E*, *Art.O*) as well as the numbers of species (*Epi*, *Acc*) ore higher-ranked taxa (*Art.O*, *Art.E*). The natural logarithm ($\log_e$) was calculated for each of these response variables (+1 due to some zero abundance) as they did now show normal distribution. In LMEs, the predictor(s) is categorized in fixed effects that influence the mean of the response variable, and random effects that influence the variance of the response variable (Eisenhart 1947 in Crawley 2007). LMEs fit by REML were calculated in R package nlme, version 3.1-105 (Pinheiro *et al.* 2012). First, a null model that only included random effects (strictly speaking, this is a random effect model) was setup for every response variable to check the variance in the data at different spatial levels and the total variance in the data.

null.model <- lme(response variable ~ 1, random = ~1 | location / plantation.ID / oilpalm.ID, data = oilpalm.level)

The total variance in data ($\mathrm{Var}_{\mathrm{total}}$) is the sum of all variances (standard deviation * standard deviation) of random effects inclusive residuals in the null model:

$$Var_{total}\ (null.model) = Var\ (location) + Var\ (plantation.ID\ in\ location) + Var\ (oilpalm.ID\ in\ plantation.ID\ in\ location) + Var\ (residuals)$$

Var (residuals) refers to the variance in data which remained unexplained by the model. At the plot level, ‘plot.ID’ was also part of the random effects (and its variance also contributed to $\mathrm{Var}_{\mathrm{total}}$):

null.model <- lme (response variable ~ 1, random = ~1 | location / plantation.ID / oilpalm.ID / plot.ID, data = plot.level)

In order to identify determinants of abundance and diversity, further models were setup. They also included one or more fixed effects (predictors in Table 2).

model.n <- lme (response variable ~ fixed effect(s), random = ~1 | Location / Plantation.ID / Oilpalm.ID, data = oilpalm.level)

The best model for each response variable was chosen based on Akaike’s Information Criterion (AIC). AIC can be used as a measure for relative support. Lower AIC values indicated better fits. Only AICs of LMEs that have the same response variable can be compared to each other. The best model was tested for significant differences to the null model, using models refitted with Maximum

Likelihood (ML) rather than Restricted Maximum Likelihood (REML) to enable comparison of the fixed rather than of the random parts of the models (Zuur *et al.* 2009).

null.model <- lme(response variable ~ 1, random = ~1 | location / plantation.ID / oilpalm.ID, data = oilpalm.level, method = "ML")

best.model <- lme (response variable ~ fixed effect(s), random = ~1 | Location / Plantation.ID / Oilpalm.ID, data = oilpalm.level, method = "ML")

anova(null.model, best.model)

Significance codes were p < 0.001 (high significance ***) < 0.01 (significance **) < 0.05 (low significance *).

Parameters of the best models were summarized in tables. Parameters of the null model are shown in Appendix 8.

3 Results

3.1 Habitat characteristics of oil palm plantations

Oil palm plantation management Interviews with plantation owners indicated that great differences in cultivation existed between locations (which makes sense because all investigated plantations in ‘pk’ had the same owner and ‘mm.m’ and ‘mm.o’ were owned by the same person). The use of herbicides and pesticides and the way of dealing with epiphytes on oil palm trunks differed between the plantations in ‘mm’ and those in ‘bm’ and ‘pk’:

- In ‘bm’ and ‘pk’, epiphytes were manually removed from oil palm trunks two times a year. In contrast, epiphytes were never removed in ‘mm’.
- The herbicide Gramoxone was applied to the ground at every plantation except at ‘bm.y’. At ‘bm.m’ and ‘bm.o’ it was also applied to oil palm trunks. Additionally, plantation owners in ‘mm’ reported usage of ‘*Eli*’, but I was not able to identify this herbicide with an internet search (the name possibly refers to a company’s name, *Eli Lilly*).
- Pesticides were not used in ‘mm.y’, ‘bm.m’, ‘bm.o’ and ‘mm.o’. However, the insecticide Matador (Matador ® 120EC) was applied at oil palm leaves at all plantations in ‘pk’. Furadan 3 g (Carbofuran) is used on the ground at ‘bm.y’. The owner of ‘mm.m’ reported the use of pesticides but did not talk about details.

Chemical fertilizers were applied on every plantation. Oil palm fruits were harvested every 2 weeks in ‘bm’ and ‘mm’ and every 10 days in ‘pk’. All plantation owners reported pest infestations. *‘Ulat api’*, a group of nettle caterpillars of the Lepidoptera family Limacodidae (see Figure 2, D) occurred as oil palm pests in every plantation. Furthermore, some owners reported problems with wild pigs, mice or rats (*‘tikus’*), hedgehogs and monkeys. From time to time, plantations in ‘mm’ had fungal infestations at oil palm fruit, xylem and phloem. Detailed answers to the interview questions are given in Appendix 2. These also give information about the time of last removal of epiphytes and last application of herbicides and pesticides. Table 3 includes characteristics of the oil palm trunks grouped by plantation. At both spatial levels, ‘plant cover’ was significantly higher in ‘pk’ than in other locations and decreased with age (Figure 7, A-B; Figure 8, A-B; see also Table 3). ‘Leaf base cover’ did not differ among locations but strongly decreased from age classes ‘y’ and ‘m’ to ‘o’ (Figure 7, C-D; Figure 8, D-E). The amount of organic matter in one leaf axil was not different between locations but showed an arch-shaped distribution with highest amounts in the middle age class (Figure 8, G-H). None of the variables differed between plots at different trunk heights (Figure 8, C, F, I).

Linear regression analyses showed a positive correlation between ‘leaf base cover’ and ‘plant cover’. ‘Leaf base cover’ explained 10% of the variation in ‘plant cover’ among oil palms (Figure 6, A) and 12% among plots (Figure 6, B). However, no relationship between ‘plant cover’ and ‘organic matter’ was found (Figure 6, C).

Table 3: Oil palm characteristics. Mean ± standard deviation are given for each oil palm characteristic, grouped by plantation. In each plantation, measurements of six oil palms were taken. ‘Staying leaves’ (of the oil palm) were same with leaves alive in most cases, ‘hanging leaves’ were mostly dead leaves. Plantation.ID = [location.age class]. Abbreviations in ‘location’: bm = Bukit Makmur, mm = Marga Mulya, pk = Permatang Kabau; in ‘age class’: y = young, m = middle, o = old.

Planta-tion.ID	Planting distance [m]	Trunk height to meristem [m]	Trunk height to lowest leaf [m]	DBH [m]	Staying leaves	Hanging leaves	Leaf base cover [%]	Plant cover [%]
bm.y	6.71 ± 0.52	1.71 ± 0.29	0.4 ± 0.25	2.4 ± 0.14	40.17 ± 3.54	1.17 ± 2.04	100 ± 0	31.67 ± 15.71
mm.y	5.75 ± 1.67	1.33 ± 0.24	0.37 ± 0.11	2.4 ± 0.27	40.33 ± 5.05	0.17 ± 0.41	100 ± 0	43.33 ± 18.89
pk.y	6.06 ± 1.03	2.35 ± 0.11	0.96 ± 0.44	2.27 ± 0.34	44.67 ± 4.03	0 ± 0	100 ± 0	62.5 ± 30.29
bm.m	5.66 ± 0.87	7.26 ± 0.82	6.01 ± 0.7	2.45 ± 0.43	29.5 ± 3.73	0 ± 0	100 ± 0	18.33 ± 6.83
mm.m	6.36 ± 1.14	7.31 ± 1.17	6.24 ± 1.1	2.51 ± 0.3	32.33 ± 2.5	1.17 ± 1.17	100 ± 0	14.17 ± 5.85
pk.m	7.59 ± 0.9	4.67 ± 0.75	3.17 ± 0.97	2.47 ± 0.36	41.33 ± 4.32	0.33 ± 0.52	100 ± 0	63.33 ± 24.43
bm.o	7.82 ± 0.32	7.52 ± 0.92	6.51 ± 0.88	1.95 ± 0.45	38 ± 7.92	0.33 ± 0.52	39.17 ± 13.57	22.5 ± 12.94
mm.o	8.21 ± 0.44	12.47 ± 0.94	11.1 ± 0.94	1.62 ± 0.03	34.17 ± 2.64	2 ± 2.68	11.67 ± 4.08	8.33 ± 2.58
pk.o	7.17 ± 2.62	8.17 ± 1.23	7.29 ± 1.27	1.95 ± 0.44	43.67 ± 4.5	5.17 ± 6.88	29.17 ± 31.53	39.17 ± 26.54

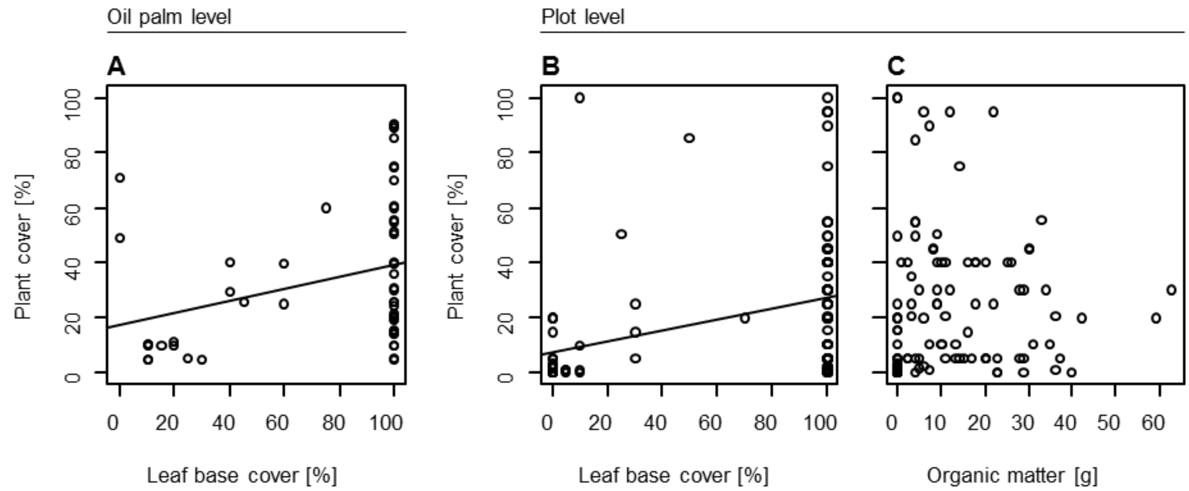

Figure 6: Relationship between habitat measurements of oil palm trunks. For a better resolution, the y-axis is jittered in all scatterplots. 'Organic matter' refers to dry weight of the whole content of organic matter in one leaf axil from each plot. A: $y = 0.22 x + 17.07$, $R^2 = 0.1018$ *; B: $y = 0.2 x + 7.41$, $R^2 = 0.12$ ***; C: $y = 0.19 x + 18.82$; $R^2 = 0.009796$ n. s.

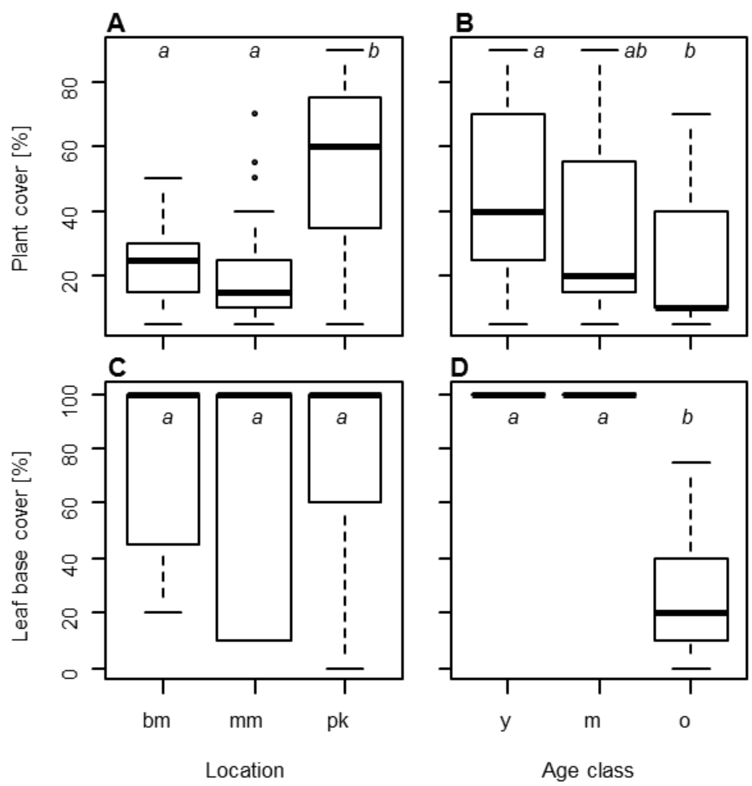

Figure 7: Habitat characteristics of oil palm trunks at the oil palm level. 'Plant cover' (A, B) and 'leaf base cover' (C, D) were estimated for each trunk. Letters in *italics* indicate group differences based on max-t-test at $p<0.05$. Abbreviations in 'location': bm = Bukit Makmur, mm = Marga Mulya, pk = Permatang Kabau; in 'age class': y = young, m = middle, o = old.

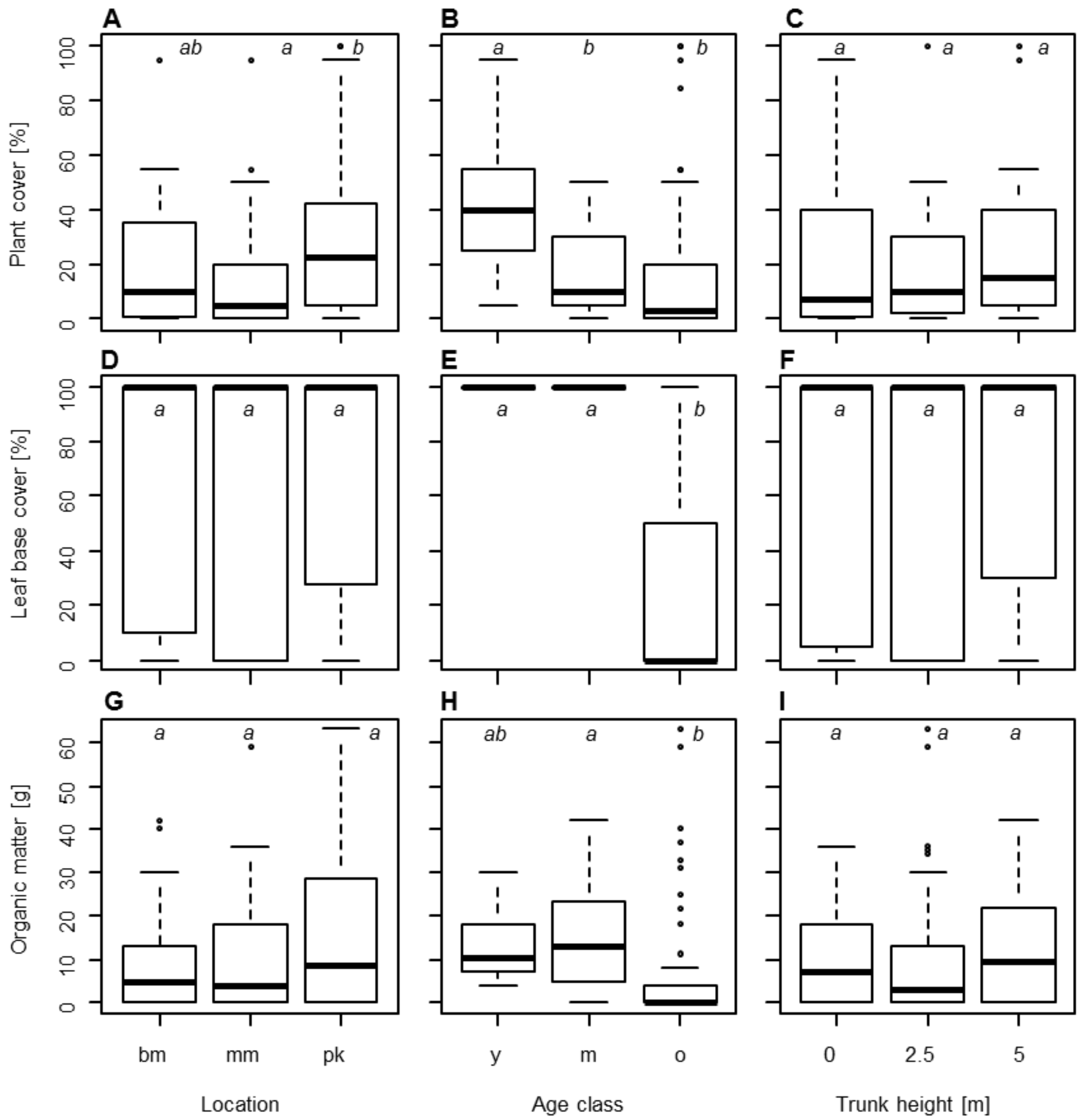

Figure 8: Habitat characteristics of the oil palm trunks at the plot level. 'Plant cover' (A-C) and 'leaf base cover' (D-F) were estimated for each plot. 'Organic matter' (G-I) refers to dry weight of the whole content of organic matter in one leaf axil from each plot. Letters in *italics* indicate group differences based on max-t-test at $p<0.05$. Abbreviations in 'location': bm = Bukit Makmur, mm = Marga Mulya, pk = Permatang Kabau; in 'age class': y = young, m = middle, o = old.

3.2 Abundance and diversity of species and higher-ranked taxa

Epiphytic plants on oil palms

In total, 50 vascular plant species were found growing on oil palm trunks including 18 epiphyte and 32 accidental epiphyte species (Table 4 and Table 5). Within epiphytes, fifteen holo-epiphyte and two hemi-epiphyte species were found; hemi-epiphytes were restricted to old oil palm plantations. All holo-epiphytes were pteridophytes and belonged to nine genera in six plant families (Aspleniaceae, Davalliaceae, Dennstaedtiaceae, Nephrolepidaceae, Vittariaceae, Polypodiaceae). Hemi-epiphytic species belonged to the angiosperm families Gesneriaceae and Moraceae. Identified accidental epiphyte species were assigned to thirteen families, but as thirteen species could not be identified, the total family diversity is probably underestimated. In contrast to epiphytes, most accidental epiphytes were angiosperms. The two pteridophyte families represented among the accidental epiphytes identified (Blechnaceae and Thelypteridaceae), were not represented among epiphytes. Accidental epiphyte species included three climbers, eleven shrubs and trees and eighteen herbs.

Table 4: List of all epiphyte species. In total, 18 species (15 holo- and 3 hemi-epiphytes) were found. Each species was given a unique number (Sp.ID). Major plant group is marked beside species names: * = Pteridophytes, all others are Angiosperms. Values: 1 = species present, 0 = species absent.

Sp.ID	Family	Species	Growth form	Location			Age class		
				bm	mm	pk	y	m	o
12	Aspleniaceae	*Asplenium* cf. *glaucophyllum*	holo-	0	1	0	0	1	0
14	Aspleniaceae	*Asplenium longissimum**	holo-	1	1	1	1	1	1
58	Aspleniaceae	*Asplenium nidus* vel aff.*	holo-	0	1	0	0	1	1
13	Aspleniaceae	*Asplenium spec.**	holo-	0	1	0	0	0	1
2	Davalliaceae	*Davallia denticulata* *	holo-	1	1	1	1	1	1
88	Dennstaedtiaceae	*Microlepia speluncae**	holo-	1	1	1	0	1	0
1	Nephrolepidaceae	*Nephrolepis spec.**	holo-	1	1	1	1	1	1
5	Polypodiaceae	*Goniophlebium percussum**	holo-	1	1	1	0	1	1
89	Polypodiaceae	*Goniophlebium* spec.*	holo-	1	1	1	1	1	1
6	Polypodiaceae	cf. *Phymatosorus* spec.*	holo-	0	0	1	0	0	1
8	Polypodiaceae	*Platycerium spec.**	holo-	0	0	1	0	0	1
87	Polypodiaceae	*Selliguea* cf. *enervis**	holo-	0	1	0	0	0	1
3	Vittariaceae	*Vittaria elongata**	holo-	1	1	1	1	1	1
4	Vittariaceae	*Vittaria ensiformis**	holo-	1	1	1	0	1	1
53		indet. Angiosperm	(holo-)	0	1	0	0	0	1
15	Gesneriaceae	*Cyrtandra* spec.	hemi-	0	0	1	0	0	1
49	Moraceae	*Ficus heteropleura*	hemi-[1]	0	1	0	0	0	1
32	Moraceae	*Ficus* spec.	hemi-[1]	0	0	1	0	0	1
Total number of epiphyte species				**8**	**14**	**12**	**5**	**10**	**16**

Table 5: List of all accidental epiphyte species observed. In total, 32 species were found. Each species was given a unique number (Sp.ID). Major plant group is marked beside species names: * = Pteridophytes, all others are Angiosperms. Values: 1 = species present 0 = species absent.

Sp.ID	**Family**	**Species**	**Growth form**	**Location**			**Age class**		
				bm	mm	pk	y	m	o
18	Acanthaceae	*Asystasia gangetica*	herb	1	1	1	1	1	1
20	Araceae	*Amorphophallus spec.*	herb	0	0	1	0	1	0
54	Arecaceae	*Elaeis guineensis*	tree	1	1	1	1	1	1
39	Asteraceae	*Ageratum conyzoides*	herb	0	1	0	0	1	0
31	Asteraceae	*Mikania micrantha*	climber	0	1	1	1	1	1
9	Blechnaceae	*Stenochlaena palustris**	climber	1	1	1	1	1	1
60	Cyperaceae	*Scleria spec.*	herb	0	0	1	1	0	0
59	Euphorbiaceae	*Hevea brasiliensis*	tree	0	0	1	0	1	0
57	Euphorbiaceae	*Macaranga triloba*	tree	0	0	1	1	0	0
47	Euphorbiaceae	*Macaranga spec.*	shrub/tree	0	1	0	1	0	0
55	Melastomataceae	*Clidemia hirta*	shrub	1	1	1	1	1	1
33	Melastomataceae	*Melastoma malabathricum*	herb	1	1	0	1	1	0
28	Phyllanthaceae	*Phyllanthus urinaria*	herb	1	0	1	1	1	0
61	Poaceae	*Isachne globosa*	herb	0	0	1	0	0	1
29	Poaceae	indet. Poaceae	herb	1	0	1	0	1	0
48	Rubiaceae	*Spermacoce latifolia*	herb	0	1	0	1	0	0
42	Rubiaceae	*Spermacoce spec.*	herb	0	1	0	0	1	0
86	Solanaceae	indet.	herb	0	0	1	1	0	0
10	Thelypteridaceae	*Cyclosorus spec.**	herb	0	1	0	0	1	0
16		indet. Angiosperm	herb	0	1	1	0	1	0
17		indet. Angiosperm	shrub/tree	0	0	1	1	1	0
19		indet. Angiosperm	shrub/tree	0	0	1	1	0	0
21		indet. Angiosperm	herb	0	0	1	0	1	0
22		indet. Angiosperm	herb	0	0	1	0	1	0
23		indet. Angiosperm	shrub/tree	0	0	1	0	1	0
24		indet. Angiosperm	shrub/tree	0	0	1	0	1	0
25		indet. Angiosperm	herb	0	0	1	0	1	0
26		indet. Angiosperm	shrub/tree	0	0	1	0	1	0
27		indet. Angiosperm	herb	0	0	1	0	1	0
30		indet. Angiosperm	climber	0	0	1	0	0	1
50		indet. Angiosperm	herb	0	1	0	0	0	1
52		indet. Angiosperm	tree	0	1	0	0	0	1
Total number of accidental epiphyte species				**7**	**14**	**24**	**14**	**22**	**9**

Species richness per oil palm was similarly low for both epiphytes and accidental epiphytes. On average, 3.98 ± 2.0 (range: 0-8) epiphyte and 3.19 ± 1.69 (range: 0-9) accidental epiphyte species were found per oil palm (n = 54).

Within the plots, 808 plant individuals, including 659 epiphytes and 149 accidental epiphytes, were sampled in total. These individuals were assigned to eleven epiphyte and fifteen accidental epiphyte species (the remaining plant species were found outside the plots). Hence, the numerical species richness of epiphytes was 11 species / 569 individuals = 0.02 species / individual. Accidentals showed a much higher numerical species richness of 15 species / 149 individuals = 0.1 species / individual. In other words, the rate at which new species were found was more than five times higher for accidental epiphytes (1 species / 9.93 individuals) than for epiphytes (1 species / 51.73 individuals). One plot contained 5.49 ± 8.46 (range: 0-68) epiphyte and 1.24 ± 2.58 (range: 0-14) accidental epiphyte individuals on average (n = 120). Note the enormous range in number of epiphyte individuals per plot. On average 1.3 ± 1.23 (range: 0-5) epiphyte and 0.62 ± 1.02 (range: 0-5) accidental epiphyte species per plot were found. For epiphytes, species accumulation curves (SACs) almost reached saturation at both the oil palm and plot levels. At the plot level, already 7 epiphyte species were found at a sampling effort of 20 plots (5 m²). In contrast, the curve progressions of SACs for accidental epiphytes are still increasing at both spatial levels, suggesting that not all species of the study area were found.

Epiphytes Number of individuals per plot differed significantly between locations. In 'mm', three times more species per plot were recorded compared to 'bm' and 'pk' (Figure 9, A). However, the number of individuals per plot did not differ significantly between age classes or trunk heights (Figure 9, B-C). Also, there was no obvious pattern in number of individuals per plot when plantations were ordered along a continuous age gradient (Appendix 6.1, A). At the oil palm level, species richness increased significantly from age class 'y' to 'm' and stagnated from 'm' to 'o' (Figure 10, B). Similar dynamics appeared along a continuous age gradient (Appendix 4). In contrast, species richness decreased significantly from age class 'm' to 'o' at the plot level, but the median did not change (Figure 11, B). When plantations were ordered by their main age but not by age class, there were no significant differences in species richness among the plots (Appendix 4). SACs for species richness of epiphytes showed similar results in comparing age classes at the plot and oil palm level (Figure 13, A-B; Figure 14, A-C). SACs were almost saturated for 'y' and 'm', but still in the rising phase for 'o'. That indicates that not all epiphyte species in old plantations were recorded yet. There were no significant differences in species richness among plots of different locations and trunk heights. SACs also approached saturation for all locations at both the plot and oil palm level. SACs calculate separately by trunk height reached saturation for plots at 0 m and 2.5 m, but not for plots at 5 m.

Accidental epiphytes Obvious changes in abundance and richness of accidental epiphytes were found along an age gradient, but these were opposite to patterns seen for epiphytes. Both number of individuals and species decreased significantly with age at the plot level (Figure 9, E; Figure 11, E). Furthermore, species richness per oil palm was significantly lower in old plantations than in younger ones (Figure 10, D). SACs for age classes 'o' and 'm' reached saturation (Figure 13, D; Figure 14, E), but SACs for young plantations, particularly at the plot level, did not saturate. Consequently, a higher sampling effort on young plantations should result in higher (cumulative) species richness. Significantly more individuals and species were observed in plots at 0 m compared to plots on higher parts of oil palm trunks (Figure 9, F; Figure 11, F). Nevertheless, SACs for every trunk height reached saturation (Figure 14, F). Locations did not show any significant differences in species richness and abundance (Figure 9, D; Figure 11, D). However, SACs for 'pk' were in the rising phase and indicate that probably more species would be found if one would have sampled more plots and oil palms (Figure 13, C; Figure 14, D).

Oil palm dwelling arthropods

Nineteen arthropod taxa were found Table 6. These included one family (Formicidae), sixteen orders (including "Hymenoptera excl. Formicidae"), and two classes. For both *Art.E* and *Art.O*, taxon accumulation curves (TACs) that included all individuals reached saturation (Figure 12, C, F). Taxon accumulation curves for the different categories in location, age class and (for Art.E) trunk height also reached saturation (Figure 13, E-F; Figure 14, G-I).

Arthropods on epiphytes In total, 508 arthropod individuals were found on epiphytes over all plots (n=90). The average number of individuals per plot was 5.64 ± 12.01 and ranged widely, from 0 to 102. The individuals were identified to fourteen taxa: Acari, Araneae, Blattodea, Coleoptera, Diplopoda, Diptera, Formicidae, Hemiptera, Hymenoptera (excl. Formicidae), Lepidoptera, Mantodea, Orthoptera, Psocoptera and Thysanoptera. No arthropods were observed in 11 plots, even though all of these plots had plant cover > 0%. Highest average arthropod abundance was observed in 'pk', in young plantations and at a trunk height of 0 m. The mean number of arthropod taxa per plot was 1.82 ± 1.29 (range: 0-5). Significantly more individuals and taxa were collected in 'pk' than in the other locations. Taxon accumulation curves for ‘pk’ and ‘mm’ pass into saturation phase. The TAC for ‘bm’ reached saturation. No significant differences in taxon richness were found among age classes or trunk heights, and all TACs pass into saturation phase.

Arthropods in organic matter In total, 1005 arthropod individuals were extracted from 2265 g organic matter (dry weight) sampled from 48 oil palm trunks. On average, 49.24 g ± 38.79 g organic matter was sampled per oil palm. Arthropods were identified to 17 taxa: Acari, Araneae, Blattodeae, Coleoptera, Collembola, Dermaptera, Diplopoda, Diptera, Formicidae, Hemiptera, Hymenoptera (excl. Formicidae), Isopoda, Isoptera, Lepidoptera, Orthoptera, Psocoptera and Symphyla. All but on individual could be assigned to a taxon. All results for arthropods in organic matter are for analyses on standardized data – numbers of arthropod individuals or taxa per 50 g organic matter (dry weight). Mean number of arthropod individuals per oil palm was 37.38 ± 100.07 (range: 0-675). Number of individuals did not differ significantly between oil palms of different locations or age classes. Also, no significant difference was found for number of taxa between oil palms of different locations. However, taxon richness decreased significantly with age class.

Table 6: List of arthropod taxa that were found in two microhabitats on oil palms.

				Microhabitat	
Class	Order	Family	English name	Epiphyte	Organic matter
Arachnida	Acari		mites; thicks	1	1
Arachnida	Araneae		spiders	1	1
Insecta	Blattodea		cockroaches	1	1
Insecta	Coleoptera		beetles	1	1
Insecta	Collembola		springtails	0	1
Insecta	Dermaptera		earwigs	0	1
Insecta	Diptera		flies	1	1
Insecta	Hemiptera		true bugs	1	1
Insecta	Hymenoptera	Formicidae	ants	1	1
Insecta	Hymenoptera	excl. Formicidae	sawflies, wasps, bees	1	1
Crustacea	Isopoda		isopods	0	1
Insecta	Isoptera		termites	0	1
Insecta	Lepidoptera		butterflies	1	1
Insecta	Mantodea		mantises	1	0
Insecta	Orthoptera		e.g. grasshoppers, crickets	1	1
Insecta	Psocoptera		booklices	1	1
Insecta	Thysanoptera		thrips	1	0
Diplopoda			millipedes	1	1
Symphyla			centipedes	0	1
Total number of taxa				14	17

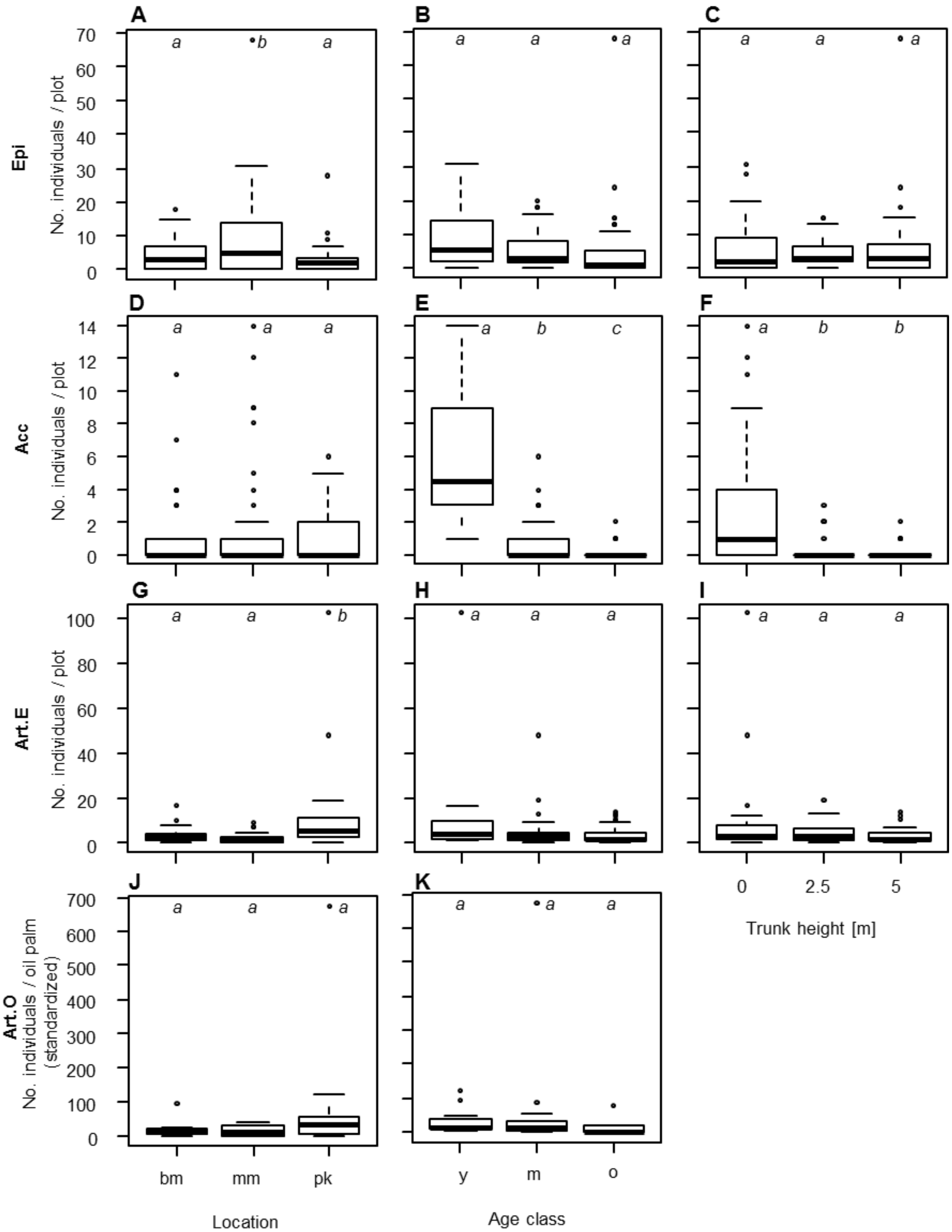

Figure 9: Number of individuals of epiphytes and arthropods per plot in different locations, age classes and trunk heights. Epiphytes (*Epi*, A-C), accidental epiphytes (*Acc*, D-F), arthropods on epiphytes (*Art.E*, G-I), arthropods in organic matter (*Art.O*, J-K). Numbers of individuals in *Art.O* were standardized to number of individuals per 50 g organic matter (dry weight) per oil palm. Number of individuals is grouped by 'location' (A, D, G, J), 'age class' (B, E, H, K) and 'trunk height' (C, F, I). Total number of individuals (n) was n(*Epi*) = 659, n(*Acc*)=149, n(*Art.E*)=508 and n(*Art.O*)=1005. Letters in *italics* indicate group differences based on max-t-test at $p<0.05$. Abbreviations in 'location': bm = Bukit Makmur, mm = Marga Mulya, pk = Permatang Kabau; in 'age class': y = young, m = middle, o = old.

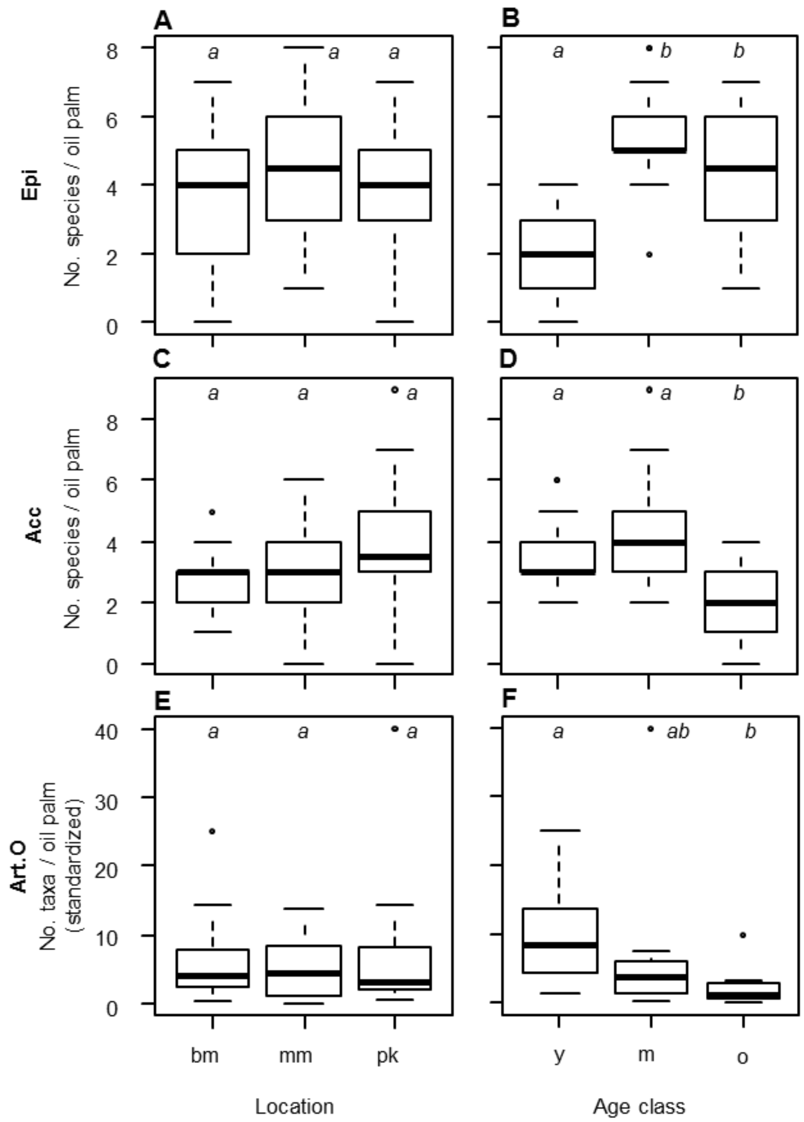

Figure 10: Richness of plant species and arthropod taxa at the oil palm level. Number of species per oil palm for epiphytes (*Epi*, A-B) and accidental epiphytes (*Acc*, C-D) and number of taxa per oil palm for arthropods in organic matter (*Art.O*, E-F). Numbers of taxa in *Art.O* were standardized to number of taxa per 50 g organic matter (dry weight) per oil palm. Species/taxon richness is grouped by location (A, C, D) and age class (B, D, F). Letters in *italics* indicate group differences based on max-t-test at p<0.05. Abbreviations in 'location': bm = Bukit Makmur, mm = Marga Mulya, pk = Permatang Kabau; in 'age class': y = young, m = middle, o = old.

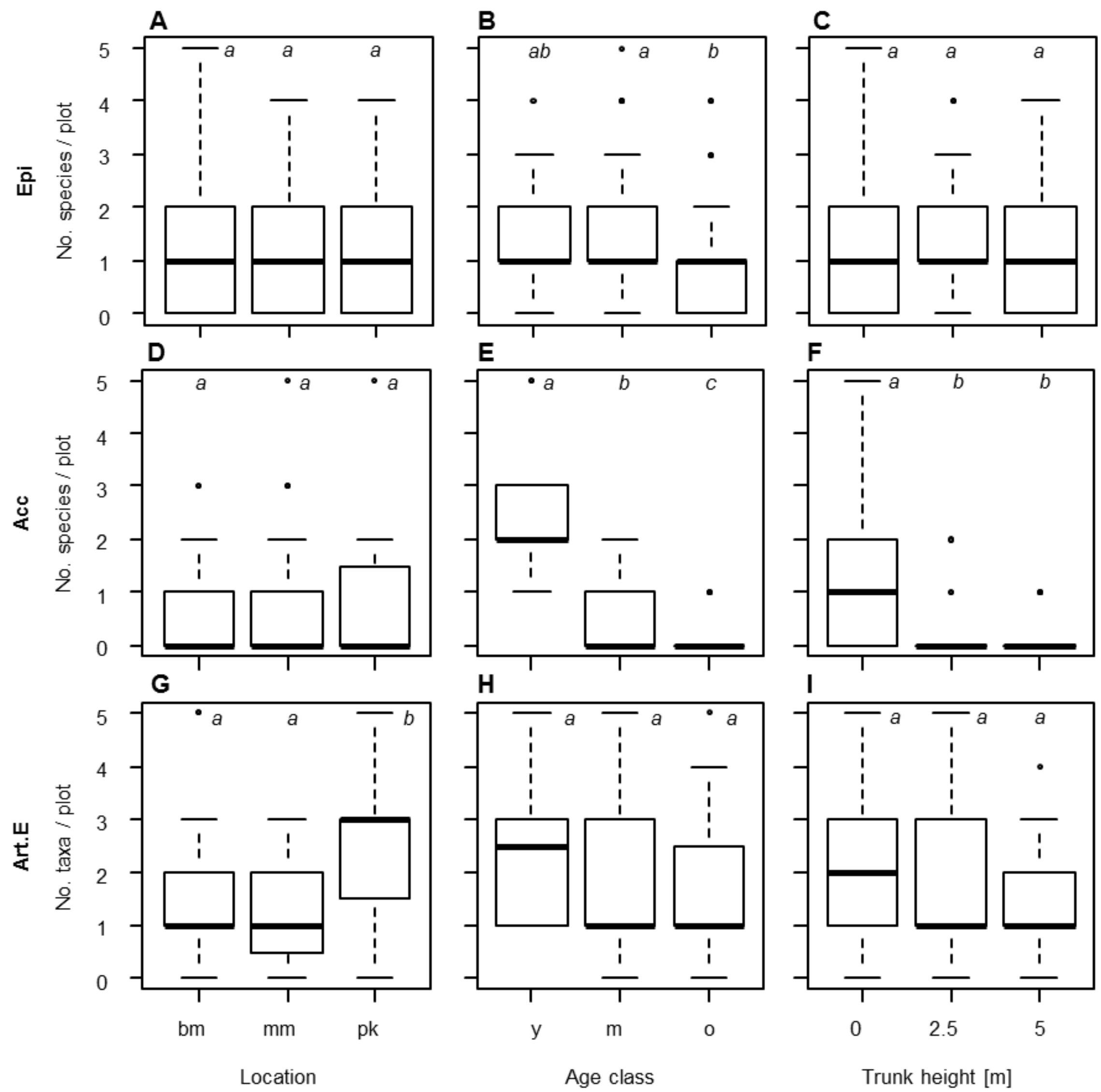

Figure 11: Richness of plant species and arthropod taxa at the plot level. Species richness of epiphytes *(Epi*, A-C) and accidental epiphytes (*Acc*, D-F) and number of arthropod taxa on epiphytes (*Art.E*, G-I) in 0.5 m x 0.5 m plots on oil palm trunks. Separated by 'location' (A, D, G), 'age class' (B, E, H) and 'trunk height' (C, F, I). Letters in *italics* indicate group differences based on max-t-test at $p<0.05$. Abbreviations in 'location': bm = Bukit Makmur, mm = Marga Mulya, pk = Permatang Kabau; in 'age class': y = young, m = middle, o = old.

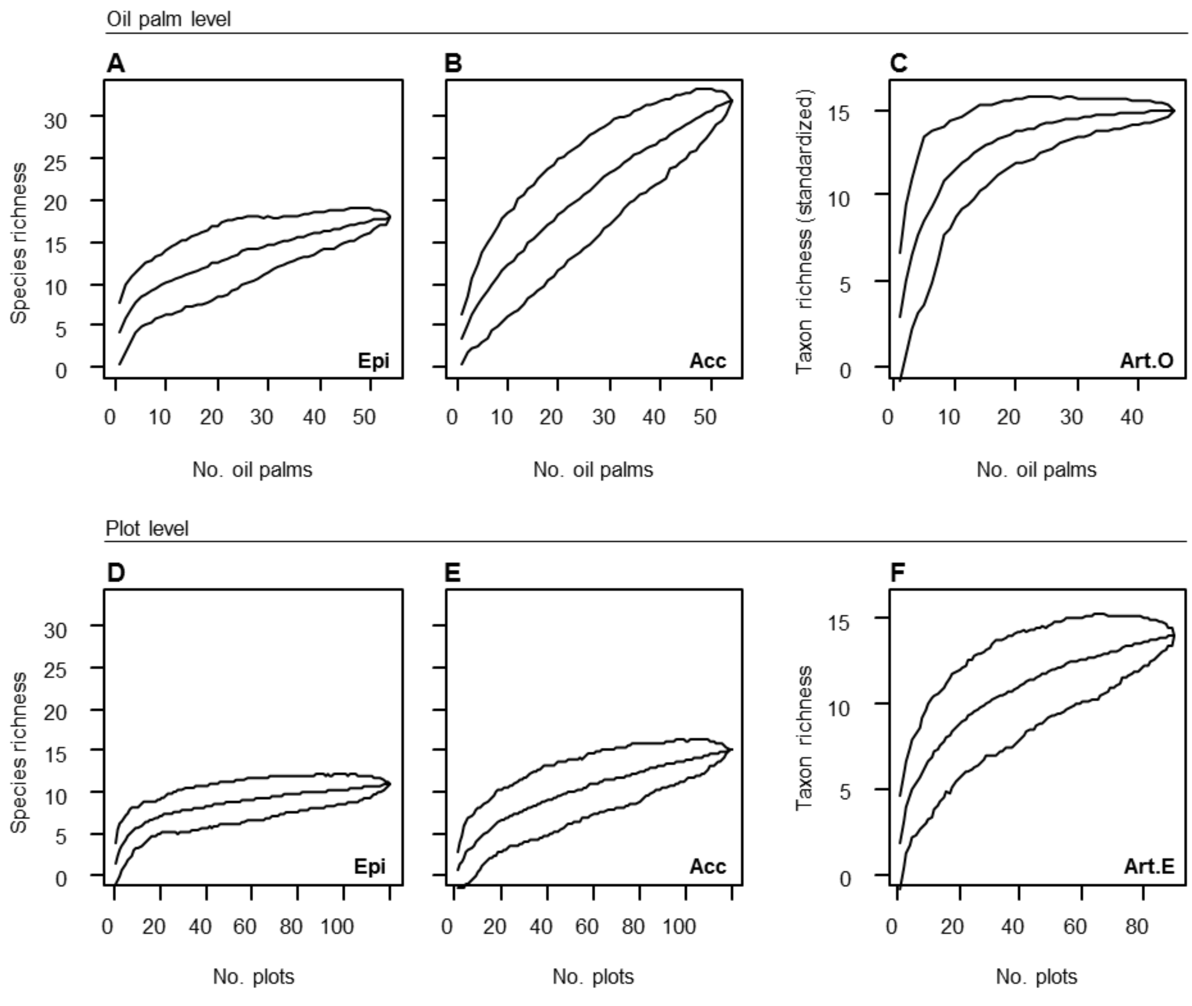

Figure 12: Species (and higher-ranked taxon) accumulation curves for all samples. Cumulative species richness of epiphytes (*Epi*) and accidental epiphytes (*Acc*) and cumulative taxon richness of arthropods on epiphytes (*Art.E*) and arthropods in organic matter (*Art.O*) in leaf axils on oil palm trunks at the oil palm (n = 54, but for *Art.O* n = 46) and plot level (n = 120, but for *Art.E* n = 90). Numbers of taxa in *Art.O* were standardized to number of taxa per 50 g organic matter (dry weight) per oil palm. 100 permutations.

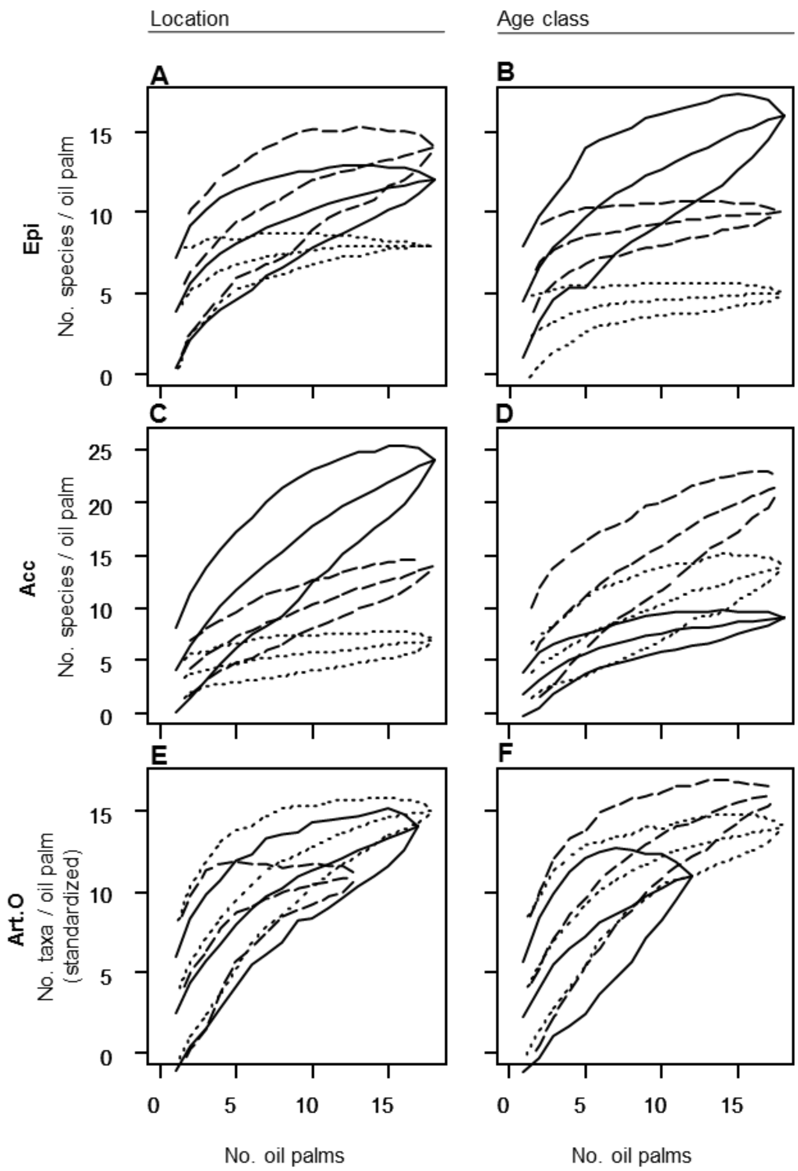

Figure 13: Species accumulation curves at the oil palm level. SACs were calculated separately for the subcategories of ‘location’ and of ‘age class’ in all cases (*Epi* = epiphyte, *Acc* = accidental epiphyte, *Art.O* = arthropods in organic matter in leaf axils). Numbers of taxa in *Art.O* were standardized to number of taxa per 50 g organic matter (dry weight) per oil palm. Line types in ‘location’ (A, C): dotted = Bukit Makmur, broken = Marga Mulya, continuous = Permatang Kabau; in ‘age class’ (B, D): dotted = young, broken = middle, continuous = old.

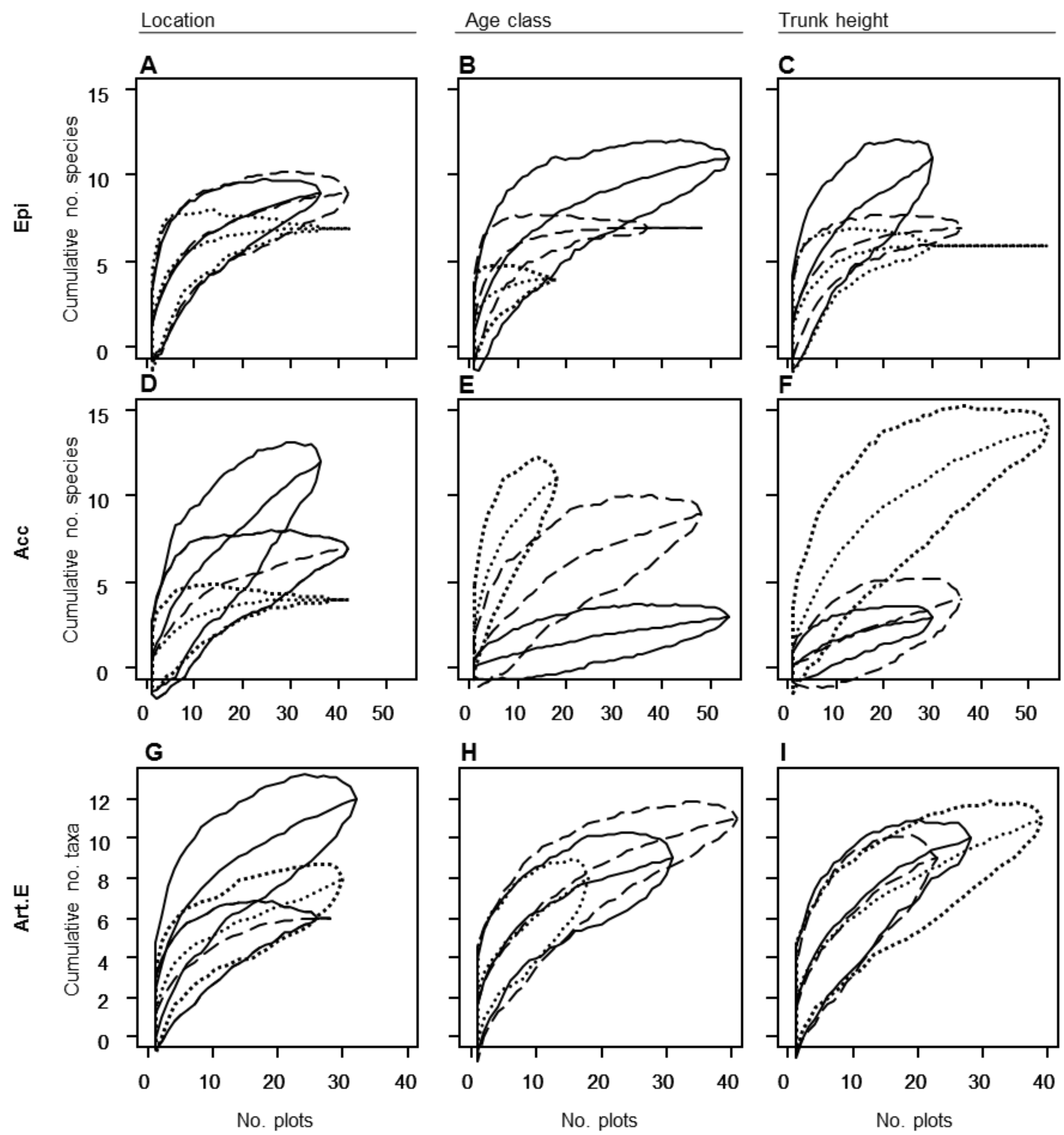

Figure 14: Species accumulation curves at the plot level. SACs were calculated separately for the subcategories of 'location', of 'age class' and of 'trunk height' in all cases (*Epi* = epiphytes, *Acc* = accidental epiphytes, *Art.E* = arthropods on epiphytes. Line types in 'location' (A, D, G): dotted = Bukit Makmur, broken line = Marga Mulya, continuous line = Permatang Kabau; in 'age class' (B, E, H): dotted line = young, broken line = middle, continuous line = old; in 'trunk height' (C, F, I): dotted line = 0 m, broken line = 2.5 m, continuous line = 5 m.

3.3 Community composition

Epiphytic plants on oil palms

Both epiphyte and accidental epiphyte species were unevenly distributed between oil palm plantations of different locations and age classes (Figure 15). Rank abundance curves show that the communities of both epiphytes and accidental epiphytes were mainly composed of individuals from a few dominant species (Figure 25).

Epiphytes All locations harbored eight common epiphyte species (Figure 15). Furthermore, six species were recorded for ‘mm’ and four species for ‘pk’, all restricted to one location. In ‘bm’, no further species were found. Five common species were shared by all age classes. No additional species were found in age class ‘y’. In contrast, eight additional species were restricted to old plantations and two species were found only in age class ‘m’. Age class ‘m’ and ‘o’ shared another 3 species.

Among epiphytes, 64.64% of the community was made up of individuals of *Vittaria ensiformis* (35.35%) and *Nephrolepis* spec. (29.29%; however note that *Nephrolepis* spec. probably includes more than one species; comment by M. Kessler). Another five species (*Asplenium longissimum, Davallia denticulata*, *Goniophlebium* spec. *Vittaria elongata*, *Goniophlebium percussum*) made up a further 34.6% of the community. The remaining four species that were found at the plot level were only represented by one or two individuals (together 0.76%). Rank abundance curves for different locations, age classes and trunk heights had similar curve shapes (Figure 26) indicating a small variation in community composition. The first four ranks in every subcategory of ‘location’, ‘age class’ and ‘trunk height’ are shared by six epiphyte species in total (Table 7). *Nephrolepis* spec. dominated the community in young plantations (65%) and also top-ranked in plantations of the age class ‘m’ (30.2). *Asplenium longissimum* (23.27%) and *Vittaria ensiformis* (17.96%) showed high abundances in this age class. The abundance of *Vittaria ensiformis* is lower on old plantations (3.15%). Individuals of *Vittaria elongata* contributed 9.76% to the epiphyte community for age class ‘m’ and were dominant in old plantations (74.4%) and at a trunk height of 5 m (60.19%).

The NMDS for epiphytes at the oil palm level did not result in obvious groups in the distance matrix (Figure 16, B). However, the stress plot is showing that this type of ordination fits the data (Figure 16, A). Also, no obvious groups are evident when different locations or age classes were marked with different colors within that distance matrix (Figure 17, A-B). Oil palms of some plantations showed a tendency for grouping, but these groups were not clearly defined (Figure 17). they did not group by age class or location.

In most epiphyte species, individuals were found on all substrates provided by the oil palm trunks (Figure 18). 78.11% of *Vittaria ensiformis* individuals occurred on the naked trunk. In contrast, *Goniophlebium spec.* was never found on the naked trunk and *Nephrolepis spec.* occurred only rarely on naked trunks. In plantations of the age class y and m, epiphytes mainly used organic matter as substrate, but in a small part also leaf bases. In old plantations, the majority of epiphytes grew on the naked trunk.

The proportion of fertile epiphyte individuals increased with age class from 3.75% in 'y' to 23.62% in 'o' and also with trunk height from 0 m (4.88%) to 5 m (25.24%) (Figure 20). The proportion of fertile individuals also varied between locations (6.14% in 'bm', 12.77% in 'mm', 17.12% in 'pk').

Accidental epiphytes Four species occurred at all locations (Figure 15). As for epiphytes, no species was restricted to 'bm'. In contrast, sixteen species only occurred at 'pk'. 'Pk' shared two more species with each 'bm' and 'mm', which again had one species in common. Five common species occurred in plantations of all age classes. Furthermore, age class 'y' and 'm' had three species in common. Age class 'm' had fourteen species that were only encountered there. Six more species were only encountered in young plantations and another four only in old plantations.

Seedlings of *Elaeis guineensis* were the most abundant in numbers of individuals (27.5%) (Figure 25, B). There were three dominant species (*Elaeis guineensis*, *Clidemia hirta* and *Asystasia gangetica*) which made up 71.14% of the community. *Stenochlaena palustris* and *Spermacoce latifolia* were each represented by ten individuals (6.71% each). The remaining 15.43% of the community was composed of ten species. Five of them were only represented by one individual. *Clidemia hirta* was among the top four most abundant species in each subcategory. *Elaeis guineensis* was also one of the four highest-ranked species in every subcategory except age class 'o'. The top four ranks in 'pk' were occupied by six species. *Stenochlaena palustris* appeared in the four top-ranked species in age class 'm' (7.68%) and was dominant in age class 'o' (66.67%). Further, Clidemia hirta and Isachne globosa completed the community of accidental epiphytes in age class 'o' (so within the plots only 3 species were found, but when the whole trunks were surveyed, nine species of accidental epiphytes were found in age class 'o'). Also, at a trunk height of 5 m, the community was composed by only three species: *Stenochlaena palustris*, *Elaeis guineensis* and *Clidemia hirta*.

Most accidental epiphyte individuals used organic matter in leaf axils along the oil palm trunks as substrate (Figure 18). Only three individuals grew on the naked trunk. All of them belong to the climbing species *Stenochlaena palustris*. The three dominant species in accidental epiphytes primarily used organic matter as substrate, although a few individuals of *C. hirta* and *A. gangetica* grew on leaf bases. Similarly as for epiphytes, the proportion of fertile accidental epiphyte individuals increased from age classes ‘y’ (6.73%) and ‘m’ (7.69%) to age class ‘o’ (16.67%). No fertile individual was found at a trunk height of 2.5 m, but 7.46% were fertile at 0 m and 14.28% at 5 m. Few fertile individuals were found in ‘mm’, but 11.11% of individuals in ‘bm’ and 14.71% of those in ‘pk’ were fertile.

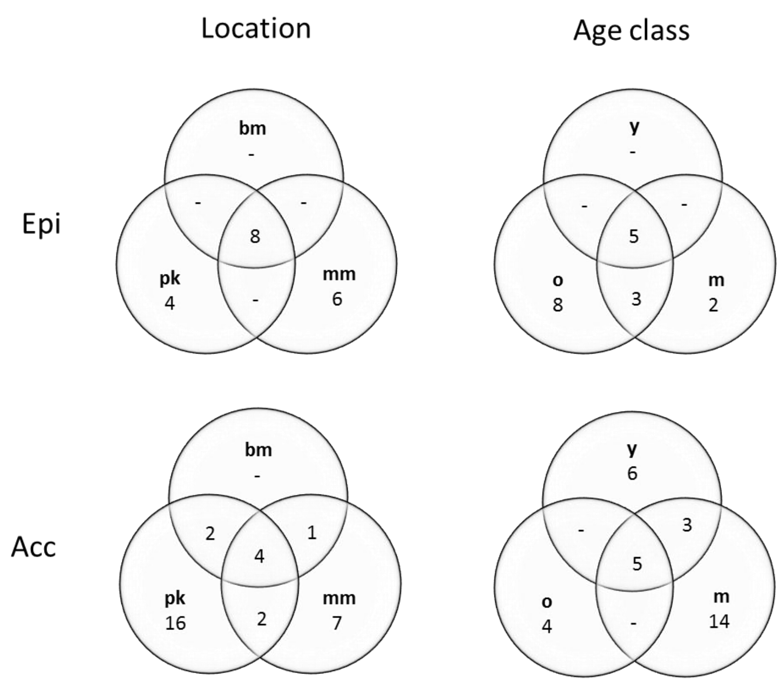

Figure 15: Distribution of plant species across locations and age classes. The circles show overlapping and non-overlapping species between locations and age classes for epiphytes (*Epi*) and accidental epiphytes (*Acc*) at the plot level. Abbreviations in ‘location’: bm = Bukit Makmur, mm = Marga Mulya, pk = Permatang Kabau; in ‘age class’: y = young, m = middle, o = old.

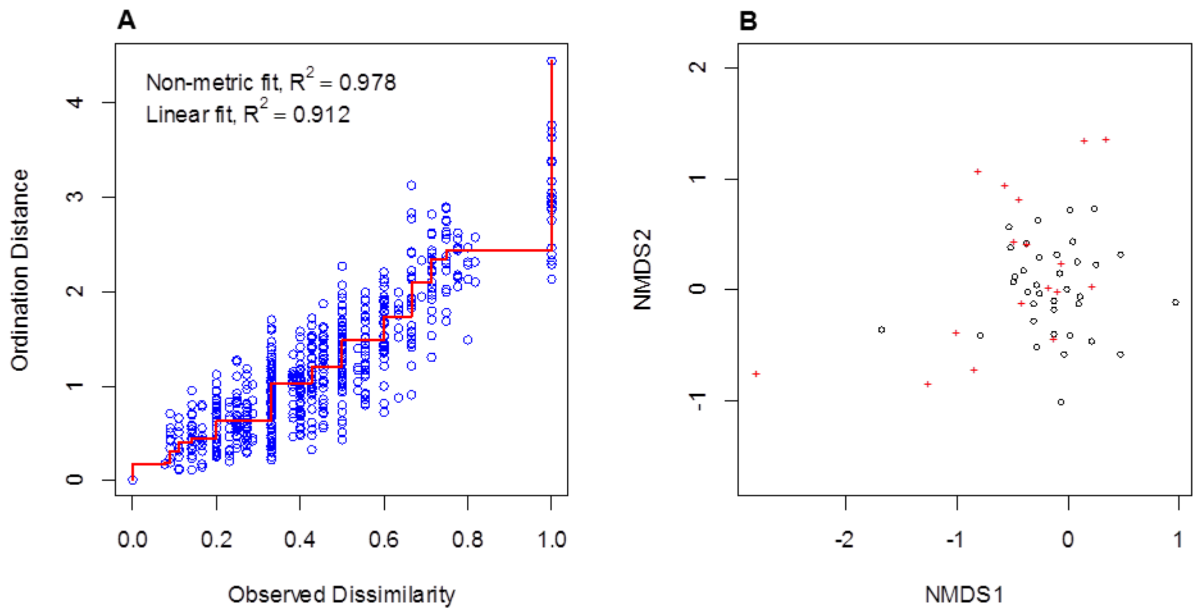

Figure 16: Non-metric multidimensional scaling (Bray-Curtis) of oil palm-based presence-absence-data for epiphytes. Each dot shows one oil palm in the distance matrix of species composition. A: Stress plot for the NMDS. B: NMDS. ᵒ = oil palms, + = epiphyte species.

Figure 17: NMDS ordination on oil palm-based presence-absence-data for epiphytes grouped in subcategories. Each dot shows one oil palm in the distance matrix of species composition. A: Locations. B: Age classes. C: Plantations.

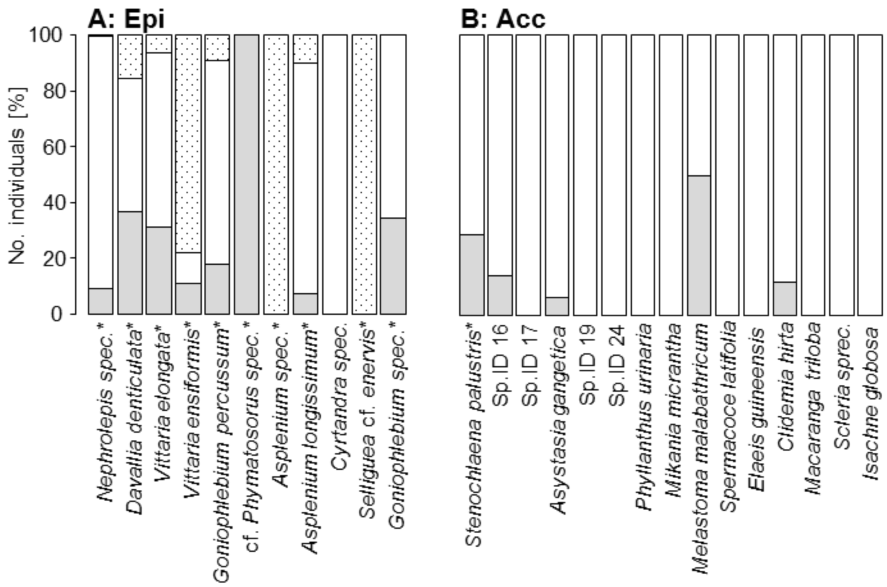

Figure 18: Substrate used by epiphytic plant species on oil palms. Grey = leaf base, white = organic matter in leaf axils, dotted = naked trunk without leaf bases. Sp.ID 16, 17, 19 and 24 refer to indet. angiosperms. * Pteridophytes. The number of individuals per species can be found Appendix 5, A-B. Note that some species were only represented by one (*Asplenium spec.*, *Cyrtandra spec.*, *Selliguea* cf. *enervis*) or two (cf. *Phymatosorus sprec.*) individuals.

Figure 19: Substrate used by epiphytic plants in comparison between age classes. Proportion of individuals in epiphytes (*Epi*, n = 659) and accidental epiphytes (*Acc*, n = 149) of all individuals observed on the substrates leaf base (grey), organic matter in leaf axils (white) and naked trunk without leaf bases (dotted) among different age classes. Three individuals (all of *Stenochlaena palustris*) in accidental epiphytes were found on the naked trunk; Abbreviations in 'age class': y = young, m = middle, o = old.

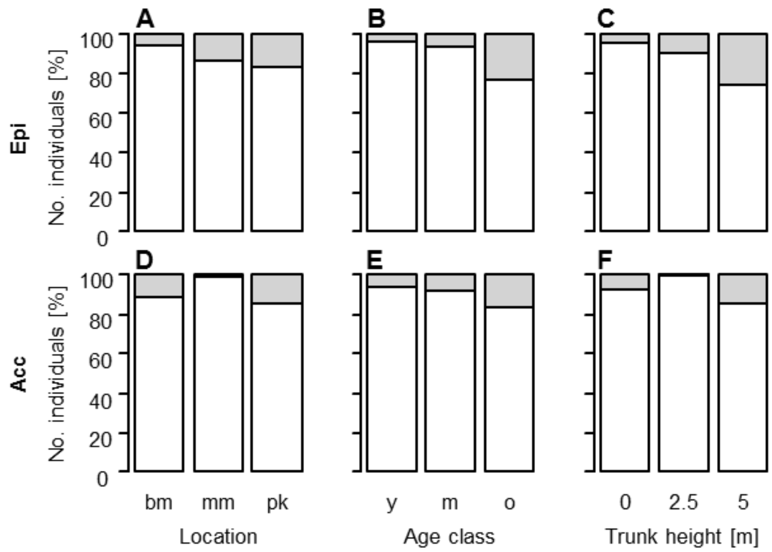

Figure 20: Proportion of sterile and fertile epiphytic individuals on oil palms. Data for epiphytes (*Epi*) and accidental epiphytes (*Acc*) at the plot level. White = sterile, grey = fertile. Sample size: n(*Epi*) = 659 (577 sterile, 82 fertile); n(*Acc*) = 149 (138 sterile, 11 fertile).

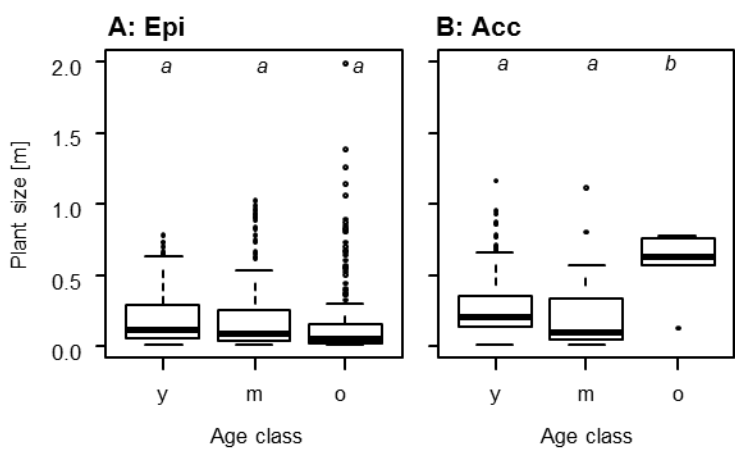

Figure 21: Size of epiphytic plants on oil palm plantations. Size of epiphyte (*Epi*, n = 659) and accidental epiphyte (*Acc*, n = 149) individuals in comparisons between age class. Letters in *italics* indicate group differences based on max-t-test at p<0.05. Abbreviations in age class: y = young, m = middle, o = old.

Oil palm dwelling arthropods

The two microhabitats of the oil palm trunk sampled for arthropods shared eleven common taxa (Figure 22). Two further arthropod taxa were found on epiphytes (*Art.E*), namely Mantodea and Thysanoptera. In organic matter, six additional taxa were found (*Art.O*): Collembola, Dermaptera, Diplopoda, Isopoda, Isoptera and Symphyla. Formicidae were the most abundant taxon in both microhabitats (Figure 25, A-B).

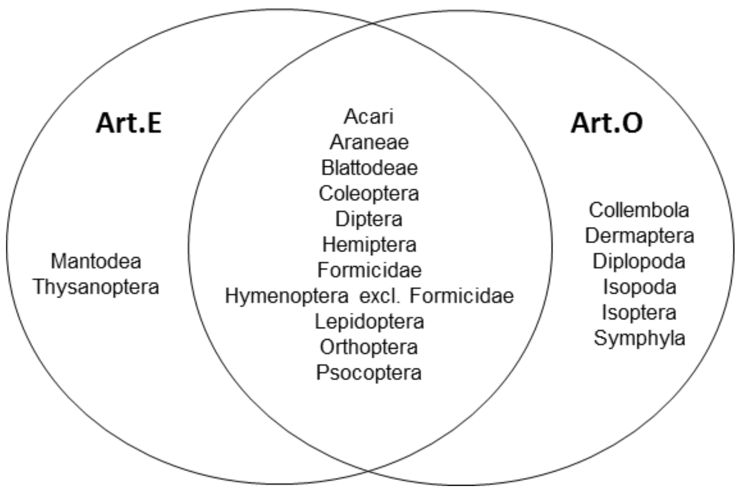

Figure 22: Overlapping and non-overlapping taxa of arthropods collected in two microhabitats. The circles summarize all taxa found using two different sampling methods. Arthropods were collected on epiphytes (*Art.E*) and in organic matter (*Art.O*) which had accumulated in leaf axils along oil pam trunks.

Arthropods on epiphytes Formicidae made up 53% of the *Art.E* individuals. Another 31.5% were Araneae, followed by Hemiptera (5.12%) and Lepidoptera (4.13%). Juvenile individuals were found for Coleoptera, Diplopoda, Hemiptera and Lepidoptera (Figure 23). Lepidoptera is the only taxon that was represented by more juvenile individuals than adults. In all age classes and all locations except 'mm', the community of *Art.E* was dominated by Formicidae, followed by Araneae and – after a gap – Hemiptera and Lepidoptera (Table 7; Figure 26, G-H). In 'mm', there were the abundance of Araneae (61.4%) was almost three times higher than the abundance of Formicidae (22.81%). Along a gradient in trunk height from 0 m to 5 m, the proportion of Formicidae within the community decreased by more than thirty percent, but that of Araneae increased by more than ten percent (Table 7).

Arthropods in organic matter After Formicidae, which accounted for 82.36% of individuals, the most abundant taxa in the *Art.O* community were Acari, Coleoptera, Isoptera, Araneae and Diptera (Figure 24). In Coleoptera and Dermaptera, more than half of all individuals were juveniles or nymphs, respectively. Adults made up the majority of individuals in the other taxa. Formicidae dominated *Art.O* communities in all locations and age classes (see Table 7; Figure 26, G-I). Isopoda were ranked in the top four taxa in abundance of individuals at all locations. The proportion of Formicidae was lowest in the community at ‘mm’ (52.67%), where Coleoptera (11.63%) and Araneae (8.03%) were also abundant. Formicidae also dominated communities in all age classes, in particular age class ‘m’ (89.88%). The rest of the community varies widely between age classes (see Table 7).

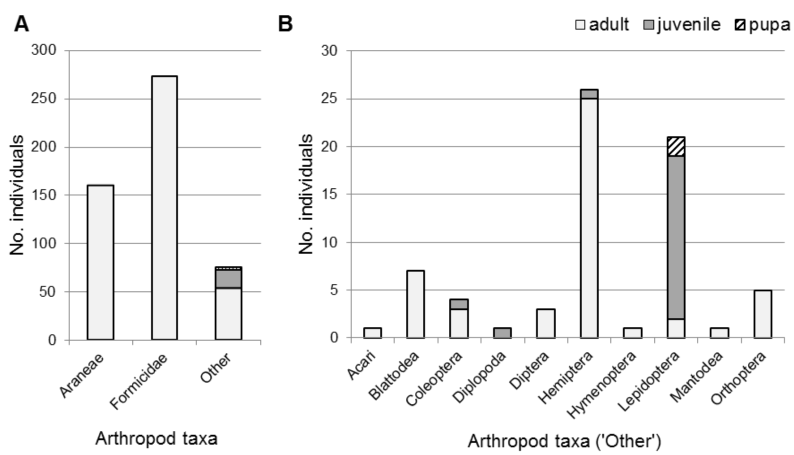

Figure 23: Life stages in arthropods collected on epiphytes on oil palm trunks. Total number of collected individuals was n = 508. A: Araneae and Formicidae in comparison to all other taxa together. B: All taxa except Araneae and Formicidae. Hymenoptera excludes Formicidae.

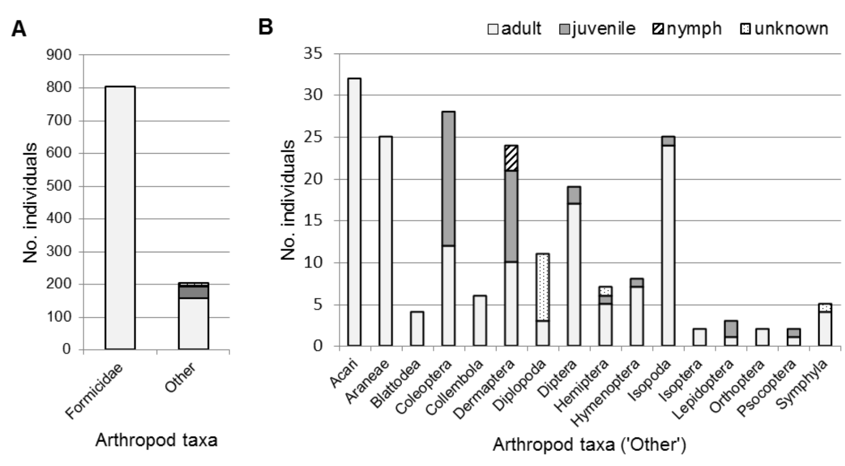

Figure 24: Life stages of arthropods extracted from organic matter in oil palm leaf axils. Total number of extracted individuals was n = 1004. (A) Formicidae in comparison to all other taxa together. (B) All taxa except Formicidae. Hymenoptera excludes Formicidae.

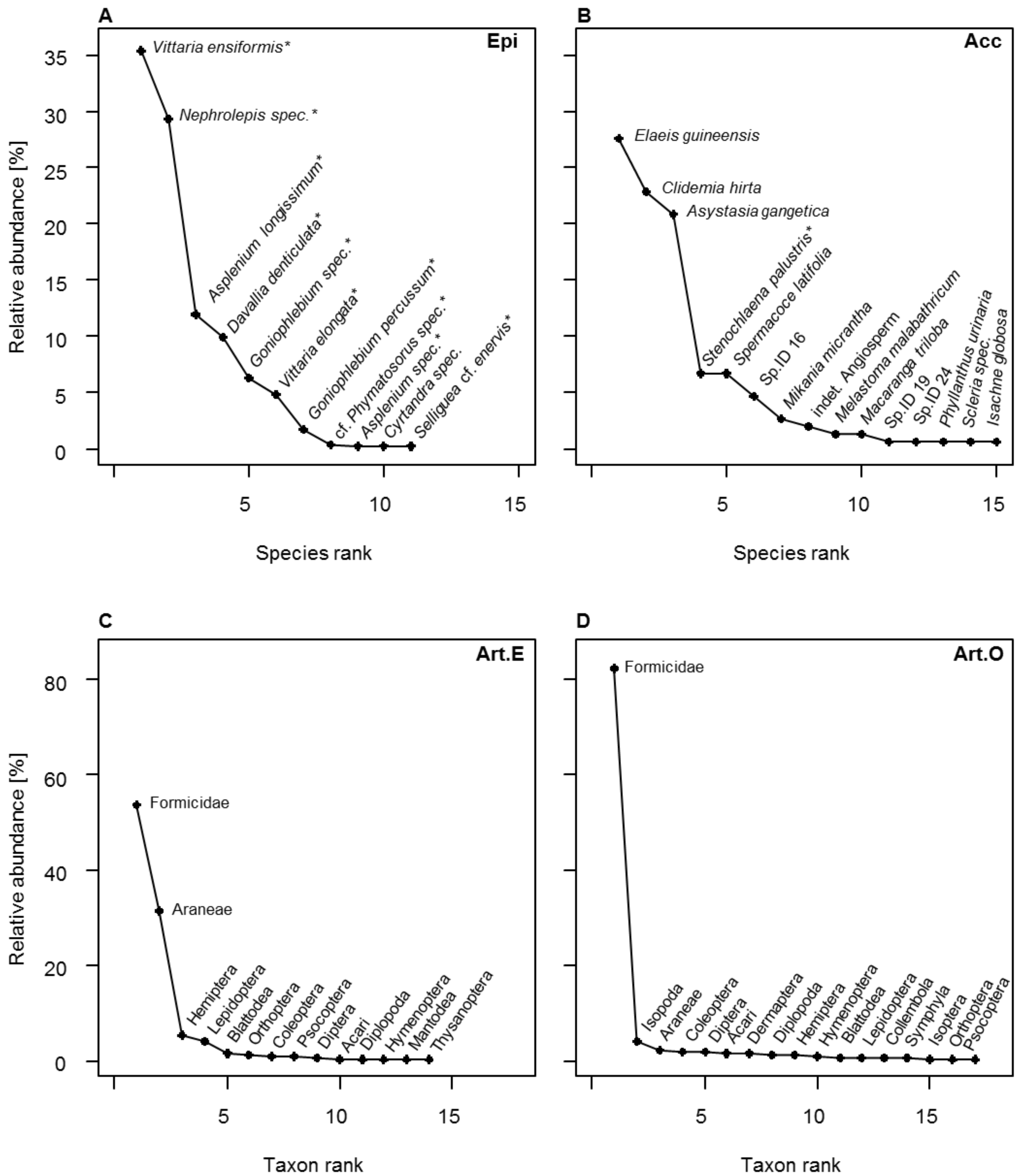

Figure 25: Overall rang abundance curves. Species and taxa are arranged in descending order according to relative abundance. Rank abundance curves are shown for epiphytes (A, *Epi*), accidental epiphytes (B, *Acc*), arthropods on epiphytes (C, *Art.E*) and arthropods in organic matter (*Art.O*), all collected on oil palm trunks. Sp.ID 16, 19 and 24 are indet. angiosperms. * Pteridophytes.

Table 7: Rank abundance table. Relative abundances for species and higher-ranked taxa which were collected on oil palm trunks. The four top-ranked species or taxa are arranged in descending order within each subcategory of the variables location, age class and trunk height. Lower ranks are not listed. The relative abundance [%] in the respective category is written in brackets beside each species or taxon. Epiphytes (*Epi*), accidental epiphytes (*Acc*) and arthropods on epiphytes (*Art.E*) were collected at the plot level. Arthropods in organic matter (*Art.O*) were collected at the oil palm level. Numbers of individuals in *Art.O* were standardized to number of individuals per 50 g organic matter (dry weight) per oil palm. Abbreviations in 'location': bm = Bukit Makmur, mm = Marga Mulya, pk = Permatang Kabau; in 'age class': y = young, m = middle, o = old.

	Epi	***Acc***	***Art.E***	***Art.O***
Location				
bm	1. *Nephrolepis spec.* (37.42) 2. *Vittaria ensiformis* (25.77) 3. *Goniophlebium spec.* (13.5) 4. *Asplenium longissimum* (11.04)	1. *Asystasia gangetica* (53.55) 2. *Clidemia hirta* (28.89) 3. *Elaeis guineensis* (11.12) 4. *Stenochlaena palustris* (6.67)	1. Araneae (45.63) 2. Formicidae (30.1) 3. Hemiptera (12.62) 4. Lepidoptera (7.77)	1. Formicidae (73.49) 2. Araneae (4.71) 3. Isopoda (4.63) 4. Diptera (3.1)
mm	1. *Vittaria elongata* (47.53) 2. *Nephrolepis spec.* (24.42) 3. *Asplenium longissimum* (11.95) 4. *Davallia denticulata* (7.01)	1. *Elaeis guineensis* (47.14) 2. *Clidemia hirta* (20) 3. *Spermacoce latifolia* (14.29) 4. *Asystasia gangetica* (10)	1. Araneae (61.4) 2. Formicidae (22.81) 3. Hemiptera (5.26) 4. Coleoptera (3.5) Lepidoptera (3.5) Psocoptera (3.5)	1. Formicidae (52.67) 2. Coleoptera (11.63) 3. Araneae (8.03) 4. Isopoda (6.23)
pk	1. *Nephrolepis spec.* (34.23) 2. *Davallia denticulata* (27.03) 3. *Asplenium longissimum* (13.51) 4. *Goniophlebium spec.* (9.01)	1. Sp.ID 18 (20.59) *Clidemia hirta* (20.59) 2. *Stenochlaena palustris* (17.65) 3. Sp.ID 17 (8.82) *Elaeis guineensis* (8.82) 4. *Macaranga triloba* (5.88)	1. Formicidae (65.8) 2. Araneae (22.4) 3. Lepidoptera (3.16) 4. Hemiptera (2.87)	1. Formicidae (90) 2. Isopoda (3.35) 3. Acari (1.08) 4. Hemiptera (0.99)
Age class				
y	1. *Nephrolepis spec.* (65) 2. *Davallia denticulata* (20) 3. *Goniophlebium* spec. (8.13) 4. *Asplenium longissimum* (6.88)	1. *Elaeis guineensis* (35.58) 2. *Asystasia gangetica* (26.92) 3. *Clidemia hirta* (14.42) 4. *Spermacoce latifolia* (9.62)	1. Formicidae (64.14) 2. Araneae (26.26) 3. Hemiptera (4.55) 4. Lepidoptera (3.03)	1. Formicidae (72.45) 2. Isopoda (7.42) 3. Coleoptera (4.24) 4. Araneae (3.8)
m	1. Nephrolepis spec. (30.2) 2. *Asplenium longissimum* (23.27) 3. *Vittaria ensiformis* (17.96) 4. *Vittaria elongata* (9.76)	1. *Clidemia hirta* (45.15) 2. Sp.ID 16 (17.95) 3. *Elaeis guineensis* (10.26) 4. *Stenochlaena palustris* (7.68) *Asystasia gangetica* (7.68)	1. Formicidae (46.84) 2. Araneae (38.95) 3. Hemiptera (3.68) 4. Lepidoptera (3.16)	1. Formicidae (89.88) 2. Diptera (1.84) 3. Acari (1.15) 4. Araneae (1.09)
o	1. *Vittaria ensiformis* (74.4) 2. *Nephrolepis spec.* (5.9) *Davallia denticulata* (5.9) 3. *Asplenium longissimum* (4.33) 4. *Vittaria elongata* (3.15)	1. *Stenochlaena palustris* (66.67) 2. *Clidemia hirta* (16.67) 3. *Isachne globosa* (16.67) 4. -	1. Formicidae (47.5) 2. Araneae (28.33) 3. Hemiptera (8.33) 4. Lepidoptera (7.5)	1. Formicidae (77.19) 2. Isopoda (8.1) 3. Hymenoptera (5.42) 4. Acari (4.24)
Trunk height				
0 m	1. *Nephrolepis spec.* (39.02) 2. *Davallia denticulata* (19.16) 3. *Asplenium longissimum* (12.89) 4. *Vittaria ensiformis* (12.2)	1. *Elaeis guineensis* (54.61) 2. *Asystasia gangetica* (23.13) 3. *Clidemia hirta* (20.9) 4. *Spermacoce latifolia* (7.46)	1. Formicidae (61.09) 2. Araneae (27.65) 3. Hemiptera (5.46) 4. Lepidoptera (2.57)	NA
2.5 m	1. *Vittaria ensiformis* (44.57) 2. *Nephrolepis spec.* (21.08) 3. *Asplenium longissimum* (16.27) 4. *Goniophlebium spec.* (8.43)	1. *Clidemia hirta* (62.5) 2. *Stenochlaena palustris* (12.5) 3. Sp.ID 24 (12.5) 4. *Elaeis guineensis* (12.5)	1. Formicidae (45.83) 2. Araneae (36.67) 3. Lepidoptera (5.83) 4. Hemiptera (3.3)	NA
5 m	1. *Vittaria ensiformis* (60.19) 2. *Nephrolepis spec.* (22.33) 3. *Asplenium longissimum* (7.28) 4. *Goniophlebium spec.* (2.91)	1. *Stenochlaena palustris* (42.86) 2. *Elaeis guineensis* (42.86) 3. *Clidemia hirta* (14.82) 4. -	1. Araneae (38.96) 2. Formicidae (36.36) 3. Lepidoptera (7.79) 4. Hemiptera (6.5)	NA

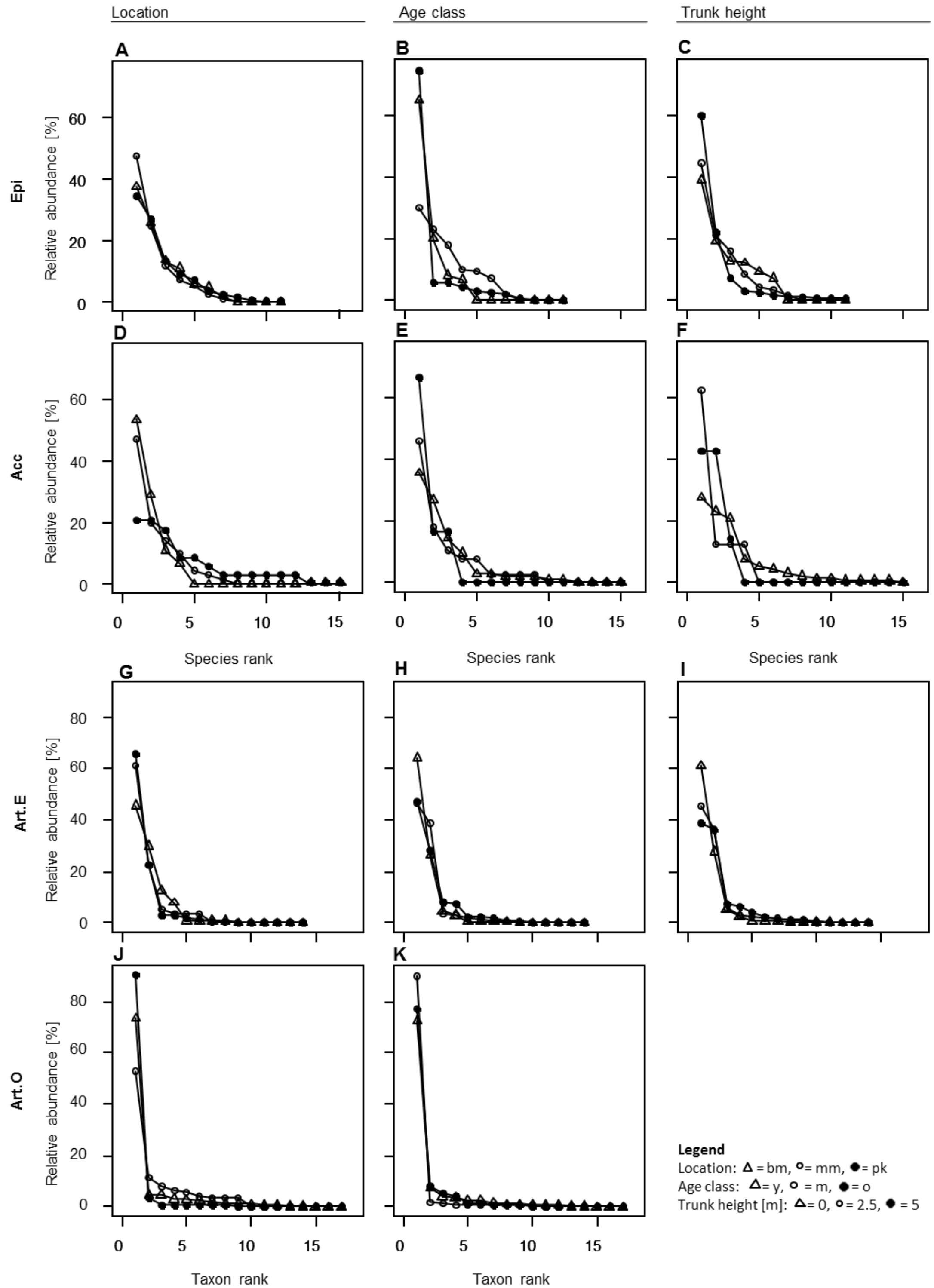

Figure 26: Rank abundance curves that differentiate between different subcategories of location, age class, and trunk height, for epiphytes and arthropods on oil palms. Species or higher-ranked taxa are arranged in descending order within each subcategory of the variables location, age class and trunk height. Epiphytes (*Epi*), accidental epiphytes (*Acc*) and arthropods on epiphytes (*Art.E*) were collected at the plot level. Arthropods in organic matter (*Art.O*) in leaf axils along oil palm trunks were collected at the oil palm level. Numbers of individuals in *Art.O* were standardized to number of individuals per 50 g organic matter (dry weight) per oil palm.

3.4 Determinants of abundance and diversity

Two types of multiple regression analyses – linear models (LMs) and linear mixed-effect models (LMEs) – were performed to identify determinants of abundance and richness of species and higher-order taxa on oil palm trunks. The best fitting LME for every response variable is shown in Table 8. Lower AIC values were always obtained, when the response variable was log-transformed (natural logarithm). Over all tested models, 'age class' was a better predictor than 'main age' or 'trunk height to meristem'. Table 9 shows the results from LMs that directly refer to the hypotheses. The direction or relationship between the explanatory variable and the predictor(s) in the models can be looked up in Table 8 and Table 9. All other LM results are shown in Appendix 7.

Epiphytic plants on oil palms

Using AIC for model selection, 'age class' was the best predictor for $\log_e$ epiphyte species richness at the oil palm level (LME). At the plot level, $\log_e$ epiphyte species richness was best explained by its $\log_e$ number of individuals (LME). In LMs 'age class' explained ~50% of the variation in the number of epiphyte species at the oil palm level. However, 'age class' was a weak predictor for both abundance and richness of epiphytes at the plot level (LM; R^2 in Table 8). The $\log_e$ number of epiphyte individuals at the plot level was best explained by 'plant cover' (LME). Trunk height had no significant effect on abundance and richness of epiphytes (LM).

The $\log_e$ species richness of accidental epiphytes at the oil palm level was best explained by 'leaf base cover' (LME). At the plot level, the $\log_e$ number of accidental epiphyte species was best explained by the number of individuals (LME). The $\log_e$ number of accidental epiphyte individuals was explained best by 'age class' (LME). In LMs, 'age class' even a stronger predictor for the abundance and species richness of accidental epiphytes at the plot level than at the oil palm level (actual values for R^2 in Table 8). Trunk height explained almost one fifth of variation in species abundance and richness (both log-transformed) of accidental epiphytes.

As a side analysis, the influence of trunk surface to the species richness per oil palm was tested (Figure 27) Trunk surface had a strong positive effect on epiphyte species richness per oil palm. In contrast, species richness of accidental epiphytes per oil palm showed a weak negative correlation with trunk surface.

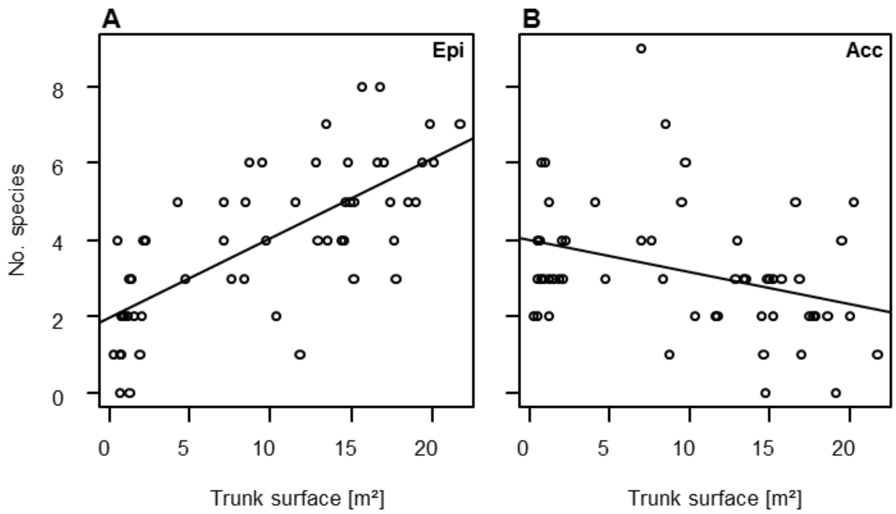

Figure 27: Species richness per oil palm in relation to trunk surface. A: Epiphytes (*Epi*), y = 0.21 x + 1.97, R^2 = 0.51 ***. B: Accidental epiphytes (*Acc*), y = -0.08 x + 3.99, R^2 = 0.12 *.

Oil palm dwelling arthropods

The $\log_e$ taxon richness of arthropods on epiphytes (*Art.E*, sampled at the plot level) was best explained by 'location' (LME). A combination of the variables 'location' and 'age class' predicted the $\log_e$ number of individuals of arthropods on epiphytes best (LME). In LMs, plant cover explained less than 10% of $\log_e$ number of individuals (R^2 = 0.07) and $\log_e$ number of taxa (R^2 = 0.09) of arthropods on epiphytes.

Similar to epiphytic plants, the $\log_e$ number of *Art.O* taxa per oil palm was best predicted by $\log_e$ number of individuals (LME). The variation in the number of individuals could not be explained by any of the explanatory variables studies. 'Age class' – tested to answer H2 – was a good predictor for $\log_e$ taxon richness of *Art.O* (R^2 = 0.32, LM).

Table 8: Results from Linear Models (LMs) that directly refer to the hypotheses. Response variables are the abundance and species or taxon richness of epiphytes (*Epi*), accidental epiphytes (*Acc*), arthropods on epiphytes (*Art.E*) and arthropods in organic matter in leaf axils (*Art.O*) on oil palm trunks. *Art.O* richness and abundance were standardized to number of individuals per 50 g organic matter (dry weight) per oil palm. If data were log-transformed, the natural logarithm was used. Significance codes: $p <$ 0.001 (high significance ***) < 0.01 (significance **) < 0.05 (low significance *) > 0.05 (not significant, n. s.). The symbols in the last column show the direction of relationship between each response variable and predictor.

Hypothesis	Level	Organism group	Response variable	Predictor	R^2	p	Direction
H2	oil palm	*Epi*	no. species	age class	0.50	***	Γ
H2	oil palm	*Epi*	log (no. species+1)	age class	0.48	***	Γ
H2	plot	*Epi*	no. species	age class	0.07	*	∩
H2	plot	*Epi*	log (no. species+1)	age class	0.09	**	˥
H2	plot	*Epi*	no. individuals	age class	0.03	n. s.	
H2	plot	*Epi*	log (no. individuals+1)	age class	0.08	**	∩
H2	oil palm	*Acc*	no. species	age class	0.32	***	∩
H2	oil palm	*Acc*	log (no. species+1)	age class	0.37	***	˥
H2	plot	*Acc*	no. species	age class	0.58	***	↘
H2	plot	*Acc*	log (no. species+1)	age class	0.57	***	↘
H2	plot	*Acc*	no. individuals	age class	0.56	***	↘
H2	plot	*Acc*	log (no. individuals+1)	age class	0.61	***	↘
H3	plot	*Art.E*	no. taxa	plant cover	0.09	**	↗
H3	plot	*Art.E*	log (no. taxa + 1)	plant cover	0.09	**	↗
H3	plot	*Art.E*	no. individuals	plant cover	0.01	n. s.	
H3	plot	*Art.E*	log (no. individuals + 1)	plant cover	0.07	**	↗
H4	oil palm	*Art.O*	no. taxa	age class	0.14	*	L
H4	oil palm	*Art.O*	log (no. taxa + 1)	age class	0.32	***	↘
H4	oil palm	*Art.O*	no. individuals	age class	0.03	n. s.	
H4	oil palm	*Art.O*	log (no. individuals + 1)	age class	0.14	*	↘
H5	plot	*Epi*	no. species	trunk height	0.00	n. s.	
H5	plot	*Epi*	log (no. species+1)	trunk height	0.00	n. s.	
H5	plot	*Epi*	no. individuals	trunk height	0.00	n. s.	
H5	plot	*Epi*	log (no. individuals+1)	trunk height	0.00	n. s.	
H5	plot	*Acc*	no. species	trunk height	0.17	***	↘
H5	plot	*Acc*	log (no. species+1)	trunk height	0.19	***	↘
H5	plot	*Acc*	no. individuals	trunk height	0.15	***	↘
H5	plot	*Acc*	$\log_e$ (no. individuals+1)	trunk height	0.20	***	↘

Table 9: Best linear mixed-effect models (LMEs) for richness and abundance of species and higher-ranked taxa. Best LMEs predicting abundance and richness of epiphytes (*Epi*), accidental epiphytes (*Acc*), arthropods on epiphytes (*Art.E*) and arthropods in organic matter in leaf axils (*Art.O*) on oil palm trunks. *Art.O* richness and abundance were standardized to number of individuals or taxa per 50 g organic matter (dry weight) per oil palm. Log-transformation by using natural logarithm. Random effects at the oil palm level: 1 | Location / Plantation.ID / Oilpalm.ID; random effects at the plot level: 1 | Location / Plantation.ID / Oilpalm.ID / Plot.ID. Significance codes: p < 0.001 (high significance ***) < 0.01 (significance **) < 0.05 (low significance *) > 0.05 (not significant, n. s.). The symbols in the last column show the direction of relationship between each response variable and fixed effect(s). The results of null models for each response variable are summarized in Appendix 8.

Organism group	Level	Response variable	Fixed effect(s)	p-value	Direction
Epi	oil palm	log (no. species + 1)	age class	***	Γ
Epi	plot	log (no. species + 1)	$\log_e$ (no. individuals (*Epi*) + 1)	***	↗
Epi	plot	log (no. individuals + 1)	plant cover	***	↗
Acc	oil palm	log (no. species + 1)	leaf base cover	***	↗
Acc	plot	log (no. species + 1)	no. individuals (*Acc*)	***	↗
Acc	plot	log (no. individuals + 1)	age class	***	L
Art.E	plot	log (no. taxa + 1)	location	*	NA
Art.E	plot	log (no. individuals)	location + age class	**	NA
Art.O	oil palm	log (no. taxa + 1)	$\log_e$ (no. individuals (*Art.O*) + 1)	***	↗
Art.O	oil palm	log (no. individuals + 1)	age class	n. s.	

4 Discussion

4.1 Biodiversity in oil palm plantations and its determinants

Epiphytes

Epiphytes were abundant on oil palms, but the diversity of epiphytes was very low. Only eighteen species were recorded in total and species accumulation curves indicated that most of the species growing on oil palm trunks were found. However, a higher diversity was found compared to the study of Altenhövel (2013), who recorded 11 epiphyte species in oil palm plantations in the same region (Jambi Province). This bias can be explained by the fact, that sampling of oil palm-dwelling epiphytes in the study of Altenhövel (2013) was restricted to approximately ten years old plantations, but the present study included a wide range of different old plantations. The present study implies that some species only occur in a certain age class of plantations. The wider the range in plantation age, the more species are expected to find. In the Bukit Duabelas lowland rainforest, Jambi Province, 48 epiphyte species were recorded (Altenhövel 2013; Böhnert 2013). An overall estimate for epiphyte species richness in the lowlands of Sumatra is not available. However, epiphyte species richness in the Bukit Duabelas rainforest seems to be low in a pantropical context: In an Amazonian lowland rainforest in Ecuador, 313 epiphyte species were recorded (Kreft, Köster & Küper 2004). In another study, 77 epiphyte species were observed in lowland rainforests in Ecuador (Haro-Carrión *et al.* 2009). Hence, the species richness of epiphytes in the oil palm plantations studied is extremely low compared to tropical rainforests both in the study area and in a global context.

Eleven out of eighteen epiphyte species were already covered by surveys within the plots, which covered a trunk surface of only 30 m². This implies a high density of epiphyte species on a small scale but also a low density of epiphyte species at higher spatial levels, such as plantation. An enormous density of epiphyte species on a small scale was observed in a Ecuadorian mountain forest, where the very 109 epiphyte species were found at a branch surface of only 20 m² (Nieder *et al.* 2001).

The epiphyte community was mainly formed by six pteridophyte species. Three of these species, *Davallia denticulata,* V*ittaria elongata* and *Goniophlebium percussum* are commonly found in disturbed habitats such as secondary forests and oil palm plantations (Wee 2005). *G. percussum* is also found on old trees in the lowland and mountains. *Vittaria ensiformis* is a common epiphyte of lowland trees. *Asplenium longissimum* is known as ground fern (but not in this study) and as epiphyte on old oil palms. Tropical species in the genus *Nephrolepis* (*N. acutifolia*, *N. biserrata*) are typically found in open places in the lowlands (Wee 2005).Hence, no forest-specialized species occurred in oil palm plantations. The result that pteridophytes are the dominant epiphytes on oil palms matches with findings of previous studies in Malaysia (Luskin & Potts 2011; Nadarajah & Nawawi 1993). Böhnert (2013) found that pteridophytes also dominated the epiphyte community in rubber plantations in Jambi Province, Sumatra. This is not surprising, as pteridophytes are a dominant taxon within epiphytes (Zotz 2013).

The highest variance in epiphyte species richness was observed at the oil palm level. The small area of 0.5 x 0.5 m² plots is not adequate for comparing species richness between different sites. At the plot level, age class had a small impact on epiphyte abundance and diversity (LMs). Species richness per plot could not be satisfactory explained: the more individuals, the more species were recorded. At the oil palm level, age class was the best predictor for epiphyte species richness in linear mixed-effect models. Species richness increased from young to middle aged oil palms and then stabilized to old oil palms. Oil palms showed a similarity of species composition (presence-absence) in a distance matrix. This result expands the finding of Altenhövel (2013), that oil palms of a similar age (approximately ten years old) show only little variation in their epiphyte species composition (Appendix 9). However, dominant species of the community within the plots changed between middle aged and old oil palms, indicating a succession. This is likely caused by the change of the substrates provided by oil palm trunks (discussed in detail in Chapter 4.2).

The higher epiphyte abundance per plot in Marga Mulya compared to the other locations is likely a result of the plantation management; Marga Mulya was the only location, where epiphytes were not removed from the trunks. In contrast to rainforests, epiphytes did not show a vertical distribution in oil palm plantations. That can be explained by the absence of vertical ecological gradients in microclimate and branche diameters in oil palm plantations, which causes vertical distribution patterns of holo-epiphytes in rainforests (Nieder *et al.* 2001).

Although most epiphytes are orchids globally (Zotz 2013), no orchid was found. Same was also noticed in the other studies that surveyed the epiphyte community in oil palm plantations (Altenhövel 2013; Danielsen *et al.* 2009; Nadarajah & Nawawi 1993). Johansson (1974) observed one single epiphytic orchid, *Habenaria procera*, on an oil palm in Liberia. In contrast, Altenhövel (2013) and Böhnert (2013) recorded seventeen epiphytic orchid species in a rainforest (Bukit Duabelas) closed to

Permatang Kabau. Orchids are also rarely found or even absent in rubber plantations (Böhnert 2013; Hietz 2005) in the lowlands of Sumatra. Possibly, the lack of orchids in oil palm plantations is partly related to the dependence of many orchids on other species; orchids with a highly specific pollination system of sexual deception (Phillips *et al.* 2011) would probably be faced by the absence of a pollinator in oil palm plantations and could not reproduce. However, this is certainly one out of many factors for explaining the lack of orchids in oil palm plantations. It was mentioned that the absence of orchids is not explainable by morphological characteristics of the oil palm, but that orchid seeds might have germination difficulties on this phorophyte (Johansson 1974).

Accidental epiphytes

In total, twice as many species were found in accidental epiphytes than in epiphytes. In contrast, species richness per oil palm and per plot was smaller in accidental epiphytes than in epiphytes. Individuals of *Elaeis guineensis* itself, *Clidemia hirta* and *Asystasia gangetica* dominated the community of accidental epiphytes. *C. hirta* and *A. gangetica* are common invasive species in the tropics (DeWalt et al. 2004; Meyer & Lavergne 2004). The composition of less abundant accidental epiphytes species was highly related to the terrestrial vegetation (pers. obs., unpublished data), which was likely influenced by the plantation management (presence of an irrigation system, time of the last application of herbicides) and by seed inflow from the surrounding area. Thus, the more plantations were surveyed, the more accidental epiphyte species were found. Species accumulation curves indicated that even more accidental epiphyte species will be found at a higher sampling effort. Local differences in the ground vegetation (pers. obs., unpublished data) explain why the total species richness and the rate of new species records were much higher in accidental epiphytes than in epiphytes.

The highest abundance of accidental epiphytes in plots next to the ground compared to higher plots can be explained by a direct spill-over of terrestrial species on the oil palm trunk. The decrease of abundance and diversity of accidental epiphytes along an age gradient is explained by a decrease of leaf base cover. The patterns indicate that accidental epiphytes strongly depend on the availability of organic matter (in leaf axils) as a substrate.

Age class was a stronger predictor of the abundance and richness of accidental epiphytes at the plot level, than at the oil palm level. At the plot level, abundance and richness decreased. In contrast, there was no significant difference in species richness between young and middle aged oil palms (however, species richness decreased from middle aged to old oil palms). This is likely explained by a species-area relationship (Arrhenius 1921): all plots had an area of 0.5 x 0.5 m^2, but the total trunk surface of middle aged oil palms was much larger than that of young oil palms.

The results do not support the finding of Luskin & Potts (2011) that Poaceae are more abundant in old plantations than in younger ones, while leafy and climbing epiphytes do not show a difference.

Arthropods on epiphytes

A wide range of oil palm-dwelling arthropod taxa was found, dominated by Formicidae and Araneae. Compared to the rest of taxa, Hemiptera and Lepidoptera were also abundant.

Previous studies on epiphyte-dwelling arthropod taxa in oil palm plantations were only conducted with respect to *Asplenium nidus* (Fayle et al. 2010; Turner & Foster 2009; Fayle et al. 2005). The arthropod community in the interior of this litter-basket fern in rainforests is similar to that in litter (Ellwood, Jones & Foster 2002). In contrast, the epiphyte-dwelling arthropods in the present study were clearly composed by typically herbivore and predator taxa (see below). That points out, that it is necessary to survey not only the bird's nest fern when investigating epiphyte-dwelling arthropods in oil palm plantations, as performed in this study.

Location was the best predictor for taxon richness and – together with age class – for abundance of epiphyte-dwelling arthropods. Abundance and taxon richness were highest in Permatang Kabau. Likely, this is favored by the Bukit Duabelas Rainforest and shrubberies in proximity to the oil palm plantations. According to the source-sink concept (Dias, 1996), there may be a spillover of forest species with a wide ecological tolerance to oil palm plantations. Shrubberies within the agricultural landscape might act as step stones. This result supports the finding of previous studies from Malaysia, that recorded an increased species richness of butterflies and birds in oil palm plantations with increasing proximity to a forest or the presence of a forest patch within a plantation or the surrounding area (Lucey & Hill 2012; Koh 2008).

Arthropods in organic matter

In all probability most taxa in the study area were covered by the sampling effort. Formicidae were the single dominant taxon in organic matter in oil palm leaf axils. This was expected, because are one of the most dominant taxon in the tropics (Hölldobler & Wilson 1990). Ant colonies in some leaf axils caused enormous numbers of individuals in some samples (pers. obs.).

The number of taxa per oil palm (always standardized) decreased with age class, a strong predictor for taxon richness in linear models. However, taxon richness was best explained by the number of individuals per oil palm (always standardized). Paradoxically, no significant differences in the number of individuals per oil palm were observed between different age classes. Also, the best model – having age class as a predictor – did not explain the number or individuals. Hence, the dynamics of arthropod diversity along the age gradient cannot be satisfactory explained with the collected data. Possibly, moisture, grade of decomposition and nutrient content of the organic matter in oil palm leaf axils would have been more telling variables. It could also be possible, that the absolute dominance of Formicidae overshadows trends in the other taxa.

Hypotheses

Accidental epiphytes were frequently recorded and therefore (H1) can be confirmed. The results also strongly support (H2), as age class of the plantation was a strong determinant of the abundance and diversity of epiphytes and accidental epiphytes. Furthermore, the community composition changed along the age gradient. Although age class strongly influences the community composition of accidental epiphytes, local characteristics of the plantations have even a stronger effect. (H3) received support from the results, but the overall variance in abundance and richness of arthropod taxa explained by plant cover was pretty low (< 10%). Diversity patterns of arthropods in organic matter in leaf axils changed with oil palm age, but ‘age class’ was a weak predictor and abundance did not differ significantly between age classes. Therefore, hypothesis (H4) can be confirmed in the term, that arthropod diversity decreased with age. The results do not confirm the second part of (H4), that arthropod abundance in organic matter changes. Probably, variables which directly refer to microhabitat qualities might be more predictive for diversity patterns in that arthropod community. The abundance and diversity of epiphytes did not differ between plots at different trunk heights. In contrast, abundance and species richness of accidental epiphytes strongly decreased with tunk height.

Hence, the results support (H5) in part. Forest-specialized species were not recorded. Hence, (H6) can be confirmed.

Limitations of the study

The space-for-time substitution method – used for investigating diversity patterns along an age gradient – is limited by a high probability of differing detailed histories among the different plantations (Facelli & Pickett 1990). The diversity of epiphytes and arthropods might be influenced by the plantation management, e.g. the application of herbicides and pesticides or the manual removal of epiphytes. Further, one should note that the range of ages within one age class differed. That might especially play a role in old plantations, as the proportion of the trunk which already lost its leaf bases differed between old plantations. Patterns in diversity of epiphytic plants would probably become even clearer, if all old oil palms would already have lost almost all leaf bases.

The sampling effort depended on the height of the oil palms and therefore differed between the categories in location, age class and trunk height. This could lead to biased species numbers according to species-area relationships (Arrhenius 1921). However, species and taxa accumulation curves indicated that almost all epiphyte species and arthropod taxa were found. Only in accidental epiphytes, a higher sampling effort would probably have resulted in higher species richness, particularly in plots at 0 m and in young plantation. Thus, a higher sampling effort would enhance the patterns found for accidental epiphytes but not change the overall trends. Also note replication in oil palms and plots between the variables location, age class and trunk height.

Some individuals of epiphyte-dwelling arthropods might have escaped before the net was pulled over the epiphytes. In particular, the abundance of winged and fast moving taxa such as Diptera, Lepidoptera or Orthoptera might be underestimated. Further it was observed, that some ants moved through the stitches, but anyway, ants were the most abundant taxon.

There are studies that doubt the Winkler extraction method as an adequate method for quantitative ecological analyses of ground-dwelling arthropods (Sabu & Shiju 2010; Krell et al. 2005). They argue that this method is suitable for the extraction of Formicidae, Coleoptera and Araneae, but underestimates the abundance of other arthropod taxa. However, the high abundance of ants is not only an artefact of the Winkler’s extraction method, because these social insects generally form large colonies and are a dominant taxon in tropical environments (Hölldobler & Wilson 1990).

Annual variation in the abundance of different taxa (Schowalter & Ganio 1999) could not be taken into account. High abundances in Formicidae and Araneae do not necessarily come along with a high diversity. For example, a study in Malaysia showed that and species richness dramatic declines from forests to oil palm plantations(Fayle *et al.* 2010). Profound statements about the habitat quality of oil palms for arthropods require closer identifications to the family, genus or species level.

4.2 Oil palms as a habitat for epiphytes and arthropods

It is clear that oil palms provide a poor-quality habitat for epiphytes, as only few epiphyte species were found in the oil palm plantations studied. The composition and quality of the substrate provided by oil palm trunks changed with plantation age. The amount of organic matter in leaf axils showed a hump-shaped distribution across age classes. Leaf bases of old oil palms start to drop off and leave a smooth, naked stem.

The organic matter in oil palm leaf axils provides nutrients and stores water. Therefore, species on young and middle aged oil palms were mostly common epiphytes of disturbed habitats and accidental epiphytes (Chapter 4.1). They did not show specific adaptions for an epiphytic growth form. There were even a few individuals of *Amorphophyllus spec.* growing in the organic matter on oil palm trunks. This is surprising, since species of this genus are geophytes (Boyce & Wong 2013). Hence, oil palm leaf axils that hold organic matter act as flower pots for humus-dependent plant species.

Plants that grow on naked trunks of old oil palms must be able to germinate on and attach to the smooth vertical trunk and to live under water and nutrient poor conditions (cp. Benzing 1990) and high sun-exposure (Luskin & Potts 2011). *Vittaria ensiformis*, a common epiphyte on lowland trees (Wee 2005), was the overall most abundant epiphyte, with particular dominance on old oil palms. This makes sense because *V. ensiformis* is a stress-resilient fern with many xeromorphic adaptions. The succulent fronds enable water storage (pers. obs.). The surface-volume ratio of the tiny, narrow succulent leaves is small, leading to reduced water loss by transpiration (cp. Benzing 1990). These xeromorphic structures are often found in epiphytes of most exposed habitats (Benzing 1990) and are obviously an important morphological adaption of epiphytes that colonize old oil palms.

Asplenium nidus vel aff. (bird's nest fern) and *Platycerium spec.* (staghorn fern), which also occurred on oil palms, have another strategy to maintain nutrients and water. They form nest-like baskets with their fronds in which they collect falling leaves from their phorophytes and other plants and water (Wee 2005). *A. nidus* vel aff. was common in old plantations (pers. obs.), but only a single individual of *Platycerium spec.* was found on oil palms in this study. *Platycerium coronarium* is known to be more common in rubber plantations (Böhnert 2013). This difference in occurrence on old oil palms between species with similar drought-tolerant adaptions is probably the result of differences in light tolerance - bird's nest ferns tolerate full sun-exposure (Wee 2005) but staghorn ferns obviously cannot grow under the full sun.

The single species of accidental epiphyte that was found growing on a naked trunk, *Stenochlaena palustris*, is a climber (Wee 2005) that had lost its contact to the ground when recorded.

Hemi-epiphytes were restricted to old plantations. Large amounts of organic matter accumulated in the dense root and branch systems of *Cyrtandra spec.* (pers. obs.) and provided nutrients and water storage to the plants. All hemi-epiphytes were large sized and woody and probably needed years for this secondary thickening. It remains in question, whether these hemi-epiphytes were only able to grow on old oil palms or if this pattern is a result of plantation management. Plantation owners might have removed hemi-epiphytes from lower parts of oil palm trunks, which would explain their occurring mainly at the top of old oil palm trunks (general pattern, pers. obs.).

Figure 28: Substrates for epiphytic plants on oil palm trunks. A: Typical plot in a young plantation (mm.y, 0 m); fresh leaf bases and a small amount of organic matter inside; this example plot holds the most abundant epiphyte (*Nephrolepis spec.* and *Davallia denticulata*) and accidental epiphyte species (*Elaeis guineensis*) found on young plantations. B: Plot in a thirty years old plantation (mm.o); leaf bases dropped down; naked trunk with poor moss cover. C: Plot in a thirty years old plantation (mm.o); leaf bases dropped down; naked trunk with dense moss cover. Note the difference in the abundance and size of epiphytes, especially *Vittaria ensiformis*, between B and C. Both plots are located in the same plantation (old) in Marga Mulya at a trunk height of 5 m, but have different grades of bryophyte (moss) cover.

The number and size of fronds as well as the number of individuals of *V. ensiformis* seemed positively related to moss cover of the smooth trunks (pers. obs.; see Figure 28, B-C). Thick moss mats were moist (pers. obs.) and should also hold nutrients. An enhanced availability of moisture and nutrients likely promotes the growth of individuals of *V. ensiformis* and other vascular epiphytes. This finding matches known epiphyte succession patterns in tropical rainforest canopy (Benzing 1990): Relatively stress-tolerant colonists such as lichens, liverworts and mosses condition the substratum, which is then settled by stress-resistant ferns and later by more demanding taxa. Similarly, Zotz & Vollrath (2003) found that the establishment of seedlings of vascular epiphytes is strongly facilitated by mosses and liverworts on the palm *Socrata exorrhiza* in Panama.

Epiphytes structure the habitat available for arthropods and in some cases also even influence temperature and humidity conditions (Stuntz *et al.* 2002). Epiphyte-dwelling arthropods might be less affected by the extreme microclimatic conditions in oil palm plantations than arthropods in other microhabitats (Turner & Foster 2009). The arthropod community on epiphytes sampled in this study compromised some mainly herbivorous taxa (Hemiptera, Lepidoptera (larvae) and Orthoptera) but also some predatory taxa (Araneae and Mantodea). However, the high abundance of Araneae was in contrast to the low abundance of the remaining taxa. Only ants were even more dominant, but they are not a preferred spider prey (Stuntz *et al.* 2002). Probably, web-building spiders on oil palms capture flying insects that visit the epiphytes, but hunting spiders forage on other epiphyte-dwelling arthropods (cp. Stuntz *et al.* 2002).

Many arthropod taxa found in the organic matter in oil palm leaf axils typically were detritivorous (Collembola, Dermaptera, Diplopoda, Isopoda, Isoptera and Symphyla). The decomposer community provides an important ecosystem service in oil palm plantations. They convert the organic matter in leaf axils into nutrients that can be utilized by epiphytic plants (cp. Foster et al. 2011). Epiphytic plants again provide a habitat for many arthropod taxa as observed in this study.

4.3 Implications for promoting epiphyte and arthropod diversity in oil palm plantations

Oil palm plantations replaced tropical lowland forests on a large scale. However, they can never provide an alternative habitat for forest species. Epiphyte diversity in the oil palm plantations studied was low and forest-specialized species were not recorded. This result coincides with biodiversity patterns of other organism groups reviewed by Foster *et al.* (2011). It is in question, if forest-related epiphytes such as orchids will be able to colonize much older oil palms. However, this is not relevant for conservation issues as oil palms in plantations get replaced by young seedlings after about thirty years (Armstrong 1999).

Nevertheless, epiphytes are an important component in the oil palm ecosystem, as they provide a habitat for various arthropod taxa. Koh (2008) showed that epiphyte prevalence enhances bird diversity in oil palm plantations, probably by the additional vegetation complexity. The interior of bird's nest ferns provides a cold and humid microclimate and therefore acts as reservoir of arthropod diversity within oil palm plantations (Fayle *et al.* 2005). However, most plantation owners in the present study removed epiphytes on the false assumption that these plants are parasites. Therefore, plantation owners should be informed about the role of epiphytes for arthropods and about biological pest control by beneficial arthropods. Advertising could be done by NGO's. Furthermore, the RSPO (Round Table of Sustainable Palm Oil) should include an epiphyte-friendly management as certification criterion for sustainable palm oil.

Furthermore, the use of highly toxic pesticides and herbicides should be stopped. Herbicides and pesticides reduce populations of important litter decomposers such as Collembola (Stenchly, Clough & Tscharntke 2012) and likely have a negative effect on populations of further organism groups, including epiphytes. The European Union banned Paraquat, a harmful agent in Gramoxone, as well as Carbofuran (syn. Furadan) already (CVRIA 2003; Kyprianou 2007), both agrochemicals that were applied in the oil palm plantations studied. However, certification bodies for sustainable palm oil like the RSPO (Round Table of Sustainable Palm Oil) still did not ban the use of toxic agrochemicals (INA-NIWG 2008). Additional to the negative effect on biodiversity, workers in oil palm plantations get in contact with these harmful agents. Instead of agrochemicals, a biological pest management should be established. Caudwell & Orrell (1997) proposed an integrated pest management for oil palms: developing a biodiversity within the plantation comes along with the presence of natural parasites and pathogens of the pest species. (Koh 2008a) showed that bird's control herbivorous pests in oil palm plantations. Spiders are known to be effective predators of herbivorous insect best in Asia's rice paddies (Maloney, Drummond & Alford 2003).

Large, often isolated shade trees in disturbed landscapes, cacao farms and coffee plantations can act as a refuge for epiphytes in anthropogenic modified landscapes (Kartzinel *et al.* 2013; Haro-Carrión *et al.* 2009; Hietz 2005). To extend this finding, I propose to establish large groups of trees in and around oil palm plantations. Single trees still would have a high sun-exposure and an unstable microhabitat, which is not adequate for sensitive species with a low tolerance to extreme microclimatic conditions.

The protection of remaining natural forests, including the establishment of buffer zones around forests, is essential for the protection of forest species (Koh 2008b). Koh *et al.* (2009) proposed a landscape mosaic of intensive oil palm plantations, high conservation areas and agroforestry zones as buffer in between. Also highly degraded forests should be protected, as they still provide an important habitat for many species such as ants (Woodcock *et al.* 2011). Intercropping with other crops is not useful due to a reduced profitability (Koh *et al.* 2009). Luskin & Potts (2011) proposed a patched plantation design of different aged small fields or stripes of oil palms to increase heterogeneity within a plantation. Small forest patches can act as refuge for forest species (Turner & T Corlett 1996).

A mosaic landscape of different aged plantations including forest patches and buffer zones within and surround the plantation, combined with the ban of agrochemicals would be a first step towards a biodiversity-friendly management. That also includes, that epiphytes are accepted to grow on the trunks. A lowering of the land-use intensity is essential to preserve the unique biodiversity in the Sundaland hotspot.

4.4 Conclusions

Epiphyte diversity in the oil palm plantations studied was extremely low. Epiphytic pteridophytes of disturbed areas and accidental epiphytes were dominant. Furthermore, the opposite patterns of epiphytes and accidental epiphytes in abundance and diversity along the age gradient and between substrates indicate that it is essential to differentiate between these two growths forms in ecological studies. Plantation age strongly determined the abundance and diversity of epiphytic plants. A succession of the epiphyte community was observed from rough young and middle aged trunks that provide organic matter in leaf axils as substrate, to smooth trunks of old oil palms. Leaf axils filled with organic matter provide a substrate for humus-dependent epiphyte species and accidental epiphytes. As a result, these species can grow on young oil palms without specific adaptions for an epiphytic growth form. In contrast, only a restricted subset of epiphytes with xeromorphic adaptations was able to grow on naked trunks of old oil palms. The lack of any vertical patterns in the distribution of epiphytes can be explained by the absence of vertical gradients in ecological factors such as microclimate (Altenhövel 2013).

Epiphytes provided an important microhabitat for arthropods in the oil palm plantations studied. The occurrence of different arthropod guilds on epiphytes and in organic matter in oil palm leaf axils implies that it is essential to sample arthropods in diverse microhabitats in order to assess the overall diversity and abundance of oil palm-dwelling arthropod taxa. Plant cover explained the abundance and richness of epiphyte-dwelling arthropods in part, but location was the best predictor. The number of arthropod taxa in organic matter strongly decreased with age. However, more work has to be done to identify the major driver(s) of diversity of oil palm-dwelling arthropods. It is possible, that drivers could be identified at the family, order or species level.

The transformation of large areas of rainforest to oil palm plantations is in particular a threat to forest-specialized epiphytes. That includes host-specific epiphytes, epiphytic orchids, and epiphytes with a narrow climatic tolerance (Köster *et al.* 2013) that are not able to cope with the extreme microclimatic conditions in oil palm plantations.

Future research should focus on methods for biodiversity-friendly plantation management. Options include designer plantations (Koh *et al.* 2009) and biological pest control (Caudwell & Orrell 1997). A landscape mosaic of oil palm plantations and forest patches within and around oil palm plantations likely enhance biodiversity (cp. Koh *et al.* 2009). In order to protect Southeast Asia’s unique biodiversity, deforestation for the establishment of new oil palm plantations must be stopped. Therefore, all stakeholders involved, including conservation biologists, NGOs, governments and the oil palm industry should cooperate.

Summary

Tropical Southeast Asia's harbors a unique biodiversity, including many endemics, but it is highly threatened by habitat loss (Koh & Wilcove 2007; Sodhi et al. 2004). The expansion of oil palm is a particularly major driver of forest loss in Southeast Asia (Wilcove *et al.* 2013). Understanding responses of different taxa to habitat transformation and accessing abundance, species richness and community composition in oil palm plantations is crucial for the development of sustainable management strategies (Turner *et al.* 2008).

This master's thesis was carried out in the Free Floater Research Group in Biodiversity, Macroecology and Conservation Biogeography in the Faculty of Forest Sciences and Forest Ecology at the University of Göttingen. The Free Floater Research Group takes part in a long-term Collaborative Research Centre (CRC 990) that is named "Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems (Sumatra, Indonesia)".(EFForTS) with the aim of understanding causes and consequences of the transformation of rainforest into agricultural landscapes. The present thesis aims to quantify and analyze the diversity and dynamics of vascular epiphytes and arthropods in oil palm (*Elaeis guineensis*) plantations with a special focus on an age gradient of oil palm plantations. Habitat characteristics of oil palm trunks change during their life cycle. First, leave bases remain on the trunk, when the leaves are cut off. In the leaf axils, organic material accumulates over the years. At an age of about twenty years (in this study), the leaf bases drop down. Now, the naked oil palm trunks are smooth. Hence, oil palms provide different substrates to other organisms.

Hypotheses are: (H1) accidental epiphytes compose a part of the plant community on oil palm trunks. (H2) Abundance, diversity and composition of epiphytes and accidental epiphytes change with plantation age. (H3) Arthropod diversity and abundance in the epiphyte microhabitat are positively related to plant cover of oil palm trunks. (H4) Arthropod diversity, abundance and composition in the organic matter microhabitat change with plantation age. (H5) Abundance, diversity and composition of epiphytes and accidental epiphytes change along the height gradient of oil palm trunks.

The study was conducted at three locations in Jambi Province, Sumatra: Bukit Makmur (unit 5 of Sungai Bahar, 2°1'56.6''S 103°23'15.7'' E, 24.2 m a.s.l.), Marga Mulya (unit 2 of Sungai Bahar, 1°57'21.1'' S 103°26'43.6'' E, 20.9 m a.s.l.) and Permatang Kabau (1°56'47.2'' S 102°35'10.2'' E, 77.4 m a.s.l.). Natural vegetation is dipterocarp tropical lowland forest but this was replaced by large

oil palm plantations. A space-for-time substitution was done to include different old oil palms: a chronosequence of each (0-6 yrs), middle (10-15 yrs) and old (20-30 yrs) plantations (one each) was surveyed in each location. Six oil palms were surveyed in each plantation (n = 54). Epiphytic plants, oil palm-dwelling arthropods and habitat characteristics were surveyed at the oil palm level and in 0.5 x 0.m m² plots (n = 120) attached to oil palm trunks at heights of 0 m, 2.5 m and 5 m, if available. Arthropods were collected from epiphytic plants with a net and extracted from organic matter in oil palm leaf axils with Winkler's traps.

Almost two thirds of the species were classified to accidental epiphytes. Eighteen epiphyte species were found. 99.24% of the epiphyte community consisted of seven pteridophyte species, headed by *Vittaria ensiformis* (34.6%). In old plantations, *Vittaria ensiformis* even built 74.4% of the epiphyte community. The species pool was almost covered by the sampling effort both at the oil palm and at the plot level; only in old plantations, few more species are expected. 31 accidental epiphytes species were recorded. More species are expected to find at higher sampling effort, in particular in plantations in Permatang Kabau, in age class 'young' and at a trunk height of 0 m. 71.14% of the community was composed by *Elaeis guineensis*, and the invasive species *Clidemia hirta* and *Asystasia gangetica*. Fourteen arthropod taxa were collected on epiphytic plants and seventeen taxa in organic matter. The sampling effort was high enough to detect almost all taxa. The majority of arthropod individuals on epiphytes were classified to Formicidae and Araneae. Formicidae alone dominated the arthropod community in organic matter. Within all organism groups, few plots were extremely rich on individuals.

'Age class' was the major driver of diversity patterns of epiphytes and accidental epiphytes. Epiphyte species richness increased with age, but the number of individuals did not differ significantly between age classes. Number of individuals and species of accidental epiphytes decreased with age and trunk height. Furthermore, accidental epiphytes were almost restricted to grow in the organic matter in oil palm leaf axils (and partly on leaf axils). Epiphytes were also able to grow at the naked trunk of old plantations. Diversity and abundance of arthropods on epiphytes did not differ among age classes, but between locations. More than the half of variance in the standardized number of arthropod taxa in organic matter was caused by the number of individuals. However, in LMEs 'age class' was not a significant predictor.

The results confirm (H1) and (H2). (H3) received support from the results, but the overall variance in abundance and richness of arthropod taxa explained by plant cover was pretty low (< 10%).

Therefore, hypothesis (H4) can be confirmed in the term, that arthropod diversity decreased with age, but not that arthropod abundance was influenced by age.

Epiphyte diversity is dramatically low in the oil palm plantations investigated. The community of epiphytic plants undergoes a succession, influenced by changes in substrate availability on oil palm trunks with palm age. Succulence seemed to enable *V. ensiformis* to grow on the naked oil palm trunks. The lack of vertical epiphyte stratification is likely caused by the absence of a vertical microclimatic gradient. The expansion of oil palm plantations endangers forest-specialized epiphytes, which were entirely lacking from the plantations investigated. Location and plant cover were drivers for arthropod abundance and diversity in part, but major determinants of arthropod diversity patterns need to be investigated further. Natural forests in proximity to plantations likely enhance arthropod diversity within plantations. The usage of highly toxic agrochemicals, applied on every plantation, should be banned and instead biological pest management techniques should be used. To manage oil-palm plantations for higher arthropod biodiversity, epiphytes should not be removed.

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Appendix

Appendix 1: Question catalogue for the interview with plantation owners

(English / Bahasa Indonesia)

1. Age of the plantation / Umur perkebunan
    - Planting year / Tahun penanaman
    - Age / umur
2. Do you remove epiphytes from oil palm trunks? / Apa epifit dihilangkan dari batang kelapa sawit?
    - How often? / Berapa kali?
    - Last time? / Kapan terakhir kali?
3. Do you use fertilizer for the plantation? / Apa anda memakai pupuk untuk perkebunan?
    - How often? / Berapa kali?
    - Last time? / Kapan terakhir kali?
    - Which one(s)? / Pupuk apa?
4. Do you use herbicides? / Apa anda memakai herbisida?
    - How often? / Berapa kali?
    - Last time? / Kapan terakhir kali?
    - Where? (Ground, oil palm trunk) / Dimano? (Di tanak, di batang)
    - Which one(s)? / Herbisida apa?
5. Do you use pesticides? / Apa anda memakai pestisida?
    - How often? / Berapa kali?
    - Last time? / Kapan terakhir kali?
    - Where? (Ground, oil palm trunk) / Dimano? (Di tanak, di batang)
    - Which one(s)? / Pestisida apa?
6. Way of cultivation? / Bagaimana cara pengolahan?
7. Any pests? / Ada serangga perusak?
8. When do you harvest the fruits? / Kapan anda memanen buah?
9. Any problems or characteristics? / Masalah dan karakteristik?
10. Comment / Komentar

Appendix 2: Answers of the plantation owners in the interviews

The answers of the plantation owners to the questions (Appendix 1) in the interviews were translated to English and are shown below. For ‘bm.o’, the village chief of Bukit Makmur, Bapak Bambang, was interviewed. Interviews were conducted between March 12 and April 13, 2013.

<u>1. Age of the plantation</u>

See Table 1

<u>2. Do you remove epiphytes from oil palm trunks?</u>

bm.y: *Yes; one time until now; November 2012*
mm.y: *No*
pk.y: *Yes; 2 times/year; October 2012*
bm.m: *Yes; 2 times/year; January 2013*
mm.m: *No*
pk.m: *Yes; 2 times/year; no answer*
bm.o: *Yes; 2 times/year; conditional*
mm.o: *No*
pk.o: *Yes; 2 times/year; February 2013*

<u>3. Do you use fertilizer for the plantation?</u>

bm.y: *Yes; 3 times/year[1], 1 time/year[2]; November 2012[1], December 2012[2]; KCl[1], SP 36[1], Poska[1], Dolomit[2], Urea[2], Mob[?]*
mm.y: *Yes; 2 times/year; April 2013, October 2012; compost, Urea, KCl, Dolomit (,CaCl)*
pk.y: *Yes; 2 times/year; December 2012; Ponska*
bm.m: *Yes; 4 times/year; January 2013; SP 36, Urea, KCl, Ponska, Dolomit (,Mob)*
mm.m: *Yes; 2 times/year; January 2013; compost, Urea, KCl, Dolomit (,CaCl)*
pk.m: *Yes; 2 times/year; no answer ; Ponska*
bm.o: *Yes; 3 times/year; January 2013; Urea, KCl, SP 36; Dolomit*
mm.o: *Yes; 2 times/year; January 2013; compost, Urea, KCl, Dolomit (,CaCl)*
pk.o: *Yes; 2 times/year; January 2013; Ponska*

<u>4. Do you use herbicides?</u>

bm.y: *No*
mm.y: *Yes; 2 times/year; November 2012; everywhere on the ground; Gramoxone, Eli*
pk.y: *Yes; 2 times/year; November 2012; ground; Gramoxone*
bm.m: *Yes; 2 times/year; ground and oil palm trunks; Gramoxone*
mm.m: *Yes; 2 times/year; December 2012; everywhere on the ground; Gramoxone, Eli*
pk.m: *Yes; 2 times/year; no answer ; ground; Gramoxone*
bm.o: *Yes; 3 times/year; January 2013; ground and oil palm trunks; Gramoxone*
mm.o: *Yes; 2 times/year; December 2012; everywhere on the ground; Gramoxone, Eli*
pk.o: *Yes; 2 times/year; December 2012; ground; Gramoxone*

5. Do you use pesticides?

bm.y: *Yes; 2 times/year; January 2013; ground; Furadan 3g*
mm.y: *No*
pk.y: *Yes; 2 times/year; November 2012; leaves; Matador*
bm.m: *No*
mm.m: Yes; no answer
pk.m: *Yes; 2 times/year; no answer; leaves; Matador*
bm.o: *No*
mm.o: *No*
pk.o: *Yes; 2 times/year; December 2012; leaves; Matador*

6. Way of cultivation?

bm.y: *Phosphat is distributed in a radius of 60 cm, after 1 month oil palm planted 50 cm deep. If no rain, chalk is used; if rain, Urea, KCl, SP 36 and Polska are used.*
mm.y: No answer
pk.y: *Use good seeds at a planting distance 8 m x 9 m and chemical fertilizer 2 times/year*
bm.m: *Gramoxone kills fern and other plants on the oil palm, but not grass. If oil palms get to much water, leaf bases drop down.*
mm.m: No answer
pk.m: *Use good seeds at a planting distance 8 m x 9 m and chemical fertilizer 2 times/year*
bm.o: No answer
mm.o: No answer
pk.o: *Use good seeds at a planting distance 8 m x 9 m and chemical fertilizer 2 times/year*

7. Any pests?

Comment: 'Ulat api' is a group of nettle caterpillars of the Lepidoptera family Limacodidae. These caterpillars feed on oil palm leaves and are a common pest on oil palm plantations (Foster *et al.* 2011; Kimura 1978).

bm.y: '*Ulat api'*
mm.y: '*Ulat api', wild pigs, mice or rats ('tikus')*
pk.y: '*Ulat api', wild pigs, hedgehogs, monkeys*
bm.m: '*Ulat api'*
mm.m: '*Ulat api' (1 time), wild pigs, mice or rats ('tikus')*
pk.m: '*Ulat api', wild pigs, hedgehogs, monkeys*
bm.o: '*Ulat api'*
mm.o: '*Ulat api', wild pigs, mice or rats ('tikus')*
pk.o: '*Ulat api', wild pigs, hedgehogs, monkeys*

8. When do you harvest the fruits?

bm.y: *Every 2 weeks on Thursday, only red fruits*
mm.y: *Every 2 weeks, fruits are given to a company*
pk.y: *Every 10 days. If the plant is healthy and gets enough fertilizer, first fruits can be harvested after 3 years.*
bm.m: *Every 2 weeks on Saturday*
mm.m: *Every 2 weeks, fruits are given to a company*
pk.m: *Every 10 days. If the plant is healthy and gets enough fertilizer, first fruits can be harvested after 3 years.*
bm.o: *Every 2 weeks on Saturday*
mm.o: *Every 2 weeks, fruits are given to a company*
pk.o: *Every 10 days. If the plant is healthy and gets enough fertilizer, first fruits can be harvested after 3 years*.

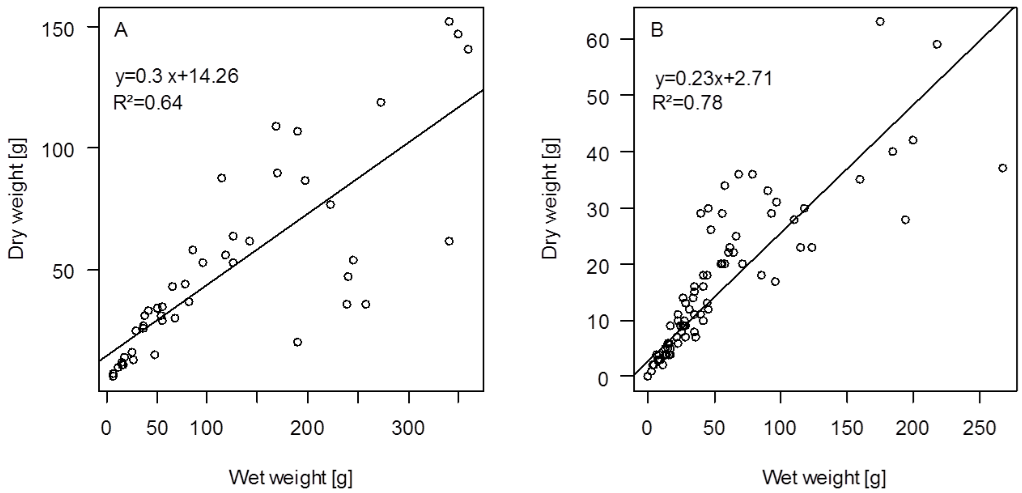
9. Any problems or characteristics?

bm.y: No answer
mm.y: *Sometimes fungal infestation at oil palm fruits, xylem and phloem (trunk)*
pk.y: No answer
bm.m: No answer
mm.m: *Sometimes fungal infestation at oil palm fruits, xylem and phloem (trunk)*
pk.m: No answer
bm.o: No answer
mm.o: *Sometimes fungal infestation at oil palm fruits, xylem and phloem (trunk)*
pk.o: No answer

10. Comment

bm.y: '*Ulat api' feed on oil palm leaves.*
mm.y: No answer
pk.y: *Plantation was originally planted in 2007 (ca. 3-4 m high oil palms). Oil palms with a trunk height of ca. 1.5 - 2 m were planted in 2009. The smallest oil palms were planted in 2012.*
bm.m: No answer
mm.m: No answer
pk.m: *Fruits are not harvested from every oil palm on the plantation, but every oil palm is controlled for mature fruits every 10 days.*
bm.o: *Gramoxone kills ferns and other plants on the palms and on the ground.*
mm.o: *Mice or rats ('tikus') feed on young oil palm fruits.*
pk.o: *Fruits are not harvested from every oil palm on the plantation, but every oil palm is controlled for mature fruits every 10 days.*

Appendix 3: Weight measurements of organic matter



Appendix 3.1: The scatterplots show the relationship between dry weight and wet weight of organic matter collected in oil palm leaf axis. A: Organic matter, from which arthropods were extracted, 1 - 3 samples (depending on oilpalm height) pooled for each oil palm, thus 1 sample = 1 oilpalm. B: Total organic matter from one leaf axis within a plot, thus 1 sample = 1 plot. The spread of samples could be explained by an error in measuring of wet weight, but the relationship between wet weight and dry weight seems to be linear.

Appendix 4: Abundance and diversity - means and standard derivations

Appendix 4.1: Number of individuals. Mean and standard deviation for number of individuals per plot for epiphytes (*Epi*), accidental epiphytes (*Acc*), arthropods on epiphytes (*Art.E*) and arthropods in organic matter (*Art.O*), grouped by locations, age classes and trunk heights of the plots.). Numbers of individuals in *Art.O* were standardized to number of individuals per 50 g organic matter (dry weight) per oil palm. Note that *Art.E* and *Art.O* cannot directly be compared to each other due to different sampling methods and units. Abbreviations in 'location': bm = Bukit Makmur, mm = Marga Mulya, pk = Permatang Kabau; in 'age class': y = young, m = middle, o = old.

	Location			**Age class**			**Trunk height [m]**		
	bm	**mm**	**pk**	**y**	**m**	**o**	**0**	**2.5**	**5**
Epi	3.88 ± 4.23	9.17 ± 12.13	3.08 ± 5.00	8.89 ± 9.21	5.10 ± 5.22	4.70 ± 10.24	5.31 ± 7.37	4.61 ± 4.24	6.87 ± 13.04
Acc	1.07 ± 2.19	1.67 ± 3.52	0.94 ± 1.47	5.78 ± 3.92	0.81 ± 1.28	0.11 ± 0.37	2.48 ± 3.42	0.22 ± 0.68	0.23 ± 0.54
Art.E	3.43 ± 3.52	2.04 ± 2.36	10.88 ± 18.78	11 ± 23.18	4.63 ± 7.96	3.87 ± 4.14	7.97 ± 17.38	4.29 ± 4.73	3.35 ± 4.05
Art.O	15.24±22.74	16.12±15.77	74.48±158.66	29.41±32.96	58.97±155.51	12.87 ± 24.7	NA	NA	NA

Appendix 4.2: Richness of plant species and arthropod taxa at the oil palm level. Mean ± standard deviation of epiphyte (*Epi*) and accidental epiphyte (*Acc*) species richness per oil palm and number of taxa per oil palm for arthropods in organic matter (*Art.O*). Numbers of taxa in *Art.O* were standardized to number of taxa per 50 g organic matter (dry weight) per oil palm. Abbreviations in 'location': bm = Bukit Makmur, mm = Marga Mulya, pk = Permatang Kabau; in 'age class': y = young, m = middle, o = old.

	Location			**Age class**		
	bm	**mm**	**pk**	**y**	**m**	**o**
Epi	3.67 ± 2.09	4.39 ± 2.15	3.89 ± 1.81	2.06 ± 1.26	5.4 ± 1.05	4.5 ± 1.58
Acc	2.78 ± 1.06	2.89 ± 1.49	3.89 ± 2.19	3.5 ± 1.2	4.17 ± 1.86	1.89 ± 1.08
Art.O	6.24 ± 6.28	5.08 ± 4.58	7.09 ± 9.58	9.21 ± 5.9	5.47 ± 8.88	2.22 ± 2.95

Appendix 4.3: Richness of plant species and arthropod taxa at the plot level. Mean ± standard deviation of epiphyte (*Epi*) and accidental epiphyte (*Acc*) species and of arthropod taxa on epiphytes (*Art.E*) per plot. Abbreviations in 'location': bm = Bukit Makmur, mm = Marga Mulya, pk = Permatang Kabau; in 'age class': y = young, m = middle, o = old.

	Location			**Age class**			**Trunk height [m]**		
	bm	**mm**	**pk**	**y**	**m**	**o**	**0**	**2.5**	**5**
Epi	1.43 ± 1.43	1.26 ± 1.19	1.19 ± 1.04	1.5 ± 1.1	1.63 ± 1.28	0.94 ± 1.16	0.24 ± 1.29	1.36 ± 1.1	1.33 ± 1.32
Acc	0.52 ± 0.8	0.6 ± 1.15	0.75 ± 1.11	2.39 ± 1.95	0.54 ± 0.71	0.09 ± 0.29	1.15 ± 1.25	0.17 ± 0.51	0.2 ± 0.41
Art.E	1.7 ± 1.26	1.18 ± 0.98	2.5 ± 1.27	2.39 ± 1.29	1.66 ± 1.33	1.71 ± 1.19	2.08 ± 1.33	1.82 ± 1.36	1.39 ± 1.08

Appendix 5: Tables corresponding to rank abundance curves

Appendix 5.1: Abundance of plant species and arthropod taxa on oil palm trunks. Taxa are listed in descending order according to abundance. The number of arthropod individuals in (D) is standardized to number of individuals per 50 g organic matter (dry weight) per oil palm.

A: Epiphytes (*Epi*)

Sp.ID	Species	No. individuals
4	*Vittaria ensiformis*	233
1	*Nephrolepis spec.*	193
14	*Asplenium longissimum*	79
2	*Davallia denticulata*	65
89	*Goniophlebium spec.*	41
3	*Vittaria elongata*	32
5	*Goniophlebium percussum*	11
6	cf. *Phymatosorus spec.*	2
13	*Asplenium spec.*	1
15	*Cyrtandra spec.*(hemi-)	1
87	*Selliguea* cf. *enervis*	1

B: Accidental epiphytes (*Acc*)

Sp.ID	Species	No. individuals
54	*Elaeis guineensis*	41
55	*Clidemia hirta*	34
18	*Asystasia gangetica*	31
9	*Stenochlaena palustris*	10
48	*Spermacoce latifolia*	10
16	indet. Angiosperm	7
31	*Mikania micrantha*	4
17	indet. Angiosperm	3
33	*Melastoma malabathricum*	2
57	*Macaranga triloba*	2
19	indet. Angiosperm	1
24	indet. Angiosperm	1
28	*Phyllanthus urinaria*	1
60	*Scleria spec.*	1
61	*Isachne globosa*	1

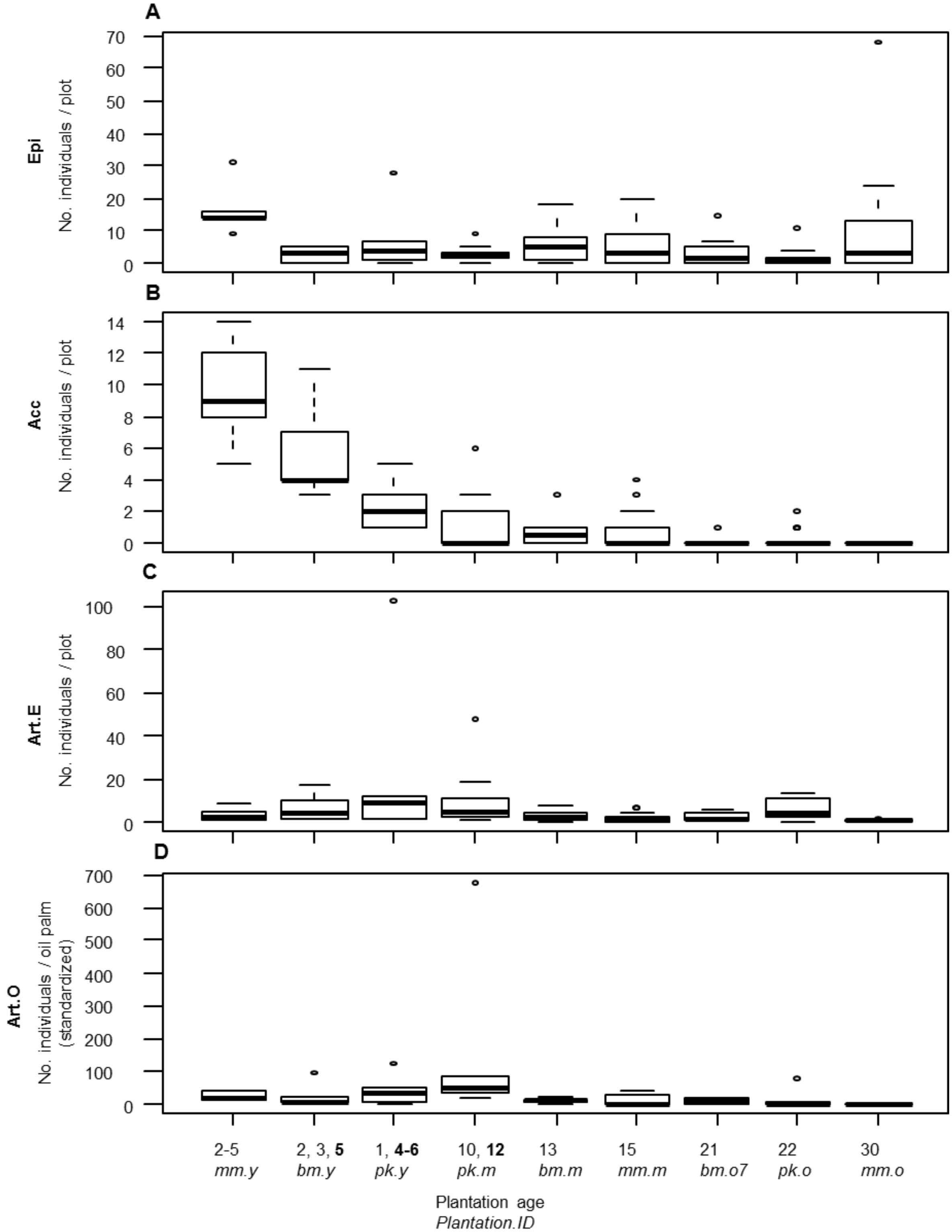
C: Arthropods on epiphytes (*Art.E*)

Taxon	No. individuals
Formicidae	273
Araneae	160
Hemiptera	26
Lepidoptera	21
Blattodea	7
Orthoptera	5
Coleoptera	4
Psocoptera	4
Diptera	3
Acari	1
Diplopoda	1
Hymenoptera excl. Formicidae	1
Mantodea	1
Thysanoptera	1

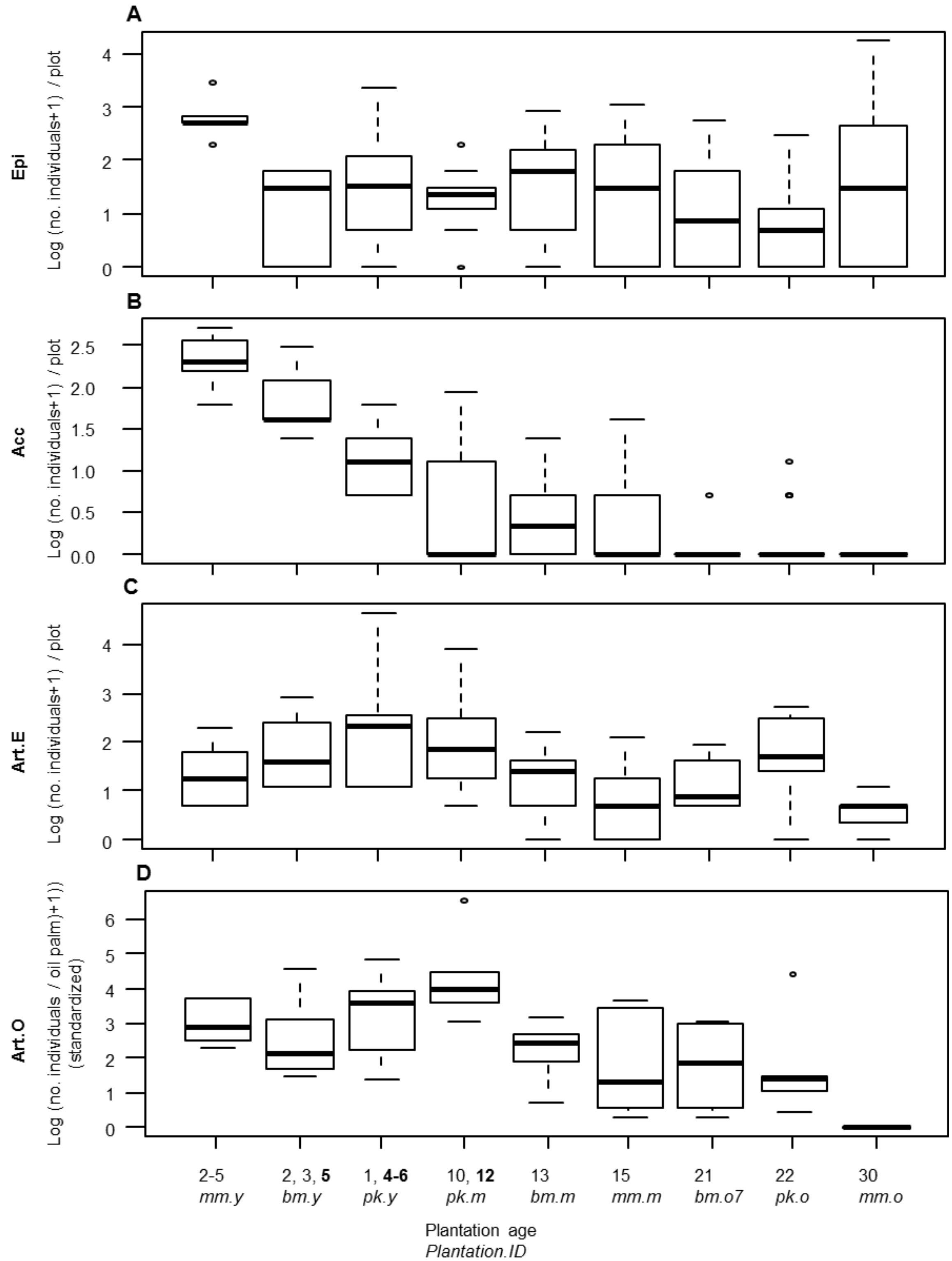
D: Arthropods in organic matter (*Art.O*, standardized)

Taxon	No. individuals
Formicidae	1589.02
Isopoda	76.55
Araneae	41.37
Coleoptera	35.90
Diptera	32.88
Acari	26.95
Dermaptera	25.00
Diplopoda	20.67
Hemiptera excl. Formicidae	19.25
Hymenoptera	12.78
Blattodea	11.98
Lepidoptera	10.45
Collembola	9.80
Symphyla	8.18
Isoptera	5.46
Orthoptera	1.85
Psocoptera	1.36

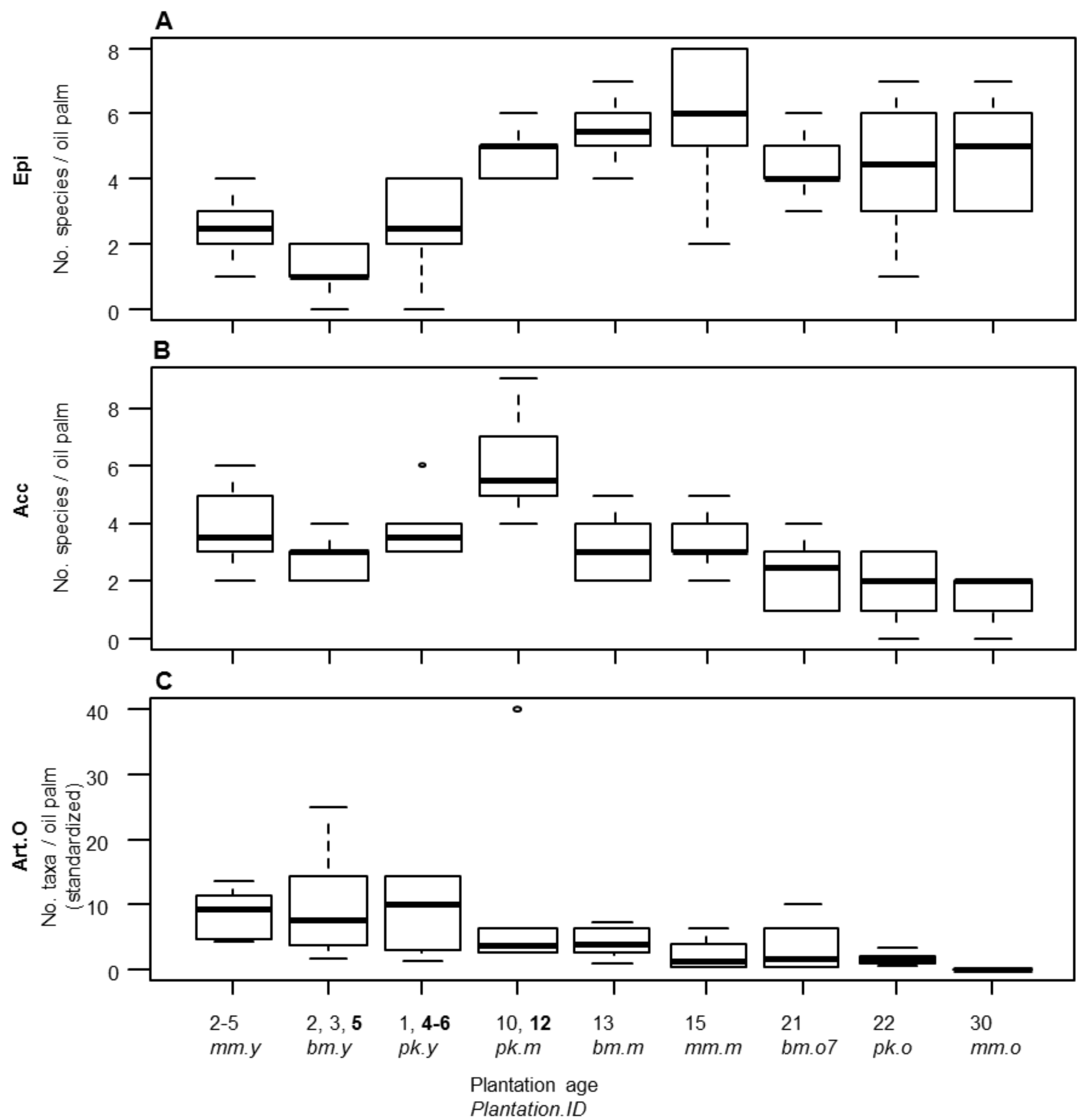
Appendix 6: Abundance and diversity along a continuous age gradient



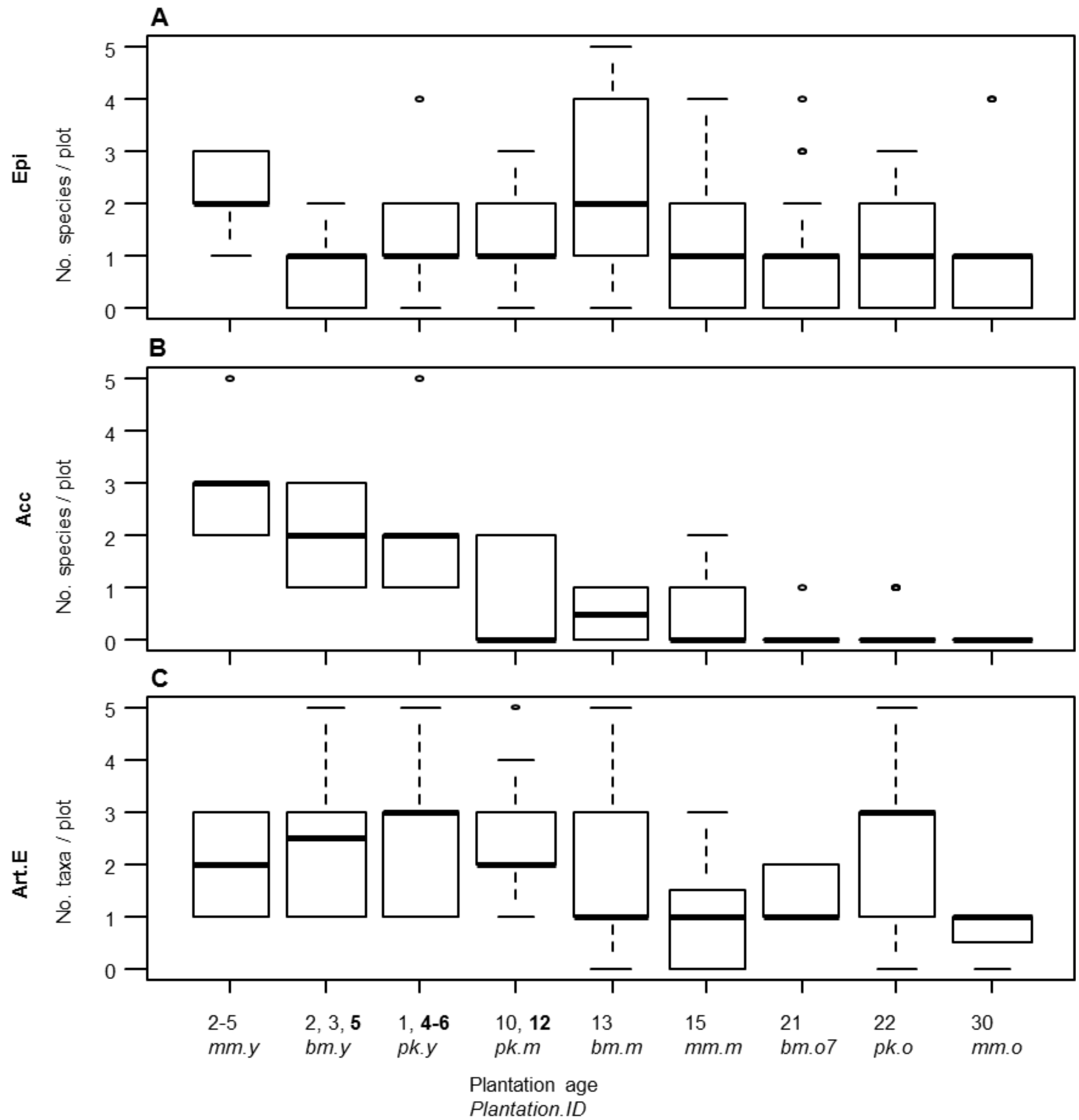
Appendix 6.1: Number of individuals along a continuous age gradient. Plantations are ordered by their main age - the age of oil palms present in this plantation. If a plantation included oil palms of different planting years, plantations were ordered by the mean trunk height of investigated oil palms. If known, main age is written in bold numbers.



Appendix 6.2: Number of individuals along a continuous age gradient. Numbers of individuals are $\log_e$-transformed (natural logarithm). Plantations are ordered by their main age - the age of oil palms present in this plantation. If a plantation included oil palms of different planting years, plantations were ordered by the mean trunk height of investigated oil palms. If known, main age is written in bold numbers.



Appendix 6.3: Richness of plant species and arthropod taxa at the oil palm level along a continuous age gradient. Plantations are ordered by their main age - the age of oil palms present in this plantation. If a plantation included oil palms of different planting years, plantations were ordered by the mean trunk height of investigated oil palms. If known, main age is written in bold numbers.



Appendix 6.4: Richness of plant species and arthropod taxa at the plot level along a continuous age gradient. Plantations are ordered by their main age - the age of oil palms present in this plantation. If a plantation included oil palms of different planting years, plantations were ordered by the mean trunk height of investigated oil palms. If known, main age is written in bold numbers.

Appendix 7: Linear Models (LMs)

Linear models for the abundance and diversity of epiphytic plants and arthropods in oil palm plantations. Number of individuals and number of species or higher-ranked taxa of epiphytes (Epi), accidental epiphytes (Acc), arthropods on epiphytes (Art.E), arhtorpods in organic matter (Art.O) at the plot level (0.5 x 0.5 m²) and at the oil palm level as response variable. Each the best model is marked in grey.

Appendix 7.1: Linear models for number of epiphyte (*Epi*) individuals.

Model	Organism group	Level	Response variable	Predictor(s)	R^2	p-value	AIC
LM.1	*Epi*	plot	no. individuals	location	0.1038	**	847
LM.2	*Epi*	plot	no. individuals	age class	0.0291	n.s.	856.6
LM.3	*Epi*	plot	no. individuals	trunk height	0.0038	n.s.	857.69
LM.4	*Epi*	plot	no. individuals	main age	0.0009	n.s.	858.04
LM.5	*Epi*	plot	no. individuals	plant cover	0.0484	**	852.2
LM.6	*Epi*	plot	no. individuals	leaf base cover	0.0002	n.s.	851.99
LM.7	*Epi*	plot	no. individuals	organic matter	0.0019	n.s.	851.54
LM.8	*Epi*	plot	no. individuals	location + plant cover	0.1911	***	836.7
LM.9	*Epi*	plot	$\log_e$ (no. individuals+1)	location	0.0638	**	355.92
LM.10	*Epi*	plot	$\log_e$ (no. individuals+1)	age class	0.0756	**	354.4
LM.11	*Epi*	plot	$\log_e$ (no. individuals+1)	trunk height	0.0026	n.s.	361.52
LM.12	*Epi*	plot	$\log_e$ (no. individuals+1)	main age	0.037	*	357.3
LM.13	*Epi*	plot	$\log_e$ (no. individuals+1)	plant cover	0.1238	***	345.98
LM.14	*Epi*	plot	$\log_e$ (no. individuals+1)	leaf base cover	0.0452	**	354.27
LM.15	*Epi*	plot	$\log_e$ (no. individuals+1)	organic matter	0.0013	n.s.	359.38
LM.16	*Epi*	plot	$\log_e$ (no. individuals+1)	location + plant cover + age class + leaf base cover	0.2785	***	330.94
LM.17	*Epi*	plot	$\log_e$ (no. individuals+1)	location + plant cover	0.2444	***	332.2049

Appendix 7.2: Linear models for number of accidental epiphyte (*Acc*) individuals.

Model	Organism group	Level	Response variable	Predictor(s)	R^2	p-value	AIC
LM.1	*Acc*	plot	no. individuals	location	0.0151	n.s.	573.47
LM.2	*Acc*	plot	no. individuals	age class	0.5645	***	457.53
LM.3	*Acc*	plot	no. individuals	trunk height	0.1502	***	553.76
LM.4	*Acc*	plot	no. individuals	main age	0.3578	***	520.15
LM.5	*Acc*	plot	no. individuals	plant cover	0.1355	***	555.8183
LM.6	*Acc*	plot	no. individuals	leaf base cover	0.1091	***	555.58
LM.7	*Acc*	plot	no. individuals	organic matter	0.0234	n.s.	566.52
LM.8	*Acc*	plot	no. individuals	age class + trunk height + plant cover + leaf base cover	0.5871	***	472.06
LM.9	*Acc*	plot	no. individuals	age class + epiphyte cover	0.5775	***	473.91
LM.10	*Acc*	plot	$\log_e$ (no. individuals+1)	location	0.0008	n.s.	268.76
LM.11	*Acc*	plot	$\log_e$ (no. individuals+1)	age class	0.6142	***	154.58
LM.12	*Acc*	plot	$\log_e$ (no. individuals+1)	trunk height	0.1955	***	240.75
LM.13	*Acc*	plot	$\log_e$ (no. individuals+1)	main age	0.4542	***	194.19
LM.14	*Acc*	plot	$\log_e$ (no. individuals+1)	plant cover	0.1603	***	245.89
LM.15	*Acc*	plot	$\log_e$ (no. individuals+1)	leaf base cover	0.1765	***	242.16
LM.16	*Acc*	plot	$\log_e$ (no. individuals+1)	organic matter	0.0284	n.s.	261.83
LM.17	*Acc*	plot	$\log_e$ (no. individuals+1)	age class + plant cover + leaf base cover + trunk height	0.6585	***	145.42
LM.18	*Acc*	plot	$\log_e$ (no. individuals+1)	age class + plant cover + trunk height	0.6573	***	144.36
LM.19	*Acc*	plot	$\log_e$ (no. individuals+1)	age class + trunk height	0.6304	***	151.43

Appendix 7.3: Linear models for number of arthropod individuals in the epiphyte microhabitat (*Art.E*).

Model	Organism group	Level	Response variable	Predictor(s)	R^2	p-value	AIC
LM.1	*Art.E*	plot	no. individuals	location	0.1081	**	699.53
LM.2	*Art.E*	plot	no. individuals	age class	0.0511	n.s.	705.1
LM.3	*Art.E*	plot	no. individuals	trunk height	0.0272	n.s.	705.34
LM.4	*Art.E*	plot	no. individuals	main age	0.0451	*	703.66
LM.5	*Art.E*	plot	no. individuals	plant cover	6.30E-03	n.s.	707.25
LM.6	*Art.E*	plot	no. individuals	leaf base cover	0.0151	n.s.	699.44
LM.7	*Art.E*	plot	no. individuals	organic matter	0.0001	n.s.	700.78
LM.8	*Art.E*	plot	no. individuals	no. individuals (Epi)	0.0205	n.s.	705.96
LM.9	*Art.E*	plot	no. individuals	no. individuals (Acc)	8.80E-06	n.s.	707.82
LM.10	*Art.E*	plot	no. individuals	no. individuals (Epi) + no. individuals (Acc)	0.0218	n.s.	707.84
LM.11	*Art.E*	plot	no. individuals	no. individuals (Epi) + no. individuals (Acc) + plant cover	0.0305	n.s.	709.027
LM.12	*Art.E*	plot	no. individuals	(no. individuals (Epi) + no. individuals (Acc)) * plant cover	0.0348	n.s.	712.62
LM.13	*Art.E*	plot	no. individuals	no. species (Epi)	0.0149	n.s.	707.47
LM.14	*Art.E*	plot	no. individuals	no. species (Acc)	0.0126	n.s.	706.68
LM.15	*Art.E*	plot	no. individuals	no. species (Epi) + no. species (Acc)	0.0314	n.s.	706.94
LM.16	*Art.E*	plot	no. individuals	location + plant cover + trunk height + leaf base cover + no. individuals (Epi) + no. individuals (Acc)	0.1313	n.s.	700.26
LM.17	*Art.E*	plot	no. individuals	location + plant cover	0.1081	**	701.53
LM.18	*Art.E*	plot	$\log_e$ (no. individuals+1)	location	0.2433	***	219.71
LM.19	*Art.E*	plot	$\log_e$ (no. individuals+1)	age class	0.5969	n.s.	239.26
LM.20	*Art.E*	plot	$\log_e$ (no. individuals+1)	trunk height	0.0395	n.s.	239.17
LM.21	*Art.E*	plot	$\log_e$ (no. individuals+1)	main age	0.0734	**	235.94
LM.22	*Art.E*	plot	$\log_e$ (no. individuals+1)	plant cover	0.0744	**	235.84
LM.23	*Art.E*	plot	$\log_e$ (no. individuals+1)	leaf base cover	0.0438	*	234.81
LM.24	*Art.E*	plot	$\log_e$ (no. individuals+1)	organic matter	3.20E-05	n.s.	238.79
LM.25	*Art.E*	plot	$\log_e$ (no. individuals+1)	no. individuals (Epi)	0.0586	*	237.35
LM.26	*Art.E*	plot	$\log_e$ (no. individuals+1)	no. individuals (Acc)	0.0044	n.s.	242.4
LM.27	*Art.E*	plot	$\log_e$ (no. individuals+1)	no. individuals (Epi) + no. individuals (Acc)	0.074	*	237.88
LM.28	*Art.E*	plot	$\log_e$ (no. individuals+1)	no. individuals (Epi) + no. individuals (Acc) + plant cover	0.1553	**	231.61
LM.29	*Art.E*	plot	$\log_e$ (no. individuals+1)	(no. individuals (Epi) + no. individuals (Acc)) * plant cover	0.1752	**	233.47
LM.30	*Art.E*	plot	$\log_e$ (no. individuals+1)	no. species (Epi)	0.009	n.s.	241.99
LM.31	*Art.E*	plot	$\log_e$ (no. individuals+1)	no. species (Acc)	0.0288	n.s.	240.17
LM.32	*Art.E*	plot	$\log_e$ (no. individuals+1)	no. species (Epi) + no. species (Acc)	0.0426	n.s.	240.88
LM.33	*Art.E*	plot	$\log_e$ (no. individuals+1)	location + main age + plant cover + leaf base cover + No. individuals (Epi) + No. individuals (Acc)	0.3275	***	251.48
LM.34	*Art.E*	plot	$\log_e$ (no. individuals+1)	location + epiphyte cover	0.02703	***	218.43
LM.35	*Art.E*	plot	$\log_e$ (no. individuals+1)	location + epiphyte cover + main age	0.3174	***	214.43
LM.36	*Art.E*	plot	$\log_e$ (no. individuals+1)	location + main age	0.3044	***	214.43

Appendix 7.4: Linear models for number of arthropod individuals in the organic matter microhabitat (*Art.O*). Numbers of individuals in *Art.O* were standardized to number of individuals per 50 g organic matter (dry weight) per oil palm.

Model	Organism group	Level	Response var.	Explanatory var.	R2	p-value	AIC
LM.1	*Art.O*	oil palm	no. individuals	location	0.0824	n.s.	557.32
LM.2	*Art.O*	oil palm	no. individuals	age class	0.0345	n.s.	559.65
LM.3	*Art.O*	oil palm	no. individuals	main age	0.0047	n.s.	559.05
LM.4	*Art.O*	oil palm	no. individuals	plant cover	0.049	n.s.	556.96
LM.5	*Art.O*	oil palm	no. individuals	leaf base cover	0.0102	n.s.	558.8
LM.6	*Art.O*	oil palm	no. individuals	trunk height to meristem	0.0042	n.s.	559.08
LM.7	*Art.O*	oil palm	$\log_e$ (no. individuals + 1)	location	0.1072	n.s.	165.12
LM.8	*Art.O*	oil palm	$\log_e$ (no. individuals + 1)	age class	0.1366	*	163.63
LM.9	*Art.O*	oil palm	$\log_e$ (no. individuals + 1)	main age	0.1622	**	160.24
LM.10	*Art.O*	oil palm	$\log_e$ (no. individuals + 1)	plant cover	0.169	**	159.87
LM.11	*Art.O*	oil palm	$\log_e$ (no. individuals + 1)	leaf base cover	0.0703	n.s.	165.03
LM.12	*Art.O*	oil palm	$\log_e$ (no. individuals + 1)	trunk height to meristem	0.1956	**	158.37
LM.13	*Art.O*	oil palm	$\log_e$ (no. individuals + 1)	trunk height to meristem + plant cover	0.2641	**	156.28
LM.14	*Art.O*	oil palm	$\log_e$ (no. individuals + 1)	wet weight (UNJA)	0.0517	n.s.	556.83
LM.15	*Art.O*	oil palm	$\log_e$ (no. individuals + 1)	wet weight (UNJA)	0.2473	***	155.32
LM.16	*Art.O*	oil palm	$\log_e$ (no. individuals + 1)	trunk height to meristem + plant cover + wet weight (UNJA)	0.3148	**	154.94
LM.17	*Art.O*	oil palm	$\log_e$ (no. individuals + 1)	plant cover + wet weight (UNJA)	0.257	**	156.72

Appendix 7.5: Linear models for number of epiphyte (*Epi*) species.

Model	**Organism group**	**Level**	**Response variable**	**Predictor(s)**	**R^2**	**p-value**	**AIC**
LM.1	*Epi*	oil palm	no. species	location	0.0231	n.s.	234.08
LM.2	*Epi*	oil palm	no. species	age class	0.5036	***	197.52
LM.3	*Epi*	oil palm	no. species	main age	0.2231	***	219.71
LM.4	*Epi*	oil palm	no. species	trunk height to meristem	0.3526	***	209.86
LM.5	*Epi*	oil palm	no. species	plant cover	0.0035	n.s.	233.15
LM.6	*Epi*	oil palm	no. species	leaf base cover	0.0202	n.s.	232.24
LM.7	*Epi*	oil palm	no. species	age class * trunk height meristem	0.5512	***	198.0795
LM.8	*Epi*	oil palm	$\log_e$ (no. species+1)	location	0.0245	n.s.	85.11
LM.9	*Epi*	oil palm	$\log_e$ (no. species+1)	age class	0.4828	***	50.84
LM.10	*Epi*	oil palm	$\log_e$ (no. species+1)	main age	0.2314	***	70.23
LM.11	*Epi*	oil palm	$\log_e$ (no. species+1)	trunk height to meristem	0.3379	***	62.17
LM.12	*Epi*	oil palm	$\log_e$ (no. species+1)	plant cover	0.0005	n.s.	84.42
LM.13	*Epi*	oil palm	$\log_e$ (no. species+1)	leaf base cover	0.0344	n.s.	82.55
LM.14	*Epi*	oil palm	$\log_e$ (no. species+1)	age class * trunk height meristem	0.5085	***	54.09
LM.15	*Epi*	oil palm	$\log_e$ (no. species+1)	age class + location	0.5073	***	52.22
LM.16	*Epi*	plot	no. species	location	0.0064	n.s.	397.23
LM.17	*Epi*	plot	no. species	age class	0.0696	*	389.34
LM.18	*Epi*	plot	no. species	trunk height	0.0012	n.s.	395.85
LM.19	*Epi*	plot	no. species	main age	0.0523	*	389.56
LM.20	*Epi*	plot	no. species	no. individuals (Epi)	0.3377	***	346.55
LM.21	*Epi*	plot	no. species	plant cover	0.1784	***	372.42
LM.22	*Epi*	plot	no. species	leaf base cover	0.0853	**	378.2
LM.23	*Epi*	plot	no. species	organic matter	0.0037	n.s.	393.241
LM.24	*Epi*	plot	no. species	no. individuals (Epi) + age class + plant cover + leaf base cover	0.5139	***	310.9775
LM.25	*Epi*	plot	$\log_e$ (no. species+1)	location	0.0016	n.s.	197.6
LM.26	*Epi*	plot	$\log_e$ (no. species+1)	age class	0.0887	**	186.65
LM.27	*Epi*	plot	$\log_e$ (no. species+1)	trunk height	0.0017	n.s.	195.59
LM.28	*Epi*	plot	$\log_e$ (no. species+1)	main age	0.0723	**	186.78
LM.29	*Epi*	plot	$\log_e$ (no. species+1)	no. individuals (Epi)	0.3172	***	150.01
LM.30	*Epi*	plot	$\log_e$ (no. species+1)	plant cover	0.1944	***	169.84
LM.31	*Epi*	plot	$\log_e$ (no. species+1)	leaf base cover	0.1141	***	177.8
LM.32	*Epi*	plot	$\log_e$ (no. species+1)	organic matter	0.0078	n.s.	194.27
LM.33	*Epi*	plot	$\log_e$ (no. species+1)	age class + number of individuals (Epi) + plant cover + leaf base cover	0.5125	***	114.73
LM.34	*Epi*	plot	$\log_e$ (no. species+1)	age class + number of individuals (Epi) + plant cover	0.5047	***	117.49
LM.35	*Epi*	plot	$\log_e$ (no. species+1)	age class + number of individuals (Epi) * plant cover	0.507	***	118.92
LM.36	*Epi*	plot	$\log_e$ (no. species+1)	number of individuals (Epi) + plant cover	0.4228	***	131.83
LM.37	*Epi*	plot	$\log_e$ (no. species+1)	age class * leafbase cover + no. individuals (Epi) * plant cover	0.515	***	116.11

Appendix 7.6: Linear models for number of accidental epiphyte (*Acc*) species.

Model	Organism group	Level	Response variable	Predictor(s)	R^2	p-value	AIC
LM.1	*Acc*	oil palm	no. species	location	0.0886	.	212.17
LM.2	*Acc*	oil palm	no. species	age class	0.3245	***	196
LM.3	*Acc*	oil palm	no. species	main age	0.2108	***	202.4
LM.4	*Acc*	oil palm	no. species	trunk height to meristem	0.1861	**	204.06
LM.5	*Acc*	oil palm	no. species	plant cover	0.1578	**	205.91
LM.6	*Acc*	oil palm	no. species	leaf base cover	0.3288	***	194.46
LM.7	*Acc*	oil palm	no. species	age class + leaf base cover	0.3469	***	196.17
LM.8	*Acc*	oil palm	$\log_e$ (no. species+1)	location	0.04258	n.s.	69.07
LM.9	*Acc*	oil palm	$\log_e$ (no. species+1)	age class	0.3669	***	46.74
LM.10	*Acc*	oil palm	$\log_e$ (no. species+1)	main age	0.2758	***	52
LM.11	*Acc*	oil palm	$\log_e$ (no. species+1)	trunk height to meristem	0.2529	***	53.68
LM.12	*Acc*	oil palm	$\log_e$ (no. species+1)	plant cover	0.1329	**	61.72
LM.13	*Acc*	oil palm	$\log_e$ (no. species+1)	leaf base cover	0.4107	***	40.86955
LM.14	*Acc*	oil palm	$\log_e$ (no. species+1)	age class + leaf base cover	0.4334	***	43.78
LM.15	*Acc*	oil palm	$\log_e$ (no. species+1)	age class * leaf base cover	0.4224	***	43.78
LM.16	*Acc*	oil palm	$\log_e$ (no. species+1)	main age + leaf base cover	0.4128	***	42.68
LM.17	*Acc*	oil palm	$\log_e$ (no. species+1)	main age + leaf base cover + plant cover	0.4512	***	41.03
LM.18	*Acc*	plot	no. species	location	0.0082	n.s.	351.84
LM.19	*Acc*	plot	no. species	age class	0.576	***	249.87
LM.20	*Acc*	plot	no. species	trunk height	0.1723	***	328.14
LM.21	*Acc*	plot	no. species	main age	0.4217	***	285.12
LM.22	*Acc*	plot	no. species	no. individuals (Acc)	0.6591	***	221.69
LM.23	*Acc*	plot	no. species	plant cover	0.1898	***	325.57
LM.24	*Acc*	plot	no. species	leaf base cover	0.1575	***	328.19
LM.25	*Acc*	plot	no. species	organic matter	0.0286	n.s.	345.13
LM.26	*Acc*	plot	no. species	no. individuals (Acc) + age class + plant cover + leaf base cover + trunk heiht	0.7376	***	199.39
LM.27	*Acc*	plot	no. species	age class + no. individuals (Acc) + plant cover	0.7294	***	199.99
LM.28	*Acc*	plot	no. species	age class + no. individuals (Acc) * plant cover	0.7321	***	200.79
LM.29	*Acc*	plot	$\log_e$ (no. species+1)	location	0.0088	n.s.	176.8084
LM.30	*Acc*	plot	$\log_e$ (no. species+1)	age class	0.5657	***	77.78
LM.31	*Acc*	plot	$\log_e$ (no. species+1)	trunk height	0.1868	***	151.06
LM.32	*Acc*	plot	$\log_e$ (no. species+1)	main age	0.453	***	103.48
LM.33	*Acc*	plot	$\log_e$ (no. species+1)	no. individuals (Acc)	0.6346	***	55.06
LM.34	*Acc*	plot	$\log_e$ (no. species+1)	plant cover	0.1755	***	152.71
LM.35	*Acc*	plot	$\log_e$ (no. species+1)	leaf base cover	0.1936	***	149.37
LM.36	*Acc*	plot	$\log_e$ (no. species+1)	organic matter	0.0342	*	170.84
LM.37	*Acc*	plot	$\log_e$ (no. species+1)	age class + trunk height + no. individuals (Acc) + plant cover + leaf base cover + organic matter	0.7296	***	31.73
LM.38	*Acc*	plot	$\log_e$ (no. species+1)	age class + trunk height + no. individuals (Acc.) + plant cover	0.7256	***	28.7
LM.39	*Acc*	plot	$\log_e$ (no. species+1)	age class + no. individuals (Acc) + plant cover	0.7128	***	32.16
LM.40	*Acc*	plot	$\log_e$ (no. species+1)	age class + no. individuals (Acc) * plant cover	0.5994	***	74.09
LM.41	*Acc*	plot	$\log_e$ (no. species+1)	age class + no. individuals (Acc)	0.699	***	35.81
LM.42	*Acc*	plot	$\log_e$ (no. species+1)	age class + no. individuals + leaf base cover	0.7017	***	37.02
LM.43	*Acc*	plot	$\log_e$ (no. species+1)	age class + trunk height + no. individuals (Acc.) * plant cover	0.7396	***	24.4

Appendix 7.7: Linear models for number of arthropod taxa in the epiphyte microhabitat (*Art.E*).

Model	Organism group	Level	Response variable	Predictor(s)	R^2	p-value	AIC
LM.1	*Art.E*	plot	no. taxa	location	0.1793	***	291.09
LM.2	*Art.E*	plot	no. taxa	age class	0.04875	n.s.	304.38
LM.3	*Art.E*	plot	no. taxa	trunk height	0.0446	*	302.77
LM.4	*Art.E*	plot	no. taxa	main age	0.0585	*	301.45
LM.5	*Art.E*	plot	no. taxa	no. individuals (Art.E)	0.1313	***	294.21
LM.6	*Art.E*	plot	no. taxa	plant cover	0.0858	**	298.79
LM.7	*Art.E*	plot	no. taxa	leaf base cover	0.059	*	297.09
LM.8	*Art.E*	plot	no. taxa	organic matter	0.0072	n.s.	301.86
LM.9	*Art.E*	plot	no. taxa	no. individuals (Epi)	0.0375	n.s.	303.43
LM.10	*Art.E*	plot	no. taxa	no. individuals (Acc)	0.0082	n.s.	306.13
LM.11	*Art.E*	plot	no. taxa	no. individuals (Epi) + no. individuals (Acc)	0.0565	n.s.	303.64
LM.12	*Art.E*	plot	no. taxa	no. individuals (Epi) + no. individuals (Acc) + plant cover	0.1437	**	296.91
LM.13	*Art.E*	plot	no. taxa	(no. individuals (Epi) + no. individuals (Acc)) * plant cover	0.1708	**	298.02
LM.14	*Art.E*	plot	no. taxa	no. species (Epi)	0.0054	n.s.	306.38
LM.15	*Art.E*	plot	no. taxa	no. species (Acc)	0.02	n.s.	305.06
LM.16	*Art.E*	plot	no. taxa	no. species (Epi) + no. species (Acc)	0.0285	n.s.	306.27
LM.17	*Art.E*	plot	no. taxa	location + plant cover + trunk height + leaf base cover + no. individuals (Epi) + no. individuals (Acc) + no. individuals (ArtE)	0.3084	***	203.68
LM.18	*Art.E*	plot	no. taxa	location + plant cover + no. individuals (Art.E)	0.2781	***	283.54
LM.19	*Art.E*	plot	no. taxa	location + plant cover	0.2204	***	288.47
LM.20	*Art.E*	plot	no. taxa	location + no. individuals (Art.E)	0.2373	***	286.49
LM.21	*Art.E*	plot	$\log_e$ (no. taxa + 1)	location	0.1836	***	113.8
LM.22	*Art.E*	plot	$\log_e$ (no. taxa + 1)	age class	0.0567	n.s.	126.81
LM.23	*Art.E*	plot	$\log_e$ (no. taxa + 1)	trunk height	0.0416	n.s.	126.24
LM.24	*Art.E*	plot	$\log_e$ (no. taxa + 1)	main age	0.0591	*	124.57
LM.25	*Art.E*	plot	$\log_e$ (no. taxa + 1)	no. individuals (Art.E)	0.1257	***	117.96
LM.26	*Art.E*	plot	$\log_e$ (no. taxa + 1)	plant cover	0.0933	**	121.24
LM.27	*Art.E*	plot	$\log_e$ (no. taxa + 1)	leaf base cover	0.0528	**	121.06
LM.28	*Art.E*	plot	$\log_e$ (no. taxa + 1)	organic matter	0.0082	n.s.	125.15
LM.29	*Art.E*	plot	$\log_e$ (no. taxa + 1)	no. individuals (Epi)	0.0396	n.s.	126.43
LM.30	*Art.E*	plot	$\log_e$ (no. taxa + 1)	no. individuals (Acc)	0.0167	n.s.	128.54
LM.31	*Art.E*	plot	$\log_e$ (no. taxa + 1)	no. individuals (Epi) + no. individuals (Acc)	0.0715	*	125.38
LM.32	*Art.E*	plot	$\log_e$ (no. taxa + 1)	no. individuals (Epi) + no. individuals (Acc) + plant cover	0.1595	**	118.42
LM.33	*Art.E*	plot	$\log_e$ (no. taxa + 1)	(no. individuals (Epi) + no. individuals (Acc)) * plant cover	0.1893	**	119.17
LM.34	*Art.E*	plot	$\log_e$ (no. taxa + 1)	no. species (Epi)	0.0059	n.s.	129.53
LM.35	*Art.E*	plot	$\log_e$ (no. taxa + 1)	no. species (Acc)	0.0301	n.s.	127.31
LM.36	*Art.E*	plot	$\log_e$ (no. taxa + 1)	no. species (Epi) + no. species (Acc)	0.0401	n.s.	128.38
LM.37	*Art.E*	plot	$\log_e$ (no. taxa + 1)	location + plant cover + trunk height + leaf base cover + no. individuals (Epi) + no. individuals (Acc) + no. individuals (ArtE)	0.3159	***	106.1
LM.38	*Art.E*	plot	$\log_e$ (no. taxa + 1)	location + no. individuals (Art.E) + plant cover	0.2839	***	106.01
LM.39	*Art.E*	plot	$\log_e$ (no. taxa + 1)	location + plant cover	0.2301	***	110.53

Appendix 7.8: Linear models for number of arthropod taxa in the organic matter microhabitat (*Art.O*). Numbers of taxa in *Art.O* were standardized to number of taxa per 50 g organic matter (dry weight) per oil palm.

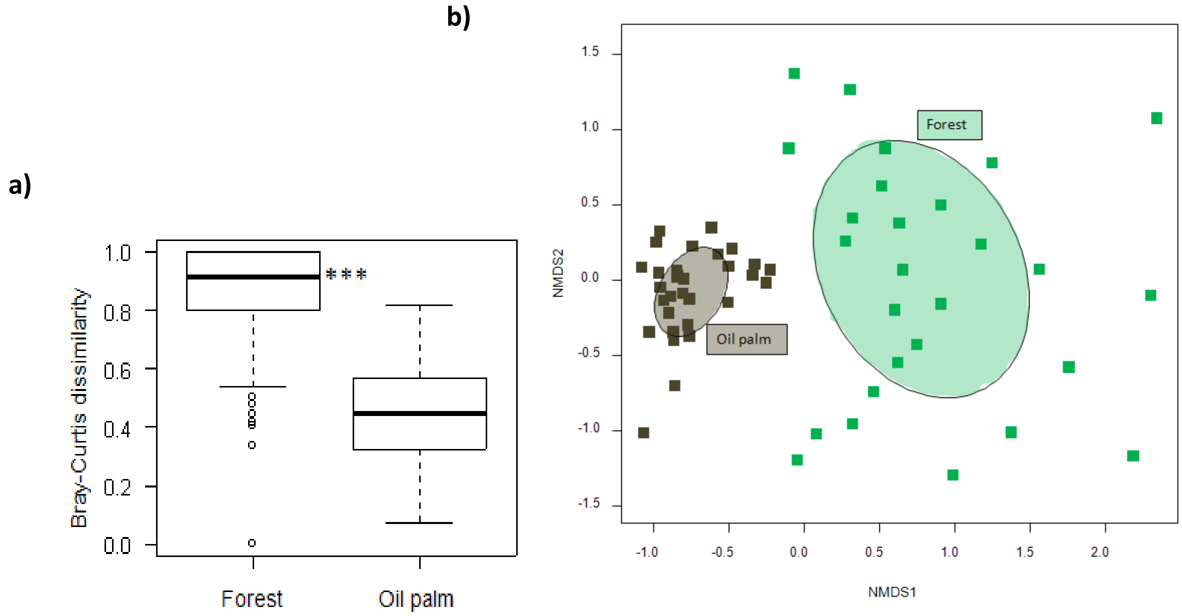
Model	**Organism group**	**Level**	**Response var.**	**Predictor(s)**	**R2**	**p-value**	**AIC**
LM.1	*Art.O*	oil palm	no. taxa	location	0.01277	n.s.	318.72
LM.2	*Art.O*	oil palm	no. taxa	age class	0.1412	*	312.32
LM.3	*Art.O*	oil palm	no. taxa	main age	0.1633	**	309.118
LM.4	*Art.O*	oil palm	no. taxa	plant cover	0.0401	n.s.	315.44
LM.5	*Art.O*	oil palm	no. taxa	leaf base cover	0.0695	n.s.	314.01
LM.6	*Art.O*	oil palm	no. taxa	trunk height to meristem	0.1789	**	308.25
LM.7	*Art.O*	oil palm	no. taxa	no. individuals	0.565	***	279.03
LM.8	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	main age + no. individuals	0.6898	***	265.48
LM.9	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	location	0.0127	n.s.	122.06
LM.10	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	age class	0.319	***	104.98
LM.11	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	main age	0.3787	***	98.76
LM.12	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	plant cover	0.0546	n.s.	118.07
LM.13	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	leaf base cover	0.1453	**	113.43
LM.14	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	no. individuals	0.1069	**	109.99
LM.15	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	$\log_e$ (no. individuals + 1)	0.5485	***	84.07
LM.16	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	trunk height to meristem	0.4151	***	95.99
LM.17	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	$\log_e$ (no. individuals + 1) + age class + main age + trunk height to meristem + leaf base cover	0.687	***	77.21
LM.18	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	$\log_e$ (no. individuals + 1) + main age + trunk height to meristem + leaf base cover	0.6796	***	74.297
LM.19	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	$\log_e$ (no. individuals + 1) + trunk height to meristem + leaf base cover	0.6733	***	73.2
LM.20	*Art.O*	oil palm	$\log_e$ (no. taxa + 1))	$\log_e$ (no. individuals + 1) + trunk height to meristem	0.6732	***	71.2
LM.21	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	$\log_e$ (no. individuals + 1) + main age	0.6686	***	71.85
LM.22	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	$\log_e$ (no. individuals + 1) + age class	0.6809	***	72.11
LM.23	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	wet weight (UNJA)	0.2619	***	303.35
LM.24	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	wet weight (UNJA)	0.4411	***	93.9
LM.25	*Art.O*	oil palm	$\log_e$ (no. taxa + 1))	wet weight (UNJA) + $\log_e$ (no. individuals + 1) + main age + leaf base cover	0.7068	***	70.22
LM.26	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	wet weight (UNJA) + $\log_e$ (no. individuals + 1) + main age + leaf base cover + trunk height to meristem	0.7068	***	72.22
LM.27	*Art.O*	oil palm	$\log_e$ (no. taxa + 1)	wet weight (UNJA) + $\log_e$ (no. individuals + 1) + main age	0.7039	***	68.66

Appendix 8: Linear mixed effect models (LMEs) – Null models

Appendix 8.1: Null models for linear mixed-effect models. Null models only include random effects, but no fixed effects. Random effects at the oil palm level: 1 | Location / Plantation.ID / Oilpalm.ID; random effects at the plot level: 1 | Location / Plantation.ID / Oilpalm.ID / Plot.ID. The table shows the percentage of the total variance (Var) explained by different spatial levels in the spatially-nested sampling. Numbers of individuals and taxa in *Art.O* were standardized to number of individuals and taxa per 50 g organic matter (dry weight) per oil palm. Abbreviations: *Epi* = epiphytes, *Acc* = accidental epiphytes, *Art.E* = arthropods on epiphytes, *Art.O* = Arthropods in organic matter in leaf axils of oil palm trunks.

Organism group	level	Response variable	$Var_{Location}$	$Var_{Plantation}$	$Var_{Oil\ palm}$	Var_{Plot}	$Var_{Residuals}$	Var_{total}
Epi	oil palm	log(no. species + 1)	5.39E-10	0.13	0.13	NA	1.94E-04	**0.27**
Epi	plot	log(no. species + 1)	2.77E-10	0.02	5.36E-11	0.27	4.40E-06	**0.29**
Epi	plot	log(no. individuals + 1)	0.06	0.15	1.27E-08	1.00	1.89E-03	**1.21**
Acc	oil palm	log(no. species + 1)	9.05E-10	0.09	0.11	NA	1.83E-04	**0.20**
Acc	plot	log(no. species + 1)	3.19E-09	0.24	0.01	0.10	4.68E-04	**0.35**
Acc	plot	log(no. individuals + 1)	6.97E-09	0.65	0.01	0.16	7.88E-04	**0.82**
Art.E	plot	log(no. taxa + 1)	0.05	0.01	0.01	0.17	1.32E-03	**0.24**
Art.E	plot	log(no. individuals)	0.26	9.51E-10	0.03	0.51	9.11E-04	**0.79**
Art.O	oil palm	log(no. taxa + 1)	2.84E-09	0.26	0.51	NA	7.08E-04	**0.77**
Art.O	oil palm	log(no. individuals + 1)	0.06	0.62	1.30	NA	0.19	**2.17**

Appendix 9: Composition of epiphyte species in oil palm plantations and in a lowland rainforest (Bukit Duabelas), Jambi Province, Sumatra



Appendix 9.1: 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. Figure and text by (Altenhövel 2013).

Hiermit erkläre ich, Judith Krobbach, dass ich die vorliegende Arbeit selbstständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt sowie Zitate kenntlich gemacht habe.

Göttingen, den 14.02.2014