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– CENTRE OF BIODIVERSITY AND SUSTAINABLE LAND-USE –

# The effect of climate variability on pollen rain-vegetation relationship in different rainforest and transformation systems in Sumatra, Indonesia

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# 1. Abstract

Sumatran rainforest ecosystems form a centre of biodiversity and endemism with manifold landscape and vegetation formations. However, during the past decades, Sumatran rainforest underwent a rapid transformation especially towards monocultures such as oil palm or rubber plantations. Climate is another important driver of ecosystem alteration. The effect of inter-annual climate variability, such as the El Niño Southern Oscillation (ENSO) is strongly influencing plant phenology and reproductive success of many species and needs to be understood. Modern pollen rain studies are essential to investigate the role of this climate variability on the palynological composition and diversity in Sumatran ecosystems.

This study aims to examine the after-effect of El Niño on the pollen production and palynological diversity in different rainforest and land-use transformation systems of Sumatra for two consecutive years 2016 and 2017. Furthermore, a synthesis with previous studies has been done to complete a five-year data set (2013-2017) and to monitor the long-term effects of ENSO on the vegetation's reproductive success and diversity patterns.

In the first year after the ENSO, the palynological composition in forest and jungle rubber agroforestry changed due to an increase in secondary forest vegetation and a decrease in primary forest in reaction to ENSO-related drought and fire activity. Pollen and spore accumulation (influx) increased due to a dominance of high pollen producers, whereby diversity ( $\alpha$ -,  $\beta$ - and  $\gamma$ -diversity) decreased significantly. In 2017 the secondary forest components re-established. Pollen and spore influx decreased slightly, and diversity increased significantly. No clear effects of the ENSO on land-use transformation systems could be determined, as the anthropogenic level of disturbance is too high.

From 2013 until 2017 the palynological composition and diversity changed annually. In 2014 influx and diversity measures decreased strongly and increased in the following year 2015, which might be related to the general flowering event. 2016 was generally marked by a decrease in palynological diversity and an increase in influx. In 2017, the influx was lower, however diversity increased significantly.

Four phases of palynological changes could be distinguished in the years before, during and after the ENSO. 1) A phase of climatic stress accompanied by a decrease in diversity and influx. 2) A phase of general flowering triggered by the aseasonal climatic changes of the ENSO. 3) A phase of succession and competition after major disturbance. 4) A phase of recovery of primary forest components. Between land-use forms a clearly decreasing gradient of diversity is visible, with tendencies to decline even further in the long-term.

## 2. Introduction

The Malayan rainforest, one of the largest global rainforests, covers large forest areas of the Malayan Peninsula, Sumatra, and Borneo (Sundaland). Sumatra Island, with an area of 476,000km<sup>2</sup> is the second largest island of Sundaland after Borneo and the largest island in the Indonesian archipelago (LAUMONIER 2010). Being one of the world's biodiversity hotspots, Sumatra harbours a high species richness and rate of endemism (5% of the global total) (MITTERMEIER et al. 2011, MYERS et al. 2000). The islands manifold landscape, history of development, location in the tropical zone, climatic conditions and many other factors favour the formation of various highly diverse plant communities reaching from maritime mangrove forests to montane cloud forests (LAUMONIER 1997).

In most parts of the island the natural vegetation is formed by lowland rainforest ecosystems (LAUMONIER 1997). These ecosystems offer high biodiversity as well as important ecosystem services (EDWARDS et al. 2014, REMBOLD et al. 2017). However, a growing economy accompanied by extensive logging events, which started in 1970 has caused great land-use transformations and exploitation of Sumatra's natural forests. In particular, the palm oil and rubber industry increased massively during the past decades, promoting the spread of oil palm (*Elaeis guineensis*) monocultures (Fig. 4) and rubber tree (*Hevea brasiliensis*) plantations (Fig. 3) throughout the island (DRESCHER et al. 2016). With increasing transformation towards monocultures and intensive land-use, biodiversity decreases heavily while ecosystem services are reduced (DISLICH et al. 2017, MURDIYARSO et al. 2002, REMBOLD et al. 2017).

However, the growing economy is not the only factor which influenced changes in Sumatran forest ecosystems. Climate is another important driver which plays a major role on the ecosystem change. Changing climatic conditions such as elongated drought events, fire and more frequent ENSO events, in combination with land-use transformation and their side effects, led to the ecological imparity of the rainforest ecosystem (Yaeger et al. 2003, Sze et al. 2019, REMBOLD et al. 2017, IPCC 2014, FREDRIKSSON et al. 2006). Climate plays an important role on the vegetation's reproductive success and directly affects plant dispersal and survival. Major changes can already be seen on the vegetation and its reproductive system, yet the extend of climatic impacts, such as the ENSO phenomenon on plant dispersal and survival in Sumatran rainforest needs to be further investigated to predict future changes of this ecosystem.

The Collaborative Research Centre (CRC) 990, an international collaboration research project between Indonesia and Germany, aims to study the effects of such land-use conversion on tropical ecosystems and their biodiversity through the *Ecological and Socio-economic Functions of Tropical Lowland Rainforest Transformation Systems* project (EFForTS) since 2012 (DRESCHER et al. 2016). The project focuses on the East Sumatran region of Jambi, being a representable study site where different land-use forms and natural ecosystems are monitored (Fig. 1).

One section of the research project examines modern pollen and spore rain to assess the influence of land-use and climate on the vegetations reproductive system. Pollen and spores offer deep insights into a landscape's diversity and its vegetation structure. Furthermore, the effect of human impact, landscape transformation and climatic changes can be monitored (SUGITA 2007, MATTHIAS et al. 2015). The analysis of modern pollen and spore rain has been proven to be a useful tool in ecosystems, where richness and evenness are difficult to monitor over a longer time period due to their inaccessibility and complex structure such as tropical forests (MATTHIAS et al. 2015). Since identifying common genera and families occur to show the same results in species richness as a detailed survey on plant species (MAZARIS et al. 2010) the identification of pollen and spores appears to be an accessible method.

The combination of landscape fragmentation and climate change causes an increase in severe ENSO-related droughts, followed by forest fires. Thus, the effect of ENSO on the vegetation, through a correlating factor such as pollen and spore production in natural rainforest and the overall present major land-use systems gains in importance and needs to be understood. This can give key information about the long-term effect of climate on vegetation reproduction in rainforests and different land-use transformation systems in Sumatran ecosystems. Furthermore, it can offer helpful material for the palynological interpretation of environmental archives.

## 2.1. Previous Studies

Since 2013, pollen traps related to the EFForTS project have been installed in different rainforest and transformation systems (EFForTS core plots) to collect pollen rain for each year. The pollen rain from 2013 for rainforest and transformation systems have been studied in a master thesis by Katharina Reuter (KR) in 2015. The results show that pollen and spore assemblages of modern pollen and spore rain are affected by land-use change and that patterns of landscape heterogeneity or landscape homogeneity are reflected in pollen and spore rain. By comparing measures of palynological and floristic diversity, patterns can be found which are driven by land-use conversion. The study results have revealed that conversion of tropical lowland rainforest to intensively managed land-use systems, oil palm monocultures in particular, causes a loss in both diversity and influx of pollen and spore rain and thus genetic dispersion might be inhibited/limited.

Pollen rain data from the lowland rainforest ecosystem from the year of 2014 and 2015 were studied by Lena-Marie Holtorf (LH) in her bachelor thesis in 2020. This study aimed to investigate pollen production and diversity in rainforest system to understand the role of climate variability (e.g. the ENSO event) on the vegetation composition, in particular the association of El Niño with mass flowering events. The results show that palynological diversity patterns were affected by the differences in climate conditions. El Niño conditions during most of the period 2015/16 are likely to have influenced the observed differences in flowering magnitude, either by triggering a

dipterocarp-led general flowering event or by supporting a more general increase in flowering magnitude. The study shows that pollen rain from two consecutive years (regular vs. El Niño year) can already reflect the effect of El Niño on pollen production and diversity related to mass flowering. However, further studies are needed to confirm this pattern. A long-term analysis of pollen rain is necessary to investigate the characteristic inter-annual climate variability of tropical lowland ecosystems.

### 3. Study Aims

Analysing the effect of changing climatic conditions or other driving factors such as land-use transformation in Sumatra's natural forest ecosystems allows not only to assess changes in floristic diversity patterns over a long time period and with a greater dataset but also offers material for the interpretation of environmental archives of Sumatra. The impact of inter-annual climatic oscillations can be observed on a continuous time series, to study before and after-effects of the ENSO event on the vegetation's reproductive system and diversity in Sumatra.

The main aim of the present study is to investigate the after-effect of ENSO on the pollen production and palynological diversity in the different rainforest and land-use transformation systems in Sumatra. Furthermore, I will integrate the data from previous studies (KR and LH), completing a dataset of five years (2013-2017) to provide a better understanding of the long-term effect of climatic events on the vegetation's reproductive success and diversity patterns. In particular, I ask the following research questions:

- I. What is the after-effect of the ENSO on palynological composition in different rainforest and land-use transformation systems?
- II. Do diversity patterns change between different agro-forestry management systems after the ENSO event?
- III. Do diversity and pollen production change before and after the influence of ENSO in rainforest ecosystems?

By studying the long terms patterns of pollen and spore rain in different rainforest and land-use systems, I hope to prove or falsify the following hypotheses:

- I. The after-effects of El Niño on the palynological composition are seen in all rainforest and transformation systems.
- II. The influence of different land-use management strategies on palynological diversity increased after the ENSO event.
- III. Inter-annual climatic events such as ENSO have long-term effects on modern pollen and spore rain: the pollen production and palynological diversity and species patterns change before and after the influence of ENSO.

This will forward the overall comprehension of the vegetations reaction to climatic changes and structural alteration in Sumatran ecosystems, focussing on plants' dispersal and reproductive success. Providing the longest monitoring of modern airborne pollen of southeast (SE) Asia with a five year dataset (2013-2017) including a period of the ENSO phenomenon, this is the first study in SE Asia to understand the phenological variation in pollen production and dispersal pattern related to a major climatic event in different rainforest and transformation systems. This will contribute to a better understanding of ecosystem functionality and stability under major climatic and anthropogenic stress-factors.

## 4. Study region

This study was conducted in two tropical lowland rainforests in Jambi province, Sumatra (Indonesia), as part of the CRC 990 project, subproject A01. In general, the subproject investigates the long-term vegetation changes, plant phenology and plant-pollinator interactions in rain forest and rain forest transformation systems of central Sumatra.

The study area is located in two different landscapes of the Jambi Province: Bukit Duabelas and Harapan. Bukit Duabelas (BD) lies about 110km westwards and Harapan (HR) is located 60km southwards of the province's capital city "Jambi city" (ALLEN et al. 2015; Figure 1). The plots are established in different rainforest ("Bukit Duabelas National Park" and "Harapan rainforest") and transformation systems (oil palm plantations, rubber plantations and rubber agroforests under natural tree cover, further referred to as "jungle rubber") in both regions. Per landscape four replicate plots have been selected, resulting in a total of eight plots, and an overall total of 32 plots (Fig. 2). Each plot measures 50m x 50m and a minimum distance of 200m was kept between the plots (ALLEN et al. 2015). Plots are located at an elevation of 50 to 100m above sea level (GUILLAUME et al. 2015).

### 4.1. Climate

The climate on the equatorial tropical island of Sumatra is fully humid (KOTTEK et al. 2006) with a mild dry period in July and August and two periods of high precipitation in December and March (DRESCHER et al. 2016). The driest month can be associated with the south-eastern monsoon, whereas the rainy season occurs during the influence of the north-eastern monsoon (TAN 2008). The regions mean annual temperature is  $26.7 \pm 1.0^{\circ}\text{C}$  and the mean annual precipitation is  $2235 \pm 385$  mm (ALLEN et al. 2015).

Inter-annual climate variability is driven by the El Niño Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD) (BIAGIONI et al. 2015; WEBSTER et al. 1999).

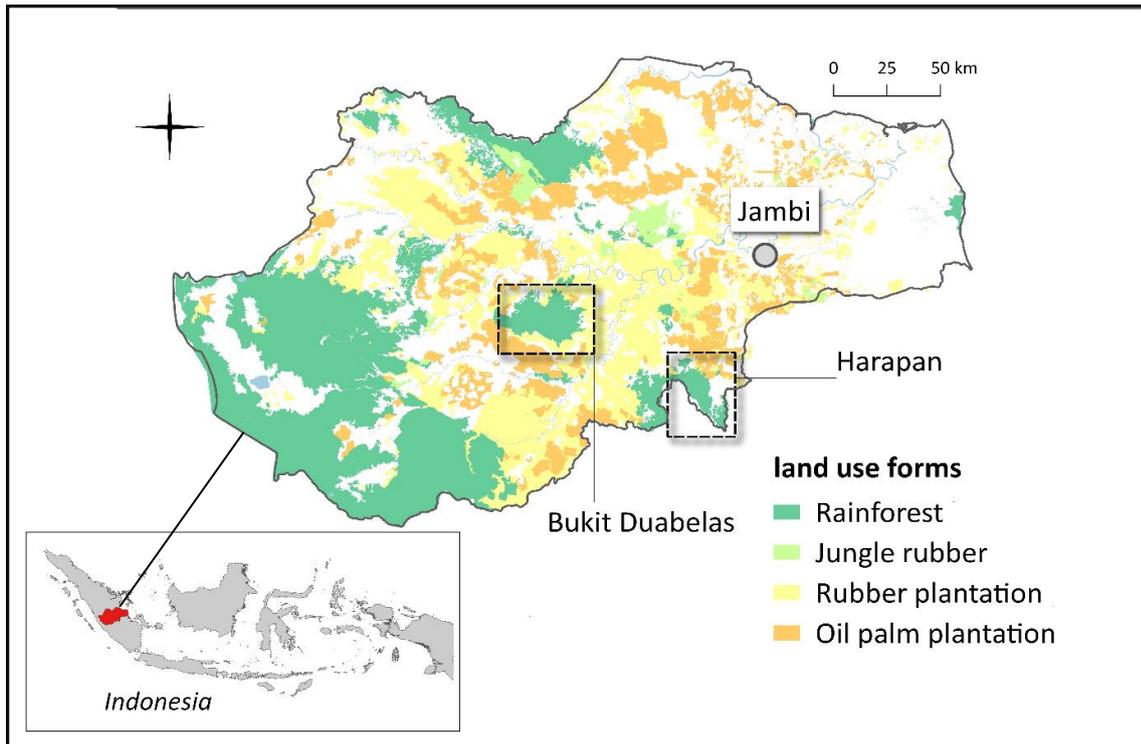


Figure 1: Location of the study region on the island of Sumatra, Indonesia. Jambi Province marked in red and magnified: Coverage of the four investigated land-use forms (Rainforest, Jungle rubber, Rubber, Oil palm) in the Province of Jambi and both natural forest remnants “Bukit Duabelas” and “Harapan” highlighted. Creation of the map was carried out in QGIS version 3.10.3-A Coruña.

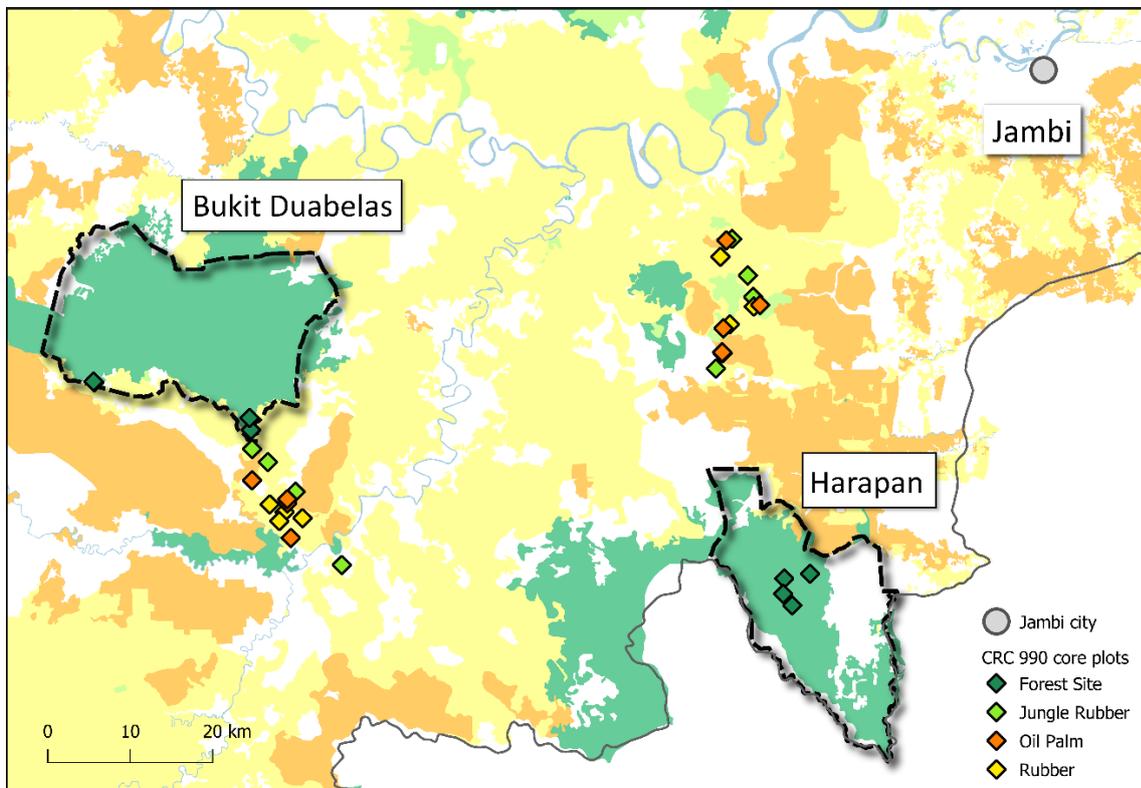


Figure 2: Both landscapes (Bukit Duabelas, left; Harapan, right) and location of core plots in close-up. CRC 990 core plots are marked with a diamond, coloured after land-use form. The border of natural forest remnant is drawn with a dashed line. Creation of the map was carried out in QGIS version 3.10.3-A Coruña.

The initiation of the ENSO phenomenon (MANTON & STEVENSON 2014) occurred from April 2015 to May 2016 where the area was affected by a strong El Niño episode which peaked in November 2015 (ISKANDAR et al. 2017). Drought correlated to such climate anomalies may have strong effects on Indonesia's ecosystems, (ERASMI et al. 2009, FREDRIKSSON et al. 2006, HOLMGREN et al. 2001), such as the mass-fruiting of the Dipterocarpaceae, a unique phenological behaviour of this family in SE Asia (SAKAI et al. 2006, WILLIAMSON & ICKES 2002). The IOD also plays a major role (MANTON & STEVENSON 2014), causing a dry period in summer.

## 4.2. Vegetation

Located within the zone of humid tropical forest, Sumatra offers a variety of landscapes. Its great altitudinal and longitudinal gradient, as well as its island characteristics allow various ecosystems to be formed. Five major ecological zones can be identified, mainly running from Northwest to Southeast: The west-coast, the Mountain, the Piedmont, the Peneplain and the Swamp zone (MURDIYARSO et al. 2002).

The region of Jambi however mainly consists of Peneplain of dense evergreen lowland natural rainforest primarily dominated by the Dipterocarpaceae family (e.g. genus *Shorea*, *Dipterocarpus* and *Parashorea*) with Myrtaceae (e.g. genus *Syzygium*), Burseraceae (e.g. genus *Canarium*) and Euphorbiaceae (e.g. genus *Croton*) standing out as well (LAUMONIER 1997, REMBOLD & KREFT 2015). Dipterocarpaceae occur in high density, which makes the Sumatran lowland dipterocarp rainforest the only forest ecosystem in the world with such a highly represented canopy forming tree family, comprising 112 species of which 11 are endemic (WHITTEN et al. 1987). Secondary forest is dominated by pioneer species, competing during gap formation with undergrowth and recruited seedlings of emergent primary forest trees. Common pioneers belong e.g. to the genera of *Mallotus* (Euphorbiaceae), *Macaranga* (Euphorbiaceae), *Trema* (Cannabaceae) and *Melastoma* (Melastomataceae) (CORLETT 1991, LAUMONIER 1997, WHITTEN et al. 1987). Gap formation and natural succession belong to the forest's natural growth cycle. However, selective logging and forest transformation may alter the relation of secondary to primary forest by triggering artificial gap formation and disturbance (LAUMONIER 1997).

The lowland Dipterocarp forest has been greatly converted into agricultural areas (Fig. 1) (LAUMONIER 1997, MURDIYARSO et al. 2002) of cash crop tree plantations, such as *Hevea brasiliensis* (Fig. 3) and *Elaeis guineensis* (Fig. 4).



Figure 4: Core plot within plantations of *Hevea brasiliensis* (rubber tree). Picture taken in September 2019 by Svea Jahnk.



Figure 3: Core plot within plantations of *Elaeis guineensis* (oil palm). Picture taken in September 2019 by Svea Jahnk.

## 5. Material and Methods

### 5.1. Pollen trap design and collection

Starting in 2013, pollen traps have been installed in each of the 32 core plots representing natural rainforest and three different agroforest management systems (jungle rubber, rubber, and oil palm plantations) in the region of Bukit Duabelas (BD) and Harapan (HR)(Fig. 1, Fig. 2).

The pollen trap is oriented on the design of Behling pollen traps (cf. JANTZ et al. 2013) where a hard-plastic tube is positioned on the ground. A test tube, filled with synthetic cotton, ca. 5ml of glycerol and covered by a mosquito net is placed within the hard-plastic tube and additionally protected by a metal net. Pollen and Spores are trapped in the synthetic cotton, soaked in glycerol which has a higher density than water and thus prevents particles from being washed out. Pollen traps were installed and recollected in September of each year, and thus remained at the plots for a one-year period, respectively.

The present study focuses on the evaluation of the pollen and spore rain of the time span from 2017 to 2018 (referred to as year 2017), retrieved in September 2018. To enlarge the dataset and provide an overview over ongoing processes I synthesized all data from 2013 (KR; 2015), 2014 and 2015 (LH; 2020) and 2016 (BIAGIONI; unpubl.) This study will cover a five-year dataset of airborne pollen and spore rain including significant climatic shifts and increasing land-use intensity.

### 5.2. Laboratory treatment

All samples were processed using standard laboratory methods after FAEGRI & IVERSEN (1989). Since pollen traps have been installed on the ground and bigger particles which are not needed for the counting are easily washed in, all samples are sieved through a 1-2 mm sieve.

Two *Lycopodium*-tablets were added ( $20848 \pm 1546$ ) to each sample to estimate the pollen concentration (STOCKMARR 1971). A treatment with 10%-hydrochloric acid (HCl) was applied to

remove washed in carbonates. The decarbonized samples were dehydrated using concentrated acetic acid and acetolyzed (ERDTMAN 1954) to remove cellulose from the samples and polysaccharides from the pollen's surface allowing an easier examination under the light microscope. Finally, the samples were filtered through a fine sieve (mesh width of 200µm) to remove particles bigger than the pollen and spores occurring within the area to ease the counting. The fixed microscope slides have been prepared with glycerine wax.

The sample collection and treatment has been done by co-workers of the CRC 990 EForTS project in Jambi before being transported to the University of Göttingen for counting and further analysis.

### 5.3. Pollen counting

The pollen traps from the year of 2013 as well as 2014 and 2015 have been studied by KR and LH, respectively. The pollen traps from the year of 2016 have been counted by Dr. SIRIA BIAGIONI (former postdoc in the sub-project A01), however they have not been fully identified. Thus, to complete the dataset, full identification of pollen and spore types from 2016 as well as counting and identification of the pollen samples from the year of 2017 has been the focus of this study.

Samples have been counted to 300 pollen grains/plot since data on 300 pollen grains per plot was available from the years before. Pollen counts were standardized to percentages based on the total pollen sum. The values of *Elaeis guineensis* and *Hevea brasiliensis* are overrepresented in the pollen assemblage due to their dominance as crop cash trees and a high production of pollen. Therefore, they are excluded from the total pollen sum for the calculation of the percentages of the remaining taxa. Fern spores were counted along with the pollen grains and are expressed as percentage of the total spore sum.

Pollen and Spores have been identified to the lowest taxonomic level possible using the tropical pollen and spore reference collection at the Department of Palynology and Climate Dynamics of the University of Göttingen, which includes specimens collected from the plots as well as additional resources including pollen keys and atlases for SE Asia (BULALACAO 1997; HUANG 1972) and online databases (The Australasian Pollen and Spore Atlas, Australian National University, Canberra, available at <http://apsa.anu.edu.au>; Pollen and Spore Image Database, University of Göttingen, available at <http://gdvh.uni-goettingen.de>). Unidentified pollen and spore types are included as indeterminate morphotypes. Relative proportions (%) of taxa and families were calculated per sample for 2016 and 2017 and visualised in a pollen diagram using the software C2 (JUGGINS 2007).

### 5.4. Pollen and spore influx

Total Pollen and spore influx (PSI) can be described as the amount of accumulated pollen per year (grains/cm<sup>2</sup>/year). The pollen concentration was calculated by multiplying the number of *Lycopodium* added ( $2 \cdot 20848 \pm 1546$ ) by the ratio of pollen to *Lycopodium* counts. PSI was

calculated by dividing the pollen concentration by the area of the pollen traps orifice (7cm<sup>2</sup>) as suggested by HICKS & HYVÄRINEN (1999).

Since the data of the years 2014 and 2015 only consist of the forest plots, PSI has been compared as the median of all forest plots and as the median of the two landscapes (BD and HR) for a five-year dataset (2013-2017). Furthermore, the pollen influx and spore influx have been calculated separately to compare which group has a higher influence on inter-seasonal shifts.

To compare the shifts within the PSI of one family, PSI has been calculated for every family occurring within the years, respectively, using the mean PSI of every family within all forest plots. To offer a constant comparison between years only families which occurred every year from 2013-2017 have been integrated into the graph. The values have been divided through 100 to reduce label crowding, yet to offer absolute values since percentages of one year's total PSI would not represent every year changes in PSI within one family. Since absolute values are shown, the scale level differs between families to reduce suppression of low PSI values within the graph, for the comparison shall only be within one family and between years respectively and not directly between all families.

To test if the PSI data per plot is normally distributed a Shapiro-Wilk-test has been performed (SHAPIRO & WILK 1965). This was followed by a Kruskal-Wallis-test to identify significant differences between years (KRUSKAL & WALLIS 1952).

## 5.5. Palynological diversity

To assess the diversity patterns after the influence of ENSO reflected in the local pollen and spore rain,  $\alpha$ -  $\beta$ - and  $\gamma$ -diversity have been determined with the pollen and spore material of 2016 and 2017 and between land-use systems. A Shapiro-Wilk test has been performed to test the data on its normal distribution (SHAPIRO & WILK 1965). To offer consistency between the analysed years diversity estimates have been calculated after the methods suggested in the thesis of KR (2015).

### *Alpha ( $\alpha$ ) -diversity*

As a measure of species richness per plot, based on the number of species and their abundance,  $\alpha$ -diversity has been calculated using the Shannon index in PAST (HAMMER et al. 2001). This diversity index includes the number of species/taxa present, as well as the relative abundance of each species/taxon. The value of this index ranges between 0 and 1, and greater values correspond to the greater diversity. The diversity increases when species/taxa richness and evenness increase. Palynological alpha diversity was calculated using pollen and spore influx data per pollen trap for a count of 300 pollen. A non-parametric test of variance (Kruskal-Wallis test, KRUSKAL & WALLIS 1952) was applied to test the significant differences in means between land-use systems.

### *Beta ( $\beta$ )-diversity*

Various measures of  $\beta$ -diversity have already been introduced (ANDERSON et al. 2011), whereby  $\beta$ -diversity is generally defined as the difference in species composition between two sites, communities, or regions (ARELLANO and HALFFTER 2003). As the variation in species composition amongst sites,  $\beta$ -diversity offers a transition from  $\alpha$ -diversity (as the diversity at local scales) to  $\gamma$ -diversity (at a regional scale) (WHITTAKER 1972). This study focuses on  $\beta$ -diversity as the dissimilarity between plots and thus on the site-to-site variation in pollen and spore composition within a land-use system (forest, jungle rubber, rubber and oil palm) using an abundance-based (Bray-Curtis, BRAY & CURTIS 1957) metric (LEYER & WESCHE 2007).

This plot-to-plot Bray-Curtis dissimilarity matrix (BACARO et al. 2012, WHITTAKER 1972) has been calculated for pollen and spore dataset for both years 2016 and 2017 in the program R.Studio 2019 (R CORE TEAM 2019) using the *vegan* R package (OKSANEN et al. 2019). When Bray-Curtis distance shows a value of 1, the objects do not have any family in common (LEYER & WESCHE, 2007). The pollen and spore influx has been chosen to represent the species' relative abundancy. A Kruskal-Wallis test has been applied to test on the significance of differences between land-use forms.

### *Gamma ( $\gamma$ ) -diversity*

$\gamma$ -diversity describes the total diversity of a landscape, including the  $\alpha$ -diversity of all its plant communities and the degree of dissimilarity between them ( $\beta$ -diversity) (WHITTAKER 1972). Thus,  $\gamma$ -diversity allows to assess landscape transformation on a larger scale. In this study the landscapes  $\gamma$ -diversity has been estimated by the total palynological richness per land-use system for both years 2016 and 2017 using PAST (HAMMER et al. 2001). To compare the richness in pollen and spore counts, a rarefaction analysis has been applied as standardization between land-use systems, creating unbiased estimates of the number of expected pollen and spore types in a sample of  $n$  pollen and spores ( $E(T_n)$ ). Here  $n$  is the smallest total count of pollen and spore types ( $n=2501$ ) (BIRKS & LINE 1992).

Thus, to analyse and compare individual rarefaction for all years (2013-2017) and land-use forms, the lowest pollen and spore count of 2501 grains ( $E(T_{2501})$ ) has been used to estimate the number of expected pollen and spore types. To express the error of estimated pollen and spore counts one standard deviation ( $1\sigma$ ) has been integrated into the graphics as error bars or as grey shade in the rarefaction curves.

## 6. Results

### 6.1. Palynological composition and diversity after ENSO (2016 and 2017)

#### 6.1.1. Pollen rain composition

A total of 266 pollen and 87 spore taxa has been identified during pollen counting for the year 2016. The majority of the pollen taxa (196) could be identified to family level with 97 taxa identified to genus and 24 taxa identified to species level. Out of the 43 determined spore taxa, 22 were identified to genus level and 9 were identified to species level.

The counting of samples of the year 2017 resulted in the differentiation of 330 pollen taxa of which 256 could at least be identified to family level. 123 pollen types could be identified to genus and 9 to species level. Moreover, 93 spore taxa have been differentiated. Of those, 74 have been identified to family level, 28 to genus and 9 to species level. To represent the pollen spectra of both years 2016 and 2017 and per landscape for HR and BD percentages of dominant families (Table 1) and dominant taxa (Table 2) have been enlisted. Furthermore, the distribution of prominent pollen and spore taxa in the different land-use forms and landscapes are visualized in figure 5 for pollen and figure 6 for spores. The overall results are summarised in the following:

#### *Rainforest*

In 2016, the pollen spectra of forest plots in both landscapes HR and BD are dominated by the Cannabaceae (38% in HR and 16% in BD), Euphorbiaceae (6% in HR and 8% in BD), Oleandraceae (90% in HR and 70% in BD) and Selaginellaceae (8% in HR and 6% in BD) families. The common dominant taxa in both landscapes are *Trema* (37% in HR and 15% in BD) and the spore *Nephrolepis* sp. (56% in HR and 68% in BD). The difference in pollen spectra can be seen in the dominance of *Elaeocarpus* (18%) in HR and Combretaceae/Melastomataceae (30%) and *Combretocarpus* (11%) in BD.

The pollen spectrum of 2017 in both landscapes is dominated by the Cannabaceae family which shows a decrease (from 38 to 14% in HR and from 16 to 11% in BD). Differences in family composition from the previous year are characterized by the dominance of Moraceae/Urticaceae (26% in HR and 10% in BD) and Davalliaceae (54% in HR and 75% in BD). The Rubiaceae and Lycopodiaceae family (8% and 12% respectively) are further dominant in HR, while Euphorbiaceae (17%) and Cyatheaceae (12%) are dominant in BD.

*Trema* sp. is still dominant in HR and BD but decreased considerably from 2016 to 2017 (from 37% to 10% in HR and from 15% to 10% in BD), whilst the spore *Davallia* is very prominent in both HR and BD (51% and 73%, respectively). *Elaeis guineensis* increased slightly in HR (from 5% to 7%). The difference between landscapes is given by the dominance of *Ficus* and *Syzygium* in HR

(11% and 7%) and *Endospermum* and *Canarium* in BD (9% for both taxa), as well as a slight increase of the spore *Stenochlaena palustris* (from 3% in 2016 to 6%).

#### *Jungle rubber*

The pollen composition of year 2016 in Jungle Rubber systems shows frequent pollen and spores of Cannabaceae (18% in HR and 29% in BD), Euphorbiaceae (24% in HR and 9% in BD), Oleandraceae (47% in HR and 48% in BD) and Lycopodiaceae (12% in HR and 15% in BD). Urticaceae/Moraceae (16%) and Elaeocarpaceae (7,93%) are only dominant in HR, while Rubiaceae (10%) and Phyllanthaceae (9,16) are dominant in BD. Dominant taxa in both landscape besides *Elaeis guineensis* (15% in HR and 7% in BD) are *Trema* sp. (17% in HR and 29% in BD) and the spore *Huperzia* (11% in HR and 14% in BD) with some variation of *Endospermum diadenum* and *Nephrolepis* in HR (16% and 45%, respectively) and *Phyllanthus oxyphyllus* in BD (8%).

The pollen spectrum from the year 2017 shows frequent occurrence of the Rubiaceae (16% in HR and 21% in BD), Elaeocarpaceae (decrease from 8% to 6% in HR and increase form 1% to 12% in BD) and Euphorbiaceae (decrease from 24% to 20% in HR and increase from 9% to 13% in BD) family. Moraceae/Urticaceae (24%) are dominant in HR and Cannabaceae (10,52%) in BD. Frequent spore families are Davalliaceae (26% in HR and 36% in BD), Cyatheaceae (27% in HR) and Lindsaeaceae (27% in BD). *Elaeis guineensis* is still dominant and increased in both landscapes (from 15% to 16% in HR and from 7% to 13% in BD) together with spores of *Davallia* (24% in HR and 32% in BD). *Endospermum* sp. slightly increased in HR (from 16 % to 17%), whereby *Ficus* became more dominant (12%). Changes in dominance can be observed through the high proportion of *Elaeocarpus* sp. (11%) in BD and the decrease of *Trema* (from 17% to 0% in HR and from 29% to 10% in BD).

#### *Rubber plantations*

The pollen spectrum from the year 2016 for Rubber plantations in both landscapes is dominated by the Cannabaceae (28% in HR and 40% in BD), Cyperaceae (6% in HR and 8% in BD) and Euphorbiaceae (4% in HR and 5% in BD) families. Prominent in HR is the Poaceae family (8%), and in BD the Boraginaceae family (7%). Frequent spore families are Oleandraceae (44% in HR and 24% in BD) as well as Cyatheaceae (27%) and Davalliaceae (21%), which both occur in BD. Dominant taxa in both landscapes are *Elaeis guineensis* (16 % in HR and 13% in BD), *Trema* sp. (26% in HR and 38% in BD) and the spore *Nephrolepis* (44% in HR and 24% in BD). The pollen spectrum changed with the dominance of *Hevea brasiliensis* and *Davallia* in HR (26% and 21%, respectively).

The pollen spectrum of 2017 is dominated by Cannabaceae which decreased abruptly (from 28 to 8% in HR and from 40% to 10% in BD), Elaeocarpaceae which increased strongly (from 0% to 12% in HR and from 0% to 8% in BD) and Euphorbiaceae which increased as well (form 4% to

6% in HR and from 5% to 20% in BD). Moraceae/Urticaceae (5%) were dominant families in HR, while the Cyperaceae family (27%) was prominent in BD. Frequent spore families are Lindsaeaceae (22% in HR and 24% in BD) with a variation between landscapes, marked by Cyatheaceae (50,23%) in BD and Davalliaceae (44,27%) in HR. *Elaeis guineensis* and *Trema* are still dominant in both, HR and BD, however the percentages differ from the previous year. *Elaeis guineensis* increased considerably (from 16% to 34% in HR and from 13% to 14% in BD), while *Trema* decreased (from 26% to 7% in HR and from 38% to 10% in BD). Changes in taxa composition per landscape from the previous year are clear. In HR, *Hevea brasiliensis* decreased significantly (from 26% to 8%), while *Davallia* increased (from 21% to 40%). Furthermore, *Mallotus/Macaranga* increased greatly in BD (from 0% to 19%).

#### *Oil palm plantations*

Frequent families in oil palm plantation plots in 2016 are Cannabaceae (13% in HR and 12% in BD), Euphorbiaceae (1% in HR and 2% in BD), Moraceae/Urticaceae (1% in HR and BD) and Poaceae (2% in HR and 6% in BD). Frequent spore families are Oleandraceae (40% in HR and 47% in BD), Lindsaeaceae (16%) in BD and Davalliaceae (9%) in HR. The most noticeable dominant taxa in both landscapes are naturally *Elaeis guineensis* (80% in HR and 70% in BD), accompanied by *Trema* (13% in HR and 12% in BD) and spores of *Nephrolepis* (40% in HR and 50% in BD). *Davallia* is prominent in HR (10%), while the genus *Lindsaea* is dominant in BD (20%).

In 2017, the frequent families are Cannabaceae, which marked an abrupt decrease (from 13% to 2% in HR and from 12% to 4% in BD) and Moraceae/Urticaceae (1% in HF) which increased only in BD (from 1% to 5% in BD). Poaceae and Euphorbiaceae are dominant in HR and increased slightly (from 2% to 3% and from 1% to 2%, respectively). The families of Melastomataceae/Combretaceae (7%) and Apocynaceae (6%) were dominant in BD. Common spore families are Davalliaceae (40% in HR and 23% in BD), Lindsaeaceae (64%) in BD and Polypodiaceae (52%) in HR. *Elaeis guineensis* is still dominant but shows different percentages in both landscapes compared to the previous year. In HR it increased (from 80% to 90%), while in BD a decrease is noticeable (from 70% to 60%). *Trema* experienced an abrupt decrease in both landscapes (from 10% to 2% in HR and from 12% to 4% in BD). Interestingly, the spore *Nephrolepis* was not the dominant taxa in both HR and BD despite its high number in 2016. Changes in taxa composition can be seen with the increasing dominance of *Davallia* in HR (from 10% to 30%) and *Lindsaea* in BD (from 20% to 60%), as well as with the presence of *Dyera polyphylla* in BD (6%).

2016

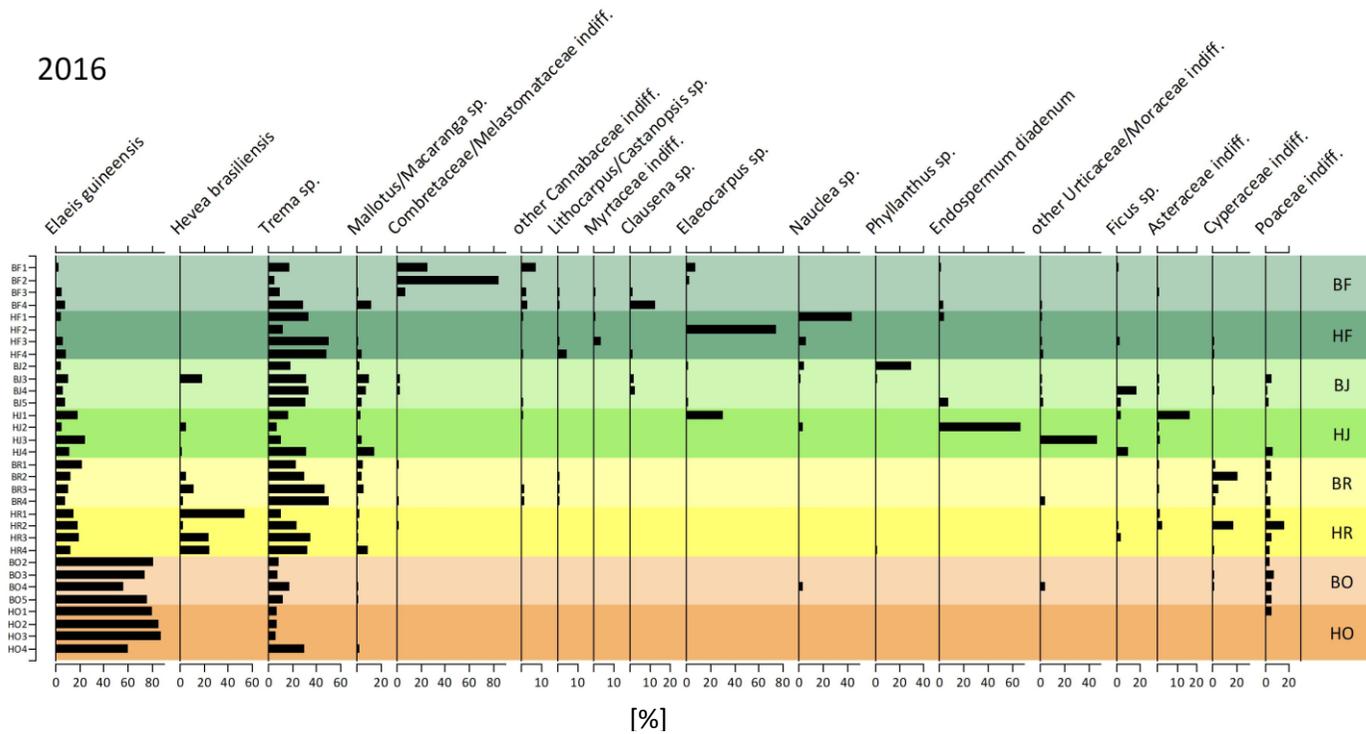
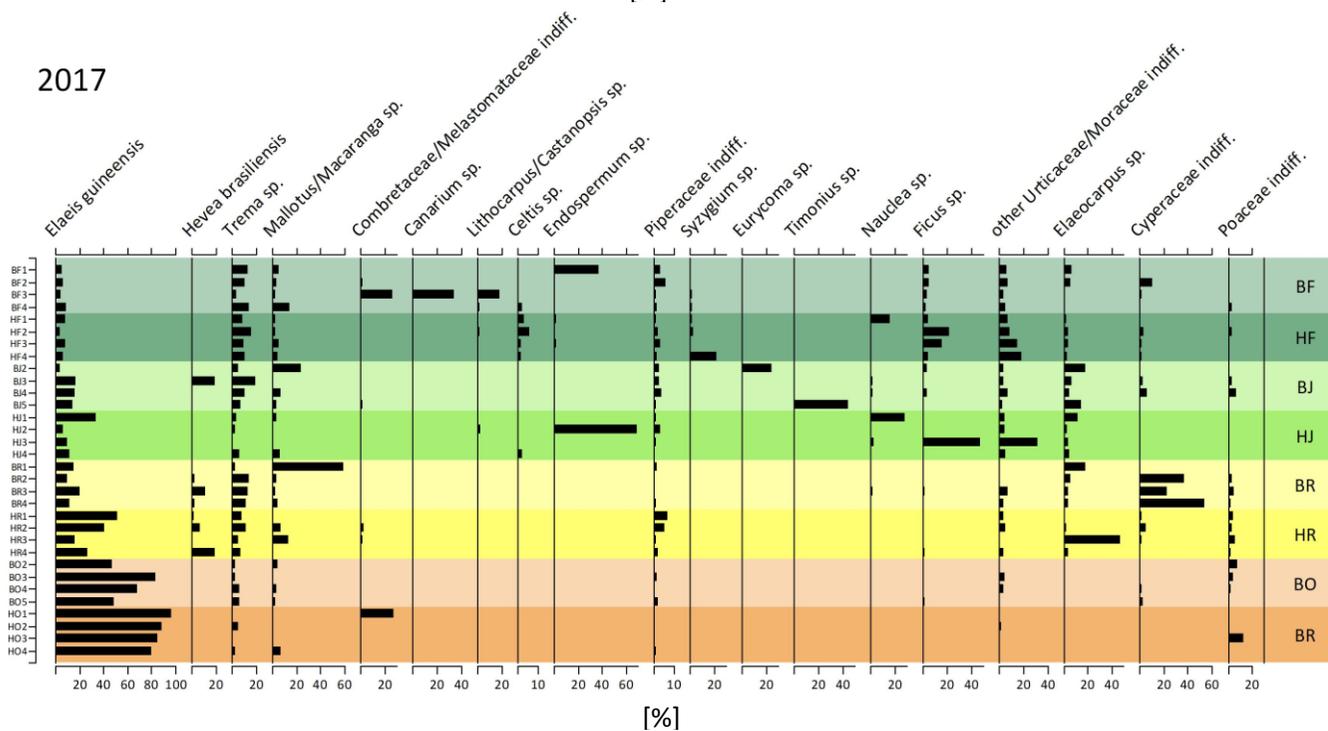
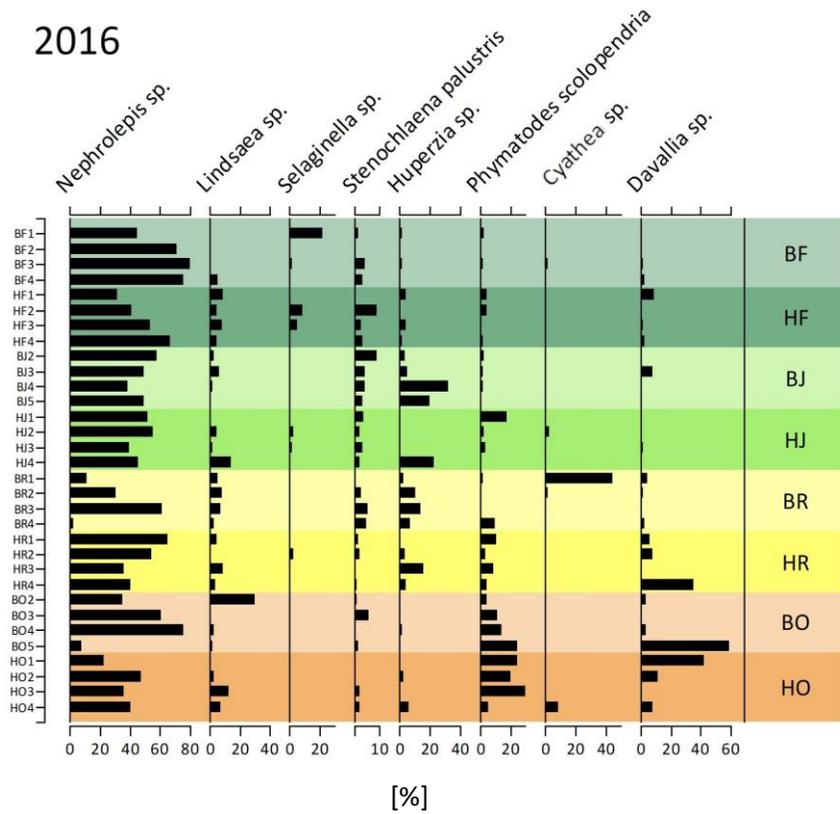


Figure 5: Pollen diagram of 2016 (above; a) and 2017 (below; b) of all analysed core plots. x-axis shows values in % of the total pollen count. Only pollen types of high percentages or frequency are visualized. Zones refer to the four land-use forms, rainforest (F, dark green), jungle rubber (J, bright green), rubber plantation (R, yellow) and oil palm plantation (O, orange), and both landscapes Bukit Duabels (B) and Harapan (H). The single plots are labelled on the left y-axis. Diagram has been generated in program C2 (JUGGINS 2016).

2017



2016



2017

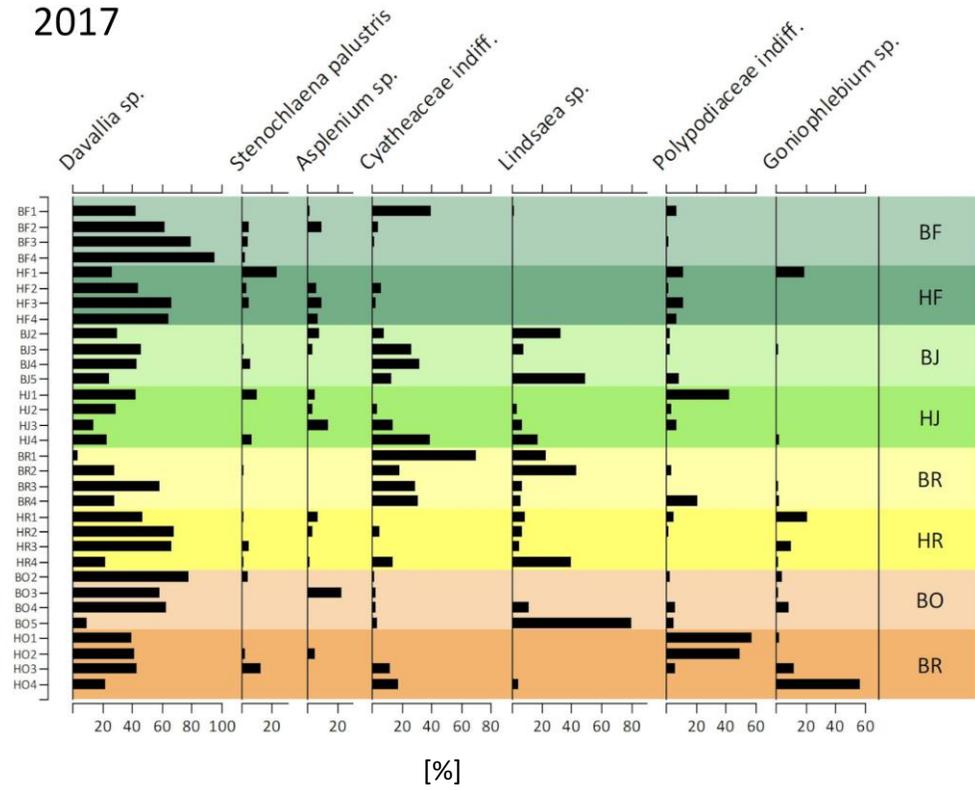


Figure 6: Spore diagram of 2016(above; a) and 2017 (below; b) of all analysed core plots. x-axis shows values in % of the total spore count. Only spore types of high percentages or frequency are visualized. Zones refer to the four land-use forms, rainforest (F, dark green), jungle rubber (J, bright green), rubber plantation (R, yellow) and oil palm plantation (O, orange), and both landscapes Bukit Duabels (B) and Harapan (H). The single plots are labelled on the left y-axis. Diagram has been generated in program C2 (JUGGINS 2016).

Table 1: Percentages of the total pollen, or rather the total spore count for the four most dominant pollen families and two most dominant spore families per land-use system and landscape (BD and HR) for the years 2016 and 2017. The major crop trees *Hevea brasiliensis* and *Elaeis guineensis* have been excluded from the families enlisted.

		2016		2017				2016		2017	
		Pollen and Spore family	%	Pollen and Spore family	%			Pollen and Spore family	%	Pollen and Spore family	%
Rainforest	Harapan	Cannabaceae	37,67	Moraceae/Urticaceae	25,87	Rubber	Harapan	Cannabaceae	27,65	Elaeocarpaceae	12,36
		Elaeocarpaceae	18,52	Cannabaceae	13,91			Poaceae	8,13	Cannabaceae	8,02
		Rubiaceae	14,18	Rubiaceae	8,16			Cyperaceae	5,58	Euphorbiaceae	5,74
		Euphorbiaceae	5,75	Myrtaceae	6,84			Euphorbiaceae	4,46	Moraceae/Urticaceae	4,78
		Oleandraceae	87,61	Davalliaceae	54,42			Oleandraceae	44,3	Davalliaceae	44,27
		Selaginellaceae	8,28	Lycopodiaceae	11,56			Davalliaceae	21,04	Lindsaeaceae	21,67
	Bukit Duabelas	Combretaceae/ Melastomataceae	28,9	Euphorbiaceae	16,59		Bukit Duabelas	Cannabaceae	39,59	Cyperaceae	27,37
		Cannabaceae	16,12	Cannabaceae	10,95			Cyperaceae	7,96	Euphorbiaceae	19,75
		Anisophylleaceae	11,05	Moraceae/Urticaceae	10,32			Boraginaceae	7,25	Cannabaceae	10,13
		Euphorbiaceae	8,1	Burseraceae	8,81			Euphorbiaceae	5,2	Elaeocarpaceae	7,97
		Oleandraceae	67,97	Davalliaceae	74,77			Cyatheaceae	27,28	Cyatheaceae	50,23
		Selaginellaceae	6,4	Cyatheaceae	11,71			Oleandraceae	23,71	Lindsaeaceae	24
Jungle rubber	Harapan	Euphorbiaceae	23,88	Moraceae/Urticaceae	23,67	Oil palm	Harapan	Cannabaceae	12,94	Poaceae	3,42
		Cannabaceae	17,75	Euphorbiaceae	20,09			Poaceae	1,97	Cannabaceae	2,38
		Moraceae/Urticaceae	16,1	Rubiaceae	16,29			Euphorbiaceae	1,34	Euphorbiaceae	1,99
		Elaeocarpaceae	7,93	Elaeocarpaceae	5,71			Moraceae/Urticaceae	0,95	Moraceae/Urticaceae	0,72
		Oleandraceae	46,59	Cyatheaceae	27,16			Oleandraceae	39,7	Polypodiaceae	51,95
		Lycopodiaceae	12,12	Davalliaceae	25,93			Davalliaceae	8,67	Davalliaceae	39,61
	Bukit Duabelas	Cannabaceae	29,41	Rubiaceae	20,88		Bukit Duabelas	Cannabaceae	11,97	Melastomataceae/ Combretaceae	7,19
		Rubiaceae	10,01	Euphorbiaceae	13,17			Poaceae	5,71	Apocynaceae	5,7
		Euphorbiaceae	9,31	Elaeocarpaceae	12,36			Euphorbiaceae	1,62	Moraceae/Urticaceae	4,77
		Phyllanthaceae	9,16	Cannabaceae	10,52			Moraceae/Urticaceae	1,31	Cannabaceae	4,45
		Oleandraceae	47,92	Davalliaceae	36,1			Oleandraceae	47,31	Lindsaeaceae	64,18
		Lycopodiaceae	15,01	Lindsaeaceae	26,95			Lindsaeaceae	15,88	Davalliaceae	22,58

Table 2: Percentages of the total pollen, or rather the total spore count for the four most dominant pollen taxa and three most dominant spore taxa per land-use system and landscape (BD and HR) for the years 2016 and 2017.

		2016		2017				2016		2017	
		Pollen and Spore type	%	Pollen and Spore type	%			Pollen and Spore type	%	Pollen and Spore type	%
Rainforest	Harapan	<i>Elaeis guineensis</i>	5,28	<i>Ficus</i>	11,05	Rubber	Harapan	<i>Trema</i>	26,05	<i>Elaeis guineensis</i>	33,99
		<i>Trema</i>	36,6	<i>Trema</i>	10,9			<i>Hevea brasiliensis</i>	25,52	<i>Elaeocarpus</i>	12,36
		<i>Elaeocarpus</i>	17,99	<i>Syzygium</i>	6,8			<i>Elaeis guineensis</i>	16,29	<i>Trema</i>	7,95
		<i>Nauclea</i>	12,63	<i>Elaeis guineensis</i>	6,5			<i>Poaceae</i> Type II	6,23	<i>Hevea brasiliensis</i>	7,65
		<i>Nephrolepis</i>	56,42	<i>Davallia</i> Type IV	50,95			<i>Nephrolepis</i>	44,3	<i>Davallia</i> Type IV	40,6
		<i>Lindsaea</i> Type II	5,96	<i>Huperzia</i> Type I	10,19			<i>Davallia</i>	21,04	<i>Lindsaea</i> Type III	14,63
		<i>Stenochlaena palustris</i>	3,21	<i>Stenochlaena palustris</i>	6,37			<i>Huperzia</i> Type I	5,85	<i>Goniophlebium</i>	7,76
	Bukit Duabelas	Combretaceae/ Melastomataceae (indiff.)	28,9	<i>Trema</i>	10,2		Bukit Duabelas	<i>Trema</i>	37,77	Cyperaceae indiff.	27,37
		<i>Trema</i>	15,38	<i>Endospermum</i>	9,49			<i>Elaeis guineensis</i>	13,02	<i>Mallotus/Macaranga</i>	19,24
		<i>Combretocarpus</i>	10,55	<i>Canarium</i>	8,78			Cyperaceae Type IV	7,3	<i>Elaeis guineensis</i>	14,09
		<i>Nephrolepis</i>	67,97	<i>Mallotus/Macaranga</i>	6,41			Boraginaceae indiff.	6,92	<i>Trema</i>	9,84
		<i>Selaginella stripulata</i>	6,05	<i>Davallia</i> Type IV	73,33			<i>Cyathea</i>	27,28	<i>Cyatheaceae</i> Type II	46,26
		<i>Lindsaea</i> Type II	2,13	Cyatheaceae Type II	10,22			<i>Nephrolepis</i>	23,71	<i>Lindsaea</i> Type I	16,35
				<i>Trepsichlore alsopteris</i>	3,1			<i>Lindsaea</i> Type II	5,96	<i>Davallia</i> Type IV	16,12
Jungle rubber	Harapan	<i>Trema</i>	17,03	<i>Endospermum</i>	16,91	Oil palm	Harapan	<i>Elaeis guineensis</i>	78,23	<i>Elaeis guineensis</i>	87,2
		<i>Endospermum</i>	16,35	<i>Elaeis guineensis</i>	15,69			<i>Trema</i>	12,75	Poaceae indiff.	3,18
		<i>Elaeis guineensis</i>	15	<i>Ficus</i>	11,83			<i>Poaceae</i> Type II	1,24	<i>Trema</i>	2,38
		<i>Elaeocarpus</i>	7,61	<i>Nauclea</i>	8,34			<i>Mallotus/Macaranga</i>	1,17	<i>Mallotus/Macaranga</i>	1,91
		<i>Nephrolepis</i>	46,59	Cyatheaceae Type II	26,51			<i>Nephrolepis</i>	39,7	Polypodiaceae (MS08)	34,81
		<i>Huperzia</i> Type II	10,98	<i>Davallia</i> Type IV	24,7			<i>Cyathea</i>	8,22	<i>Davallia</i> Type IV	31,01
		<i>Lindsaea</i> Type II	8,33	<i>Lindsaea</i> Type I	12,65			<i>Davallia</i>	8,67	<i>Goniophlebium</i>	10,13
	Bukit Duabelas	<i>Trema</i>	28,61	<i>Elaeis guineensis</i>	12,69		Bukit Duabelas	<i>Elaeis guineensis</i>	71,79	<i>Elaeis guineensis</i>	62,11
		<i>Phyllanthus oxyphyllus</i>	8,39	<i>Timonius</i>	11			<i>Trema</i>	11,69	<i>Dyera polyphylla</i>	5,7
		Rubiaceae Type IV	7,64	<i>Elaeocarpus</i>	10,84			<i>Poaceae</i> Type II	4,15	<i>Trema</i>	4,45
		<i>Elaeis guineensis</i>	7,26	<i>Trema</i>	10,44			<i>Mallotus/Macaranga</i>	1,36	<i>Mallotus/Macaranga</i>	2,66
		<i>Huperzia</i> Type I	14,06	<i>Davallia</i> Type IV	32,5			<i>Nephrolepis</i>	47,31	<i>Lindsaea</i> Type I	55,95
		<i>Davallia</i>	3,19	<i>Lindsaea</i> Type I	24,17			<i>Lindsaea</i> Type II	15,88	<i>Davallia</i> Type IV	19,35
		<i>Lindsaea</i> Type II	3,03	Cyatheaceae Type II	18,83			<i>Phymatodes scolopendria</i>	9,73	<i>Lindsaea</i> Type III	7

### 6.1.2. Pollen and spore influx

Median pollen and spore influx per landscape (HR and BD) and per land-use system are enlisted in Table 3. The total Pollen and Spore influx (PSI) in year 2016 and 2017 for all four land-use forms shows a similar trend. The PSI shows the same pattern as the pollen influx, with the highest influx in the forest plots, followed by oil palm plantations, jungle rubber and rubber plantations. However, the spore accumulation rate occurs to behave differently. In 2016, the highest spore influx can be seen in oil palm plantations followed by jungle rubber, forest and finally rubber plantations. While in 2017 the highest influx was found in forest plots, followed by jungle rubber systems, oil palm plantations and lastly rubber plantations.

Table 3: Median pollen and spore influx values for year 2016 and 2017 per land-use system

<b>2016</b>	<b>rainforest</b>	<b>jungle rubber</b>	<b>rubber</b>	<b>oil palm</b>
$\bar{x}$ pollen influx (grains/cm <sup>2</sup> /year)	~ 5885	~ 3391	~ 1217	~ 5176
$\bar{x}$ spore influx (grains/cm <sup>2</sup> /year)	~ 759	~ 843	~ 465	~ 926
$\bar{x}$ PSI (grains/cm <sup>2</sup> /year)	~ 6691	~ 4151	~ 2307	~ 6073
<b>2017</b>	<b>rainforest</b>	<b>jungle rubber</b>	<b>rubber</b>	<b>oil palm</b>
$\bar{x}$ pollen influx (grains/cm <sup>2</sup> /year)	~ 4897	~ 3678	~ 1558	~ 3836
$\bar{x}$ spore influx (grains/cm <sup>2</sup> /year)	~ 1016	~ 876	~ 311	~ 727
$\bar{x}$ PSI (grains/cm <sup>2</sup> /year)	~ 5913	~ 5640	~ 1796	~ 4568

### 6.1.3. Palynological diversity

#### *$\alpha$ -diversity*

The  $\alpha$ -diversity between year 2016 and 2017 shows a similar trend (Fig. 7). In 2016,  $\alpha$ -diversity in forest (median ~ 0,82), jungle rubber (median ~ 0,87) and rubber plantations (median ~ 0,86) shows less variation compared to the lowest index of oil palm plantations (median ~ 0,68). The Shapiro-Wilk test on normal distribution shows that pollen and spore abundancy data is not normally distributed and thus the application of a Kruskal-Wallis test is appropriate. With a p-value < 0.05 the Kruskal-Wallis test signals significant differences between plots. Statistically significant differences can be found between jungle rubber and oil palm plots.

In 2017,  $\alpha$ -diversity shows a decreasing trend from forest (median ~ 0,91) to jungle rubber (median ~ 0,87) and rubber plantations (median ~ 0,83) to the less diverse oil palm plantations (median ~ 0,55). The Kruskal-Wallis test shows that differences between land-use systems are statistically significant, whereby Oil palm plantations are significantly different from forest and jungle rubber plots.

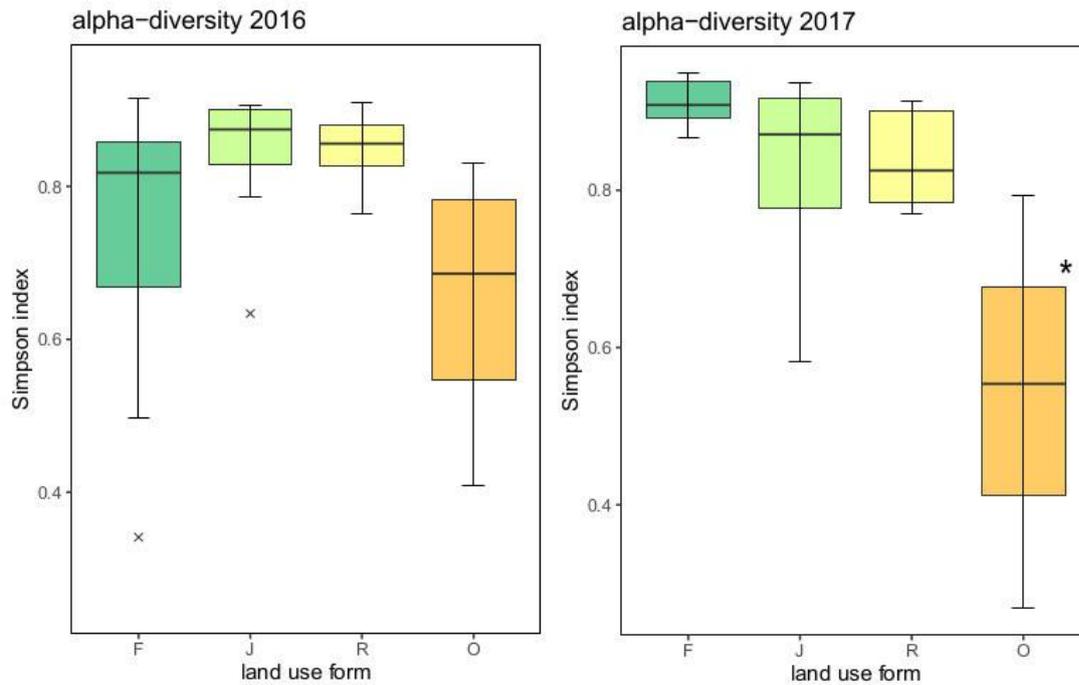


Figure 7: Simpson-Index per land-use form for all plots of 2016 and 2017. x-axis: land-use as F (rainforest), J (jungle rubber), R (rubber plantations), O (oil palm plantations). Outliers are marked with an x. y-axis: Simpson-Index. Statistically significant difference from all other plots with an asterisk (\*).

### *$\beta$ -diversity*

The  $\beta$ -diversity of the years 2016 and 2017 does not differ significantly from each other (Fig. 8). The results show a p-value higher than the significance level ( $> 0.05$ ) for both years, indicating no statistically significant differences between land-use systems. The palynological dissimilarity seems to be rather similar between plots of each land-use systems.

In 2016,  $\beta$ -diversity is higher in forest plots (median  $\sim 0,75$ ) and decreases slightly in jungle rubber and oil palm plantations (median  $\sim 0,73$ ) and even further in rubber plantations (median  $\sim 0,6$ ). Anyhow, the oil palm plantation records the highest error range of values (from  $\sim 0,1$  until  $\sim 0,98$ ) compared to other land-use forms.

In 2017, the highest diversity index can be seen in the jungle rubber (median  $\sim 0,8$ ) followed by rubber plantations (median  $\sim 0,78$ ) and forest (median  $\sim 0,77$ ). The lowest diversity was found in oil palm plantations (median  $\sim 0,71$ ) with a vast error range ( $\beta$ -diversity values between  $\sim 0,16$  and  $\sim 0,92$ ).

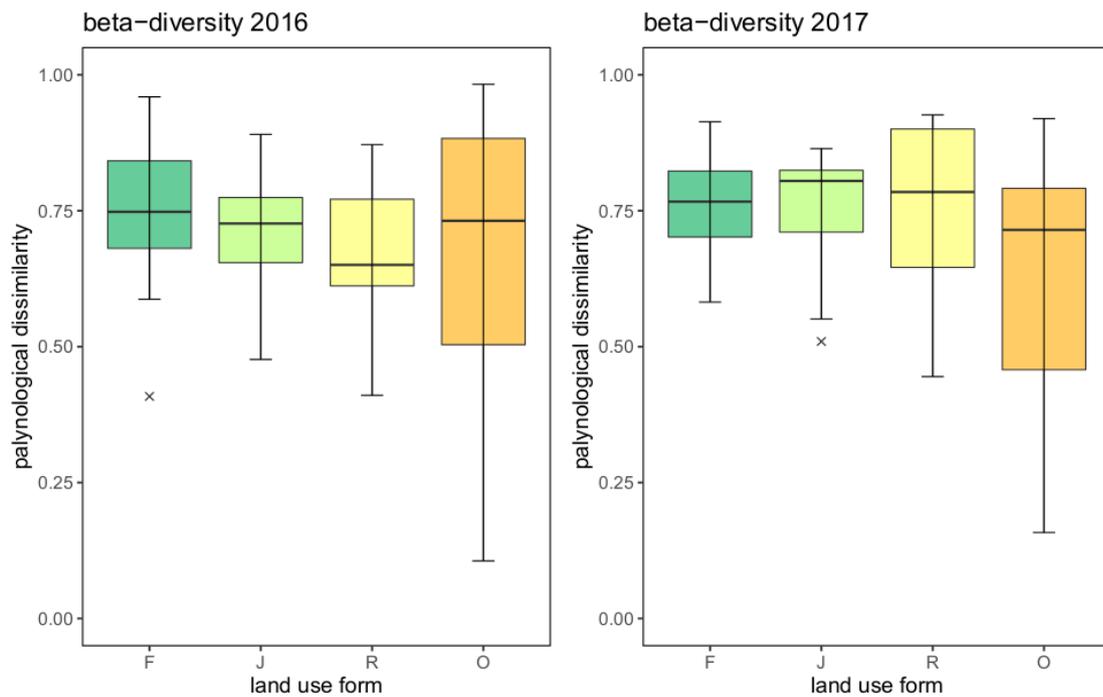


Figure 8: Plot-to-plot dissimilarity comparing within each land-use form. X-axis: land-use as F (rainforest), J (jungle rubber), R (rubber plantations), O (oil palm plantations). Y-axis: palynological dissimilarity after Bray-Curtis. Outliers are marked with an asterisk (\*).

### *γ-diversity*

Rarefaction analysis to estimate palynological richness ( $E(T_n)$ ) in all land-use systems of 2016 and 2017 shows a clear decrease in richness with increasing land-use intensity (Fig. 10). Rarefaction curves for 2016 are steep and do not reach their plateau. Only oil palm plots seem to exit their linear phase and go towards saturation. The result from 2017 shows less-steep curves and all curves potentially reach their plateau earlier than in 2016 (Fig. 9).

In 2016 estimated pollen and spore types (lowest identification level) for  $E(T_{2501})$  are 179 types in forest plots, 166 types in jungle rubber systems, 136 types in rubber plantation and the lowest number of taxa was found in oil palm plots with only 104 types (Fig. 10).

The results in 2017 show a similar trend with estimated pollen and spore counts for  $E(T_{2501})$  of 192 types in forest plots, 158 types in jungle rubber systems, 120 types in rubber plantations and 89 types in oil-palm plantations (Fig. 10).

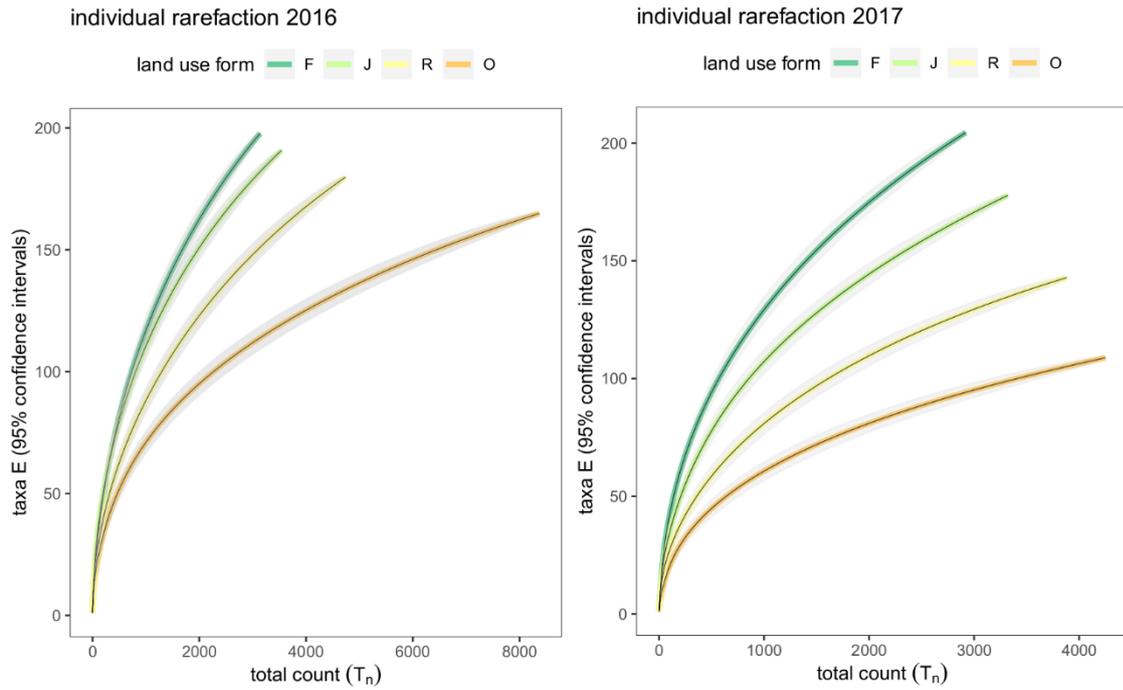


Figure 9: Rarefaction analysis to estimate palynological richness: Left: estimates for year 2016. Right: estimates for year 2017. x-axis: total projected grain count ( $T_n$ ). y-axis: estimated count of taxa (E) per year with in 95% confidence intervals. Gray shade indicates the standard deviation ( $1\sigma$ ).

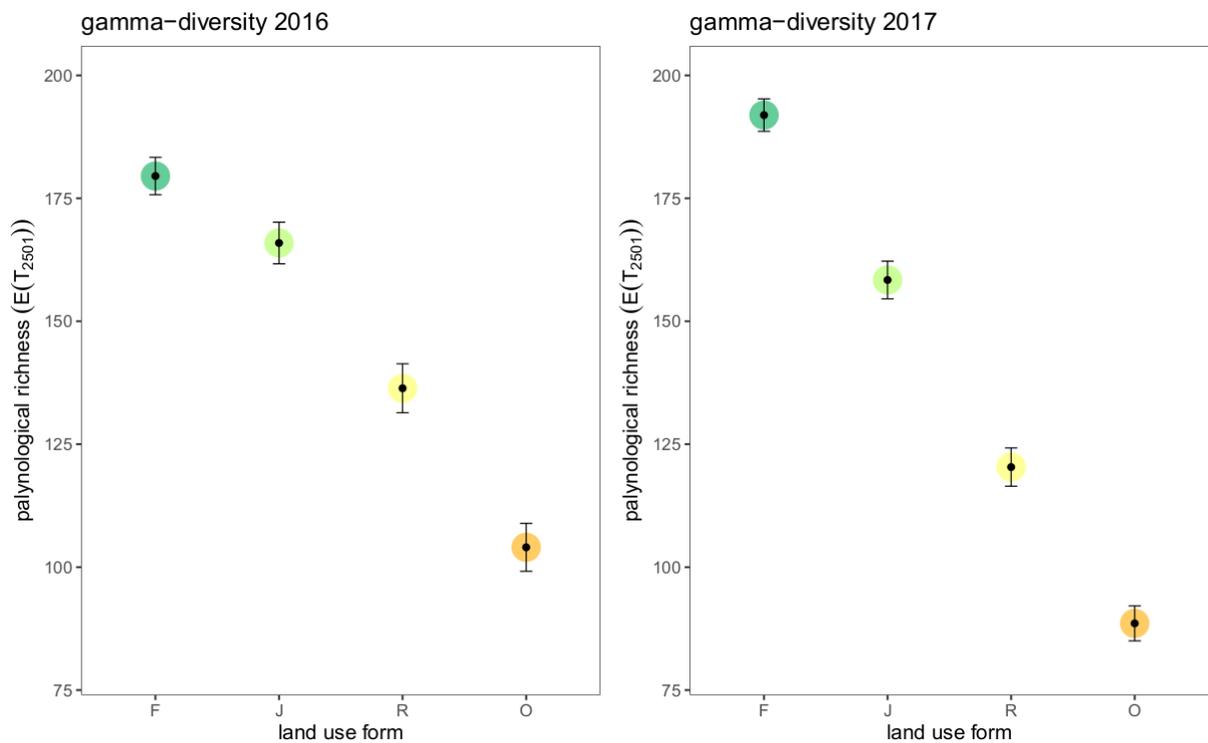


Figure 10: Palynological richness per land-use form for 2016 and 2017. Both x-axes: land-use as F (rainforest), J (jungle rubber), R (rubber plantations), O (oil palm plantations). Both y-axes: estimated palynological richness ( $E(T)$ ) for an estimated pollen and spore count of 2501 grains ( $E(T_{2501})$ ). Error-bars show  $1\sigma$ .

## 6.2. Long-term palynological composition and diversity in the rainforest system (2013-2017)

### 6.2.1. Pollen rain composition and influx

Out of 84 pollen families occurring from year 2013 to 2017, 19 families are represented every year. While out of 22 spore families, 5 families can be found every year. The overall PSI of these 24 dominant families is shown in figure 17 in the appendix (S1). The main families which occurred every year, including Euphorbiaceae, Rubiaceae, Dipterocarpaceae and Fagaceae amongst others, show a similar trend in their pollen accumulation rate. The influx of half of these families (12 out of 24 families) reached its peak in 2015 when the major ENSO event occurred, and it decreased right after the event (Fig. 13). In general, the PSI for all forest plots per year (Fig. 11) show that the influx data is not normally distributed ( $p$ -value = 0.0244) thus significant differences between the years are given. A multi-comparison test shows that the data of year 2014 behaves significantly different from other years.

Data is shown as median values for all forest plots of one year. The error-bars refer to the upper and lower quantile (25th and 75th percentiles) to show the range of values within one sample set. The PSI for all investigated years shows that in 2013 the PSI is relatively high (median ~ 10166 grains/cm<sup>2</sup>/year). It then abruptly decreases in 2014, where it shows the lowest values of all years (median ~ 2258 grains/cm<sup>2</sup>/year). In 2015, the PSI shows a high increase and records the highest value amongst the investigated years (median ~ 10204 grains/cm<sup>2</sup>/year). This is followed by a decrease in 2016 (median ~ 6528 grains/cm<sup>2</sup>/year), and again in 2017 (median ~ 5913 grains/cm<sup>2</sup>/year).

Comparing the influx between pollen and spores for all investigated years, pollen influx seems to differ stronger from year to year than spore influx (Fig. 12a, Table 4). Both show statistically significant differences from each other. Pollen influx records the highest value in 2015 when the ENSO occurred, whereby spore influx recorded the highest value in 2013.

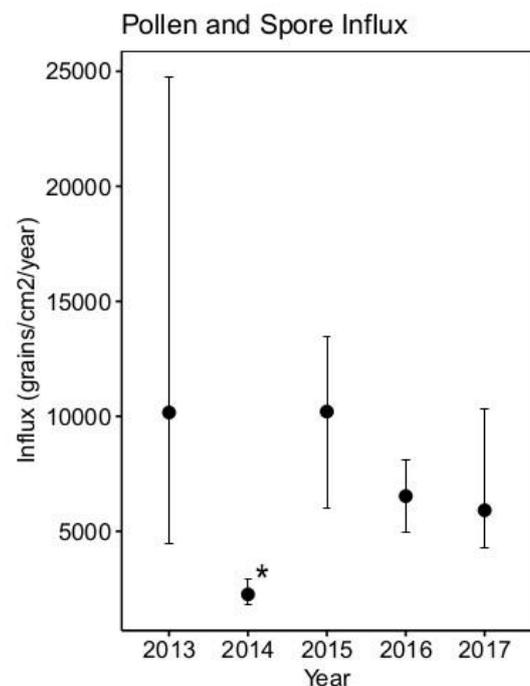


Figure 11: Total annual pollen and spore influx for rainforest plots. X-axis: all analysed years. Y-axis: total Influx in grains/cm<sup>2</sup>/year. Points show median values for each year. Error-bars: using the 25<sup>th</sup> and 75<sup>th</sup> percentiles as confidence limits. Statistically significant difference from all other years is marked with an asterisk (\*)

Both, pollen, and spore influx show the lowest value in 2014.

While comparing the PSI between landscapes, a similar trend (Fig. 12b, Table 5) was recorded in both, HR and BD. The PSI tends to be higher in 2013 for both regions, then experiences an abrupt decrease in 2014 before it finally increases again in 2015. The PSI in BD shows a decreasing trend after the ENSO event in 2015, while the opposite trend is given in HR. Here, the PSI decreases abruptly in 2016 and then increases again in the year 2017.

Table 4: Median values ( $\bar{x}$ ) for each, pollen, and spore influx of all forest plots per year.

Year	2013	2014	2015	2016	2017
$\bar{x}$ pollen influx (grains/cm <sup>2</sup> /year)	~ 7729	~ 1886	~ 8672	~ 5722	~ 4919
$\bar{x}$ spore influx (grains/cm <sup>2</sup> /year)	~ 1604	~ 315	~ 1532	~ 759	~ 1016

Table 5: Median values ( $\bar{x}$ ) for both landscapes, Bukit Duabelas and Harapan, of all forest plots per year.

Year	2013	2014	2015	2016	2017
$\bar{x}$ Bukit Duabelas PSI (grains/cm <sup>2</sup> /year)	~ 13923	~ 3333	~ 10204	~ 8006	~ 5913
$\bar{x}$ Harapan PSI (grains/cm <sup>2</sup> /year)	~ 4976	~ 1933	~ 10585	~ 4849	~ 11397

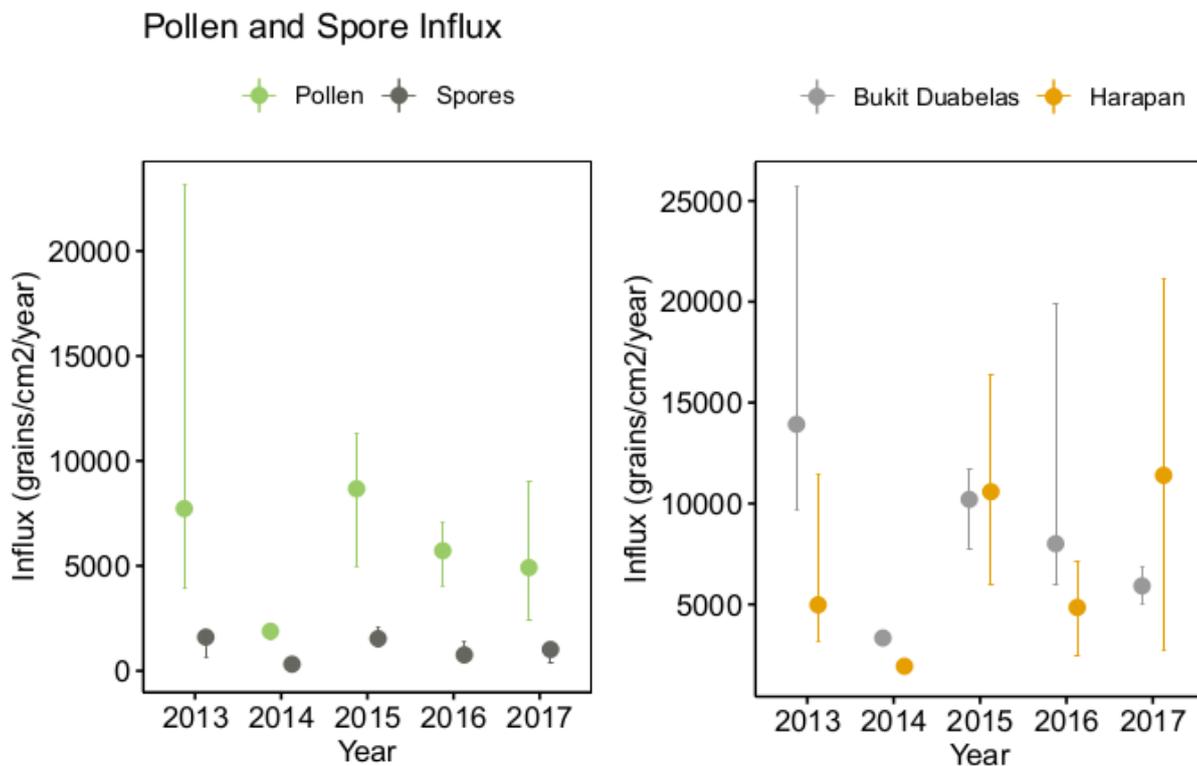


Figure 12: Annual Influx for pollen vs. spores (right; a) and Bukit vs. Harapan rainforest plots (left; b). Both graphs: x-axis: all analysed years. y-axis: total Influx in grains/cm<sup>2</sup>/year. Points show median values for each year. Error-bars: using the 25<sup>th</sup> and 75<sup>th</sup> percentiles as confidence limits.

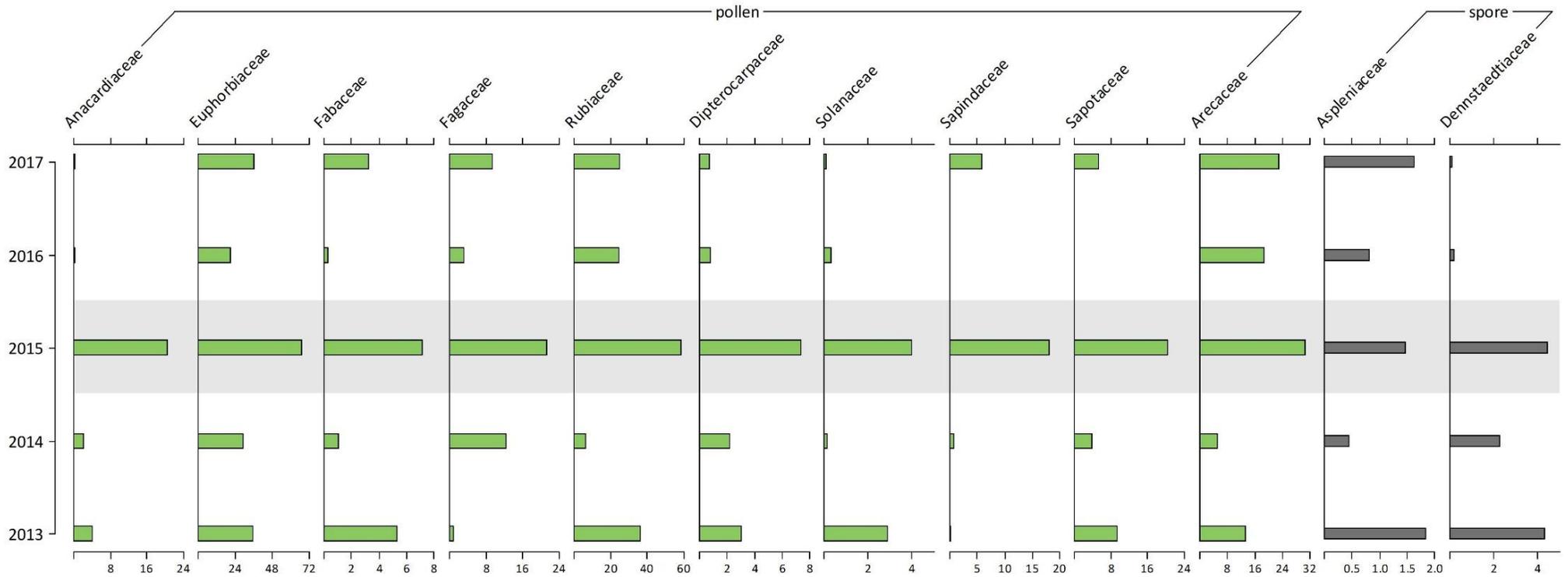


Figure 13: PSI diagram of continuous families with max. PSI values in 2015 for rainforest plots of all five years. x-axis shows absolute **influx values (grains/cm<sup>2</sup>/year)** divided by a factor of 100 to reduce label crowding. Only families are visualized, which **occur every year** to provide a thorough comparison. Diagram has been generated in the program C2 (JUGGINS 2016).

## 6.2.2. Palynological diversity

### *$\alpha$ -diversity*

$\alpha$ -diversity has been calculated to see the diversity index of a five-year dataset (2013-2017) for all forest plots. The Simpson index for all forest plots for each year based on the families' PSI are shown in figure 14a. The Kruskal-Wallis test shows a p-value  $<0.05$  and thus indicates significant differences between years. Statistically significant differences have been detected between the years 2013 and 2016. The year 2013 represents the highest Simpson index (median  $\sim 0,91$ ). It then decreases slightly in 2014 (median  $\sim 0,87$ ). The diversity index increases slightly in 2015 (median  $\sim 0,9$ ) and decreases noticeably in 2016 to record the lowest Simpson index of all years (median  $\sim 0,81$ ), before it finally increases again in 2017 (median  $\sim 0,88$ ).

### *$\beta$ -diversity*

No statistically significant differences in palynological dissimilarity can be detected between the investigated years (Fig. 14b). The results show the lowest  $\beta$ -diversity in 2014 (median  $\sim 0,63$ ), which reflects less dissimilarities between plots compared to other years. Furthermore, the highest  $\beta$ -diversity can be found in 2015 (median  $\sim 0,72$ ).

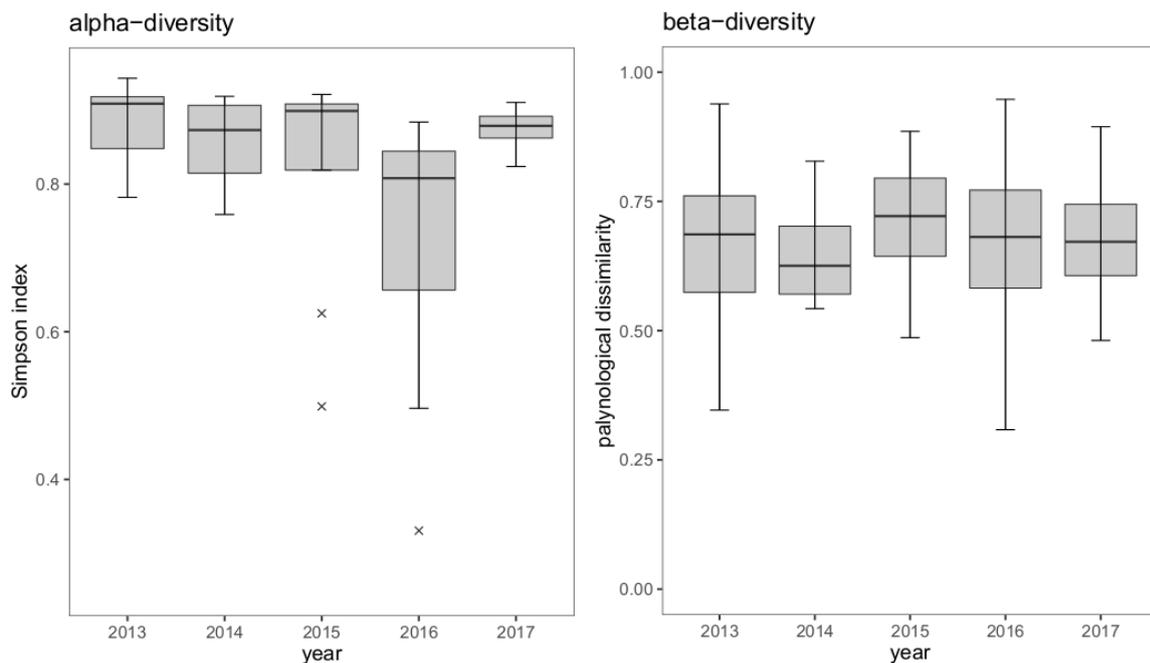


Figure 14: Left (a): Simpson-Index per year for all rainforest plots. x-axis: analysed years. y-axis: Simpson-Index. Right (b): Plot-to-plot dissimilarity compared within each year. x-axis: analysed years. y-axis: palynological dissimilarity after Bray-Curtis. Outliners are marked with an x.

### $\gamma$ -diversity

Rarefaction analysis for all five years resulted in rather different saturation curves of the estimated species counts (Fig. 15). The results from 2013 show a different trend compared to other years. The individual rarefaction curve for 2013 seemingly reaches its plateau, while the other curves still increase. However, 2014 occurs with a curve rather similar to 2013 followed by 2015, which is less steep and rather close to its estimated saturation. 2016 and 2017 are yet increasing steeply and still in their linear phase.

The number of estimated taxa indicating palynological richness per year varies (Fig. 16). Palynological richness in the forest plots increases between 2013 and 2015, along with the estimated pollen and spore counts. The  $E(T_{2501})$  records 52 families in 2013, increasing to 55 families in 2014 and finally to 63 families in 2015. This is followed by a strong decrease to the lowest palynological richness in 2016 with 52 families. The highest palynological richness was recorded in 2017 with 69 families.

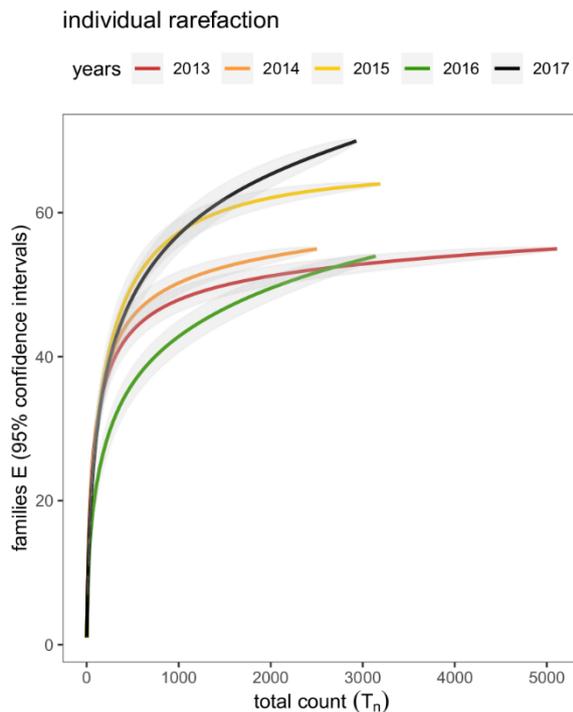


Figure 15: Rarefaction analysis to estimate palynological richness: x-axis: total projected grain count ( $T_n$ ). y-axis: estimated count of families (E) per year with in 95% confidence intervals. Gray shade indicates the standard deviation ( $1\sigma$ ).

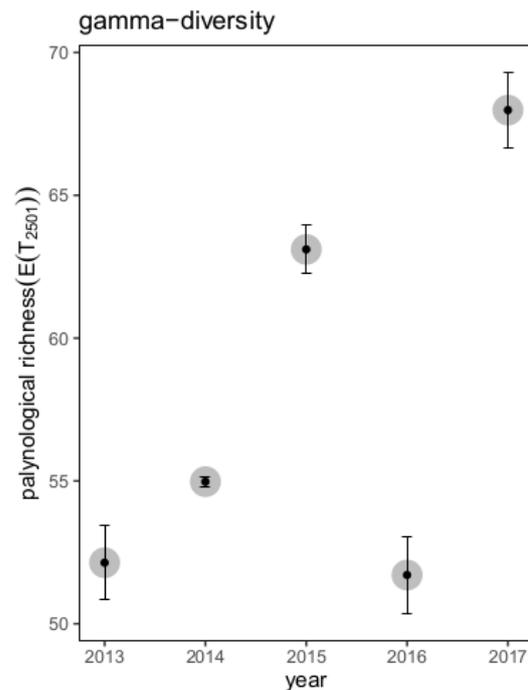


Figure 16: Total palynological richness per year. x-axis: analysed years. y-axis: estimated palynological richness ( $E(T_n)$ ) for an estimated pollen and spore count of 2501 grains ( $E(T_{2501})$ ). Error-bars show the standard deviation ( $1\sigma$ ).

## 7. Discussion

Modern airborne pollen rain can give essential information about the effects of climate and seasonality on vegetation (e.g. DONDERS et al. 2013; FLETCHER 2015 and HASELHORST et al. 2013). However, a pollen rain study has not been performed in the rainforest ecosystems of Sumatra before, even though pollen trapping is a common method in palynology. An investigation of the species patterns reflected in modern pollen and spore rain allows assessing palynological biodiversity and richness on a local and regional scale, through time and on different landscape management intensities (KR 2015). Thus, studying modern airborne pollen and spore rain on Sumatra, which is already suffering under intense land-use change and climate change can give important information about the after-effects of climate and land-use change on the plants' reproductive system.

### 7.1. The after-effect of ENSO on the palynological composition in different rainforest and land-use transformation systems (HI)

The palynological composition after the ENSO event in both investigated years (2016 and 2017) shows a change in pollen and spore rain composition of major families and pollen accumulation between land-use systems and per year. The pollen and spore composition shows that both landscapes, HR and BD, are dominated by families which include pioneer species such as Cannabaceae, Combretaceae/Melastomataceae and Elaeocarpaceae. However, there is a shift in pollen and spore composition from a higher dominance of secondary forest components towards an increasing admixture of primary forest representatives. Interestingly, these dominant families occurred in both, the forest system as well as in the transformation systems. This suggests that despite the differences in pollen and spore production and their dispersal strategies, the composition of dominant families is not merely affected by the changes in land-use types. The distance between the different land-use types is a feasible factor affecting the family composition. Generally, in both landscapes, the forest plots are located relatively close to the transformation system plots (Fig. 2). Therefore, the local pollen rain in the transformation systems could also include some pollen and spores from the forest, which were transported over a short (neighbouring regions) or a long distance into the study area (BEHLING et al. 1997).

The important taxa in forest plots in 2016 are represented by *Elaeocarpus*, *Trema*, *Combretocarpus* and the spore *Nephrolepis*. *Trema* is a fast-growing pioneer and plays a major role in regrowth communities. Thus, it is often dominant in early stages of succession (LAUMONIER 1997, CORLETT 1991). It flowers all year long hence it offers a frequent and high pollen production (COOMBE 1960). Therefore, it is not surprising that pollen of *Trema* is well represented in all plots and contributes to the pollen spectrum of both landscapes HR and BD. However, a decrease of *Trema* in 2017 indicates higher importance of other species or new species which are better

adapted to more stable climatic conditions after ENSO. Some taxa which indicate higher ecosystem functions and diversity within natural rainforests such as *Ficus* and *Syzygium* in HR, and *Canarium* and *Endospermum* in BD (Table 2, Fig. 5) become more abundant.

*Ficus* plays an important role in forest construction and offers a great food supply for various animals. Therefore, almost every vegetation type of the Malayan area includes at least one species of *Ficus*, which may occur in primary and secondary forest formations (BERG & CORNER 2005). *Syzygium*, the largest genus in the Myrtaceae family forms a key component of Sumatran lowland forest ecosystems by providing nectar, pollen and fruit for various animals (WIDODO et al. 2010). The genus *Endospermum* occurs mostly in mixed lowland primary and partially secondary forest formations, where it can be canopy forming (SCHAEFFER 1971). *Canarium* plays an important role in forest structure and diversity in moist lowland forests (DALY et al. 2015).

Besides *Trema*, the fern *Nephrolepis* is prominent in both landscapes in 2016. *Nephrolepis* is commonly found in severely disturbed areas, forest margins, open forest, or pioneer forest in the Sumatran lowland (HOVENKAMP & MIYAMOTO 2005). *Elaeocarpus* and *Combretocarpus* are only dominant in 2016, particularly. Some *Elaeocarpus* species are early succession species with a fast growth rate. They can also persist in primary forest and thrive under full grown canopy (ROSETTO et al. 2004), while *Combretocarpus* occurs abundantly in secondary forest or forests with open canopy, partially as pioneer species after fire (HOSCILO et al. 2008). These taxa were not prevailing in 2017, indicating that competition plays an important role in the overall taxa composition in which taxa of secondary forest and succession are outcompeted against primary forest taxa with better adaptations to a stable environment.

In the transformation systems, jungle rubber plots in both HR and BD are dominated by secondary forest taxa such as *Trema*, *Elaeocarpus* and *Nephrolepis*, concurrent with the presence of primary forest taxa such as *Ficus* and *Endospermum*. The Jungle rubber agroforestry under natural tree cover is an extensive land-use form, thus its forest functionality is not as high as in natural lowland forest. However, even though the canopy is not as closed as in natural forests and such disturbance is frequent, the jungle rubber comprises both pioneer and secondary forest species.

In general, *Trema* is still the dominant taxon in both landscapes in both years. However, like in the forest plots, it decreased from 2016 to 2017. This again indicates that other species or new species which are better adapted to a more stable climatic condition after ENSO gained more importance in the pollen and spore composition after a phase of competition. The taxa composition also shows components of natural and functional primary forest such as *Endospermum* and *Ficus*, complemented by secondary forest taxa such as *Elaeocarpus* and ferns such as *Nephrolepis* and *Huperzia* which is usually found at higher elevation and often in open areas (RUSEA et al. 2009). Interestingly, *Elaeis guineensis* was found dominant in both landscapes in both years considering

that oil palm is mostly pollinated by beetles such as weevils, whereby pollen dispersal by wind is present but not very effective (HENDERSON 1988, MAYFIELD 2005). Thus, pollen of *Elaeis guineensis* has a short distance dispersal strategy. However other land-use forms are closely located to oil palm plantations, explaining the concurrence of oil palm pollen in all plots. In particular, the transformation system plots are located closer to each other than to the forest plots. The forest plots are more isolated and have denser vegetation cover, which might not allow strong influx of *Elaeis guineensis* pollen. Albeit they also bear a dense vegetation cover, the jungle rubber plots show a higher percentage of *Elaeis guineensis* as they are located in ultimate proximity to oil palm plots (Fig. 2 ) There are changes in taxa composition between forest and rubber jungle plots and the rubber plantations. Rubber plantations in both landscapes show no components of natural forest systems amongst the present dominant taxa. The already mentioned pioneer species such as *Trema*, *Elaeocarpus* or *Nephrolepis* and pollen of the major crop cash trees such as *Hevea brasiliensis* and *Elaeis guineensis* are overall present. The dominant pioneer taxa such as *Trema* have the same pollen production pattern as in the forest and rubber jungle. Their representation decreased from 2016 to 2017 when the climatic conditions were more stable and more beneficial for natural forest taxa. *Hevea brasiliensis* is the main crop tree in Rubber plantations and thus is expected to be dominant. Interestingly, it was only found dominant in HR and shows less dominance in BD. This might be related to the distance between plots within the land-use forms. In HR, the rubber plantations are located closer to other transformation system plots than to the forest plots. While in BD, the transformation system plots are located closer to the forest (Fig. 2). Considering this, it is possible that an extensive surrounding of jungle rubber and rubber plantations cause higher proportions of *Hevea brasiliensis* in rubber plantations in HR. Whilst in BD, rubber plantations are located at the rainforest margin. Therefore, the taxa composition has been influenced by the forest taxa and resulted in a lower proportion of *Hevea brasiliensis*.

The oil palm *Elaeis guineensis* was found prominent in both HR and BD. Again, this is related to the proximity of oil palm plantation plots and rubber plantation plots in both landscapes. With the high proportion of *Elaeis guineensis*, various ferns such as *Nephrolepis*, *Asplenium* and *Davallia* also increased, as they originate from epiphytes which grow on the stems of *Elaeis guineensis* (BÖHNERT et al. 2016). A clear change in taxa composition can also be observed in the oil palm plantation plots. The extreme dominance of *Elaeis guineensis* is striking, suppressing other pollen types within the monoculture. This is followed by pioneers and secondary forest taxa such as *Trema* and *Mallotus/Macaranga*. Furthermore, Poaceae were present in both landscapes indicating more open areas and disturbed undergrowth vegetation (REMBOLD et al. 2017).

Overall, a major difference in taxa dominance has been observed between the years. In 2016, taxa composition was dominated by secondary forest and pioneer taxa, while in 2017, a more stable composition of primary to secondary forest taxa was prominent. Sumatra experienced an

elongated dry period related to ENSO (El Niño phase) starting in July 2015 and accompanied by a fire season, peaking in September 2015. This could have caused a major decrease in the vegetation's reproductive efforts and fitness which could have increased mortality in natural forests (SPESSA et al. 2014, YEAGER et al. 2003, MIETTINEN et al. 2017, HARRISON et al. 2016, SZE et al. 2019). This ENSO-related drought and other environmental factors triggered an aseasonal mass flowering between the years 2015 and 2016. However, the after-effects of stress still seem to remain as species of secondary forests and pioneers happen to compete against species of the primary forest. A higher canopy tree mortality and fire correlated leaf shedding possibly caused more canopy gaps and thus allowed an increase in secondary forest growth (NISHIMUA et al. 2007, YAEGER et al. 2003, CORLETT 1991). Secondary species are mostly part of the undergrowth. They grow and flower faster than species of the primary forest to use the opportunity of higher light and nutrient availability quickly after i.e. a canopy opening (NISHIMUA et al. 2007, YAEGER et al. 2003, CORLETT 1991). Therefore, it is logical, that a year after fire and drought stress, pioneer species are more dominant (DAVIES et al. 1999). Furthermore, species of the primary forest need to preserve resources after a major stress event and the effort of intensive flowering, and thus need time to recover before further reproduction.

The effect of climatic events such as ENSO was not pronounced in rubber and oil palm plantations. The vegetation in rubber and oil palm plantations is already under strong disturbance due to land-use intensification which includes measures such as weeding, fragmentation of the tree cover or mowing (REMBOLD et al. 2017). Therefore, climatic events such as ENSO might not have a visible after-effect, which is reflected in the pollen and spore composition.

In general, changes in pollen and spore accumulation, reflected in the PSI, can be observed between both years (see i.e. Table 3). In 2017, the PSI decreased noticeably in almost all land-use forms except jungle rubber, where the influx is higher. This might be related to the better growth of primary taxa, compared to pioneer and secondary taxa, due to more stable climatic conditions after the ENSO.

The pollen accumulation in both rubber plots (rubber jungle and rubber plantation) experienced an increase in 2017, contrary to the influx in the forest and the oil palm plantations. The jungle rubber plots show, amongst others, high percentages of Moraceae/Urticaceae such as *Ficus* (Table 5, Fig. 1). *Ficus* is a high pollen producer (GALIL & MAIRI 1981), thus the effect of a reduction in pioneer pollen influx might be less pronounced. The same effect can be seen in rubber plantations (Table 5, Fig. 1). The pollen accumulation increases with the sudden dominance of *Mallotus/Macaranga* and *Elaeocarpus*, as well as the growing dominance of Cyperaceae. *Mallotus/Macaranga* and *Elaeocarpus* are species of late succession and high pollen producers, persisting under canopy (DAVIES et al. 1999, CORLETT 1991, LAUMONIER 1997). An increase in pollen

production of such indicators of late succession would rather point towards ongoing long-term disturbance, which allows secondary forest to grow and expand.

On the other hand, the pollen accumulation in forest plots and in oil palm plantations decreased (Table 3). In the forest plots, constant pollen producers such as Melastomataceae, *Trema* or *Elaeocarpus* are reduced and replaced by the dominance of primary forest taxa which do not depend on strong pollen production (BENTOS et al. 2008, DAVIES et al. 1999). Whilst in oil palm plantations, a reduction in pollen influx can be explained by the effect of intensive management over the years, reducing undergrowth regularly.

However, changes in PSI are more prominent between the land-use forms. The PSI marked a decrease from forest to transformation system. A remarkable change can be seen between the forest and the rubber system as the PSI strongly decreased from forest to jungle rubber and rubber plantations. The PSI in the oil palm plantation remained high, as *Elaeis guineensis* being the main species contributed to the total pollen composition. This overall suggests that the climatic conditions after the ENSO do not merely affect pollen production and dispersal as changes are more visible between land-use types.

## 7.2. Changes in diversity patterns between different agro-forestry management systems after the ENSO event (HII)

The results from both investigated years show that despite differences in pollen and spore production and dispersal strategies, the  $\alpha$ -diversity is mostly affected by the different land-use types included in this study (forest, jungle rubber, rubber and oil palm) even though slight trends between years can be monitored as well. Alongside a gradient of land-use intensification, the Simpson index decreased from forest to jungle rubber and rubber plantations, to the lowest in oil palm plantations.

Such a decrease in  $\alpha$ -diversity can be caused by long-term intensive management. Oil palm plantations represent monocultures under partially intense management, which offers little possibilities for the establishment of more complex landscape and species patterns (EDWARDS et al. 2014). Considering the possible long-term effects of ongoing intervening measures, such as weeding or fertilization on species patterns (REMBOLD et al. 2017), further decrease in the diversity of indigenous plant communities can be expected (EDWARDS et al. 2013). Therefore, lowest floristic diversity was found in the intensively managed oil palm plantations, followed by rubber plantations (REMBOLD et al. (2017)). The same result was already discussed in the work of KR (2015), which showed that palynological  $\alpha$ -diversity in oil palm plantations shows tendencies to decrease even further with ongoing intensive management. However, an extended period of

pollen trapping is needed to confirm this pattern as five years do not monitor such long-term trends sufficiently.

The results between the investigated years show that the Simpson index in 2017 slightly increased in the forest plots. The forest plots experienced a shift in the composition of dominant families which is reflected in the pollen influx between years. In 2016, the forest was mostly dominated by pioneer species, which led to a partially lower species richness (Table 2, Fig. 7). On the other hand, the primary forest taxa increased in 2017 after a phase of succession and competition against the secondary taxa, which resulted in the increase of the Simpson index.

Meanwhile, the  $\alpha$ -diversity in rubber jungle and rubber plantations shows no significant difference between years. As already stated, the land-use transformation systems are constantly under disturbance and partially dominated by pioneers and secondary forest taxa. Being constant pollen producers throughout the year (BENTOS et al. 2008), pioneer taxa overlay the pollen and spore signal of other species which possibly did not profit from stressors such as drought or fire in 2015. Therefore, the Simpson index of jungle rubber and rubber plantations does not vary much between 2016 and 2017.

The  $\beta$ -diversity from both investigated years shows no significant differences between land-use forms. Different land-use forms in 2016 and 2017 are no more significantly different from each other in their palynological dissimilarity. A less distinguishable gradient in dissimilarity between plots might be the effect of continuous landscape fragmentation in all land-use forms. Even though the types of management are highly different from each other, all land-use forms are equally dissimilar from each other. It should be expected that the plots become more similar to each other with increasing management. This is also reflected in the results of the year 2013 (KR; 2015). If all land-use systems show equally dissimilar plots, perhaps all plots are equally disengaged from each other and show an equal level of fragmentation (JAMONEAU et al. 2012).

A change in  $\beta$ -diversity was more prominent between years, as the dissimilarity between land-use types (forest, rubber jungle, rubber plantation and oil palm plantation) increased in 2017. Once again, this can be explained by the effect of dominant secondary forest taxa in 2016, which decreased in 2017. Since all plots show pioneer and succession taxa equally, taxa abundancies become similar. This suggests a decrease in palynological dissimilarity in 2017 when primary forest taxa become more abundant. Their occurrence can vary strongly between plots as different systems can show a local variety in distributed taxa.

Palynological richness decreases steadily with increasing land-use intensity (Fig. 9, Fig. 10). Less pollen taxa are found in transformation systems under intensive management for the same pollen amount. This suggests that the loss in pollen taxa might be connected to intensive management

strategies such as weeding or regular mowing of the undergrowth (REMBOLD et al. 2017). The number of species decreased along with land-use intensification. This shows the same result as the palynological richness from 2013 where  $\gamma$ -diversity decreased in a gradient between different land-use forms (KR 2015). However, estimated grain counts for rubber plantations in 2013 show a less significant decline to the years 2016 and 2017 (KR 2015, Fig. 9). This is due to the effect of low pollen production of *Hevea brasiliensis*, causing an over representation of other species. Considering this presumption, rubber plantations in 2016 and 2017 could have an even lower species richness than visualized within the values. This shows the effect of time and continuous intensive management on a landscape's diversity and species richness along the years.

Further decreasing trends can be seen in the rarefaction curves of 2016 and 2017. Curves in 2016 are still increasing steeply, indicating that higher grain counts could resolve into a higher variety of pollen taxa. On the other hand, curves in 2017 of the transformation systems in particular head towards their plateau earlier. All indicates a decrease in each landscapes species richness from 2013 to 2016 and further to 2017 in land-use transformation systems.

### 7.3. The long-term effect of ENSO on the pollen production and diversity in the rainforest system (HIII)

The BF and HF are natural rainforest conservation areas consisting of a mixture of intact primary forest and secondary forest. Both landscapes have undergone massive deforestation and fragmentation, mostly through illegal logging and other processes such as small holder conversion of natural forest to oil palm monocultures (DRESCHER et al. 2016). However, the HR and BD landscapes show differences in their total pollen and spore influx (PSI) between the years.

Firstly, the PSI from 2013 shows a strong difference in the amount of influx between BD and HR (Fig. 12b, Table 5). A wide variety of PSI values has been detected in BD (between 46991 grains/cm<sup>2</sup>/year and 1876 grains/cm<sup>2</sup>/year), which resulted in the highest influx of all years (median ~ 13923). This suggests a higher PSI in BD in the beginning of the investigated years than in HF. Comparing the influx between landscapes in the following years, the influx in BD was significantly higher in 2014 and 2016 as well, with a slightly higher influx in 2015. Only in 2017 the PSI showed a higher influx in HR.

Additionally, a wide variety in values indicates strong differences in influx between forest plots. Considering the location of forest plots in BD, some are situated closer to the forest margin and transformation systems. Certainly, those plots are more prone to disturbance, logging, or the ingrowth of secondary forest species which thrive at forest margins (LAUMONIER 1997). Perhaps this heterogeneity in forest plots altered the PSI. Furthermore, the species composition might play

an important role where high pollen producers such as Urticaceae or Melastomataceae might occur in one landscape but lack in the other.

On the other hand, forest plots in HR are located close together and inside the rainforest, isolated from the forest margin and disturbance. Thus, constant pollen producers and succession taxa are perhaps not as prominent in the pollen spectrum.

The annual pollen and spore influx shows that the pollen influx was higher than the spore influx (Fig. 12a). Pollen and spores have different dispersal strategies, which are part of basic plant reproduction (MARTIN et al., 2009). Ferns are mostly part of the undergrowth, where they are more protected from regional climate variations and generally react to changes in microclimate. This independence from regional climate can be seen in the spore influx (Fig. 12a), which shows less variance between years than pollen influx. Fern spores are commonly dispersed by water thus are only occasionally transported from further distance. Therefore, they represent a rather local signal, while pollen has various dispersal strategies as it can be dispersed by wind, animals, mainly insects, or by water (RAVEN et al. 2006). Thus, pollen can represent taxa from further distance. For example, the pollen of wind pollinated taxa can be released and carried with the wind over a long distance before it is “captured” in a trap. This might explain why in general the pollen influx was higher than the spore influx.

In the following year, the PSI in both landscapes showed a strong decrease in 2014 especially in BD, while the extensive difference in PSI is no longer prominent between HR and BD (Fig. 12b). On a tropical island like Sumatra, the rainfall patterns throughout the year can determine flowering phenology and its offer (c.f. OPLER et al. 1976, ROUBIK et al. 2005, BENDIX et al. 2006). An inter-annual climate variability, such as ENSO could affect rain intensity by producing extreme weather conditions (driest or rainiest seasons; CHRISTENSEN et al. 2013). As such, ENSO could strongly influence floral phenology and in consequence the pollen availability in tropical ecosystems (CHANG-YANG et al. 2016, CHAPMAN et al. 2018, DETTO et al. 2018). Therefore, the strong decrease in PSI within this year could be related to the early impacts of ENSO, causing drought (LESTARI et al. 2018).

A biotic or abiotic stressor such as ENSO-related drought in combination with a high fire frequency, related to drought and landscape conversion, could cause a general decline in plant productivity and fertility. This would lead to higher tree mortality and the invasion of pioneer species (HARRISON et al. 2016, SLIK 2004, NISHIMUA et al. 2007). Fires occurred close to the plots, and the beginning drought affected the landscape, which might have an impact on pollen and spore productivity of most dominant families. Therefore, a strong decline in PSI in 2014 can be explained. However, not only fire itself has an impact on vegetation. Developing haze from forest fires which lasts over months within the surrounding region can have a short term influence on

photosynthetic success, causing partial leaf shedding and other subsequential reactions including a decrease in flower and fruit production (DAVIES & UNAM 1999, HARRISON et al. 2007, 2016). Depending on the individual dispersion strategy, surrounding fires, and following haze could affect the pollen and spore representation within local pollen traps. In BD forest plots are stronger exposed to disturbance, as they occur close to the forest edge. Fire tends to spread more successfully at fragmented forest sites, where the fire-resistant primary forest is reduced (SPESSA et al. 2014, DENNIS & COLFER 2006). This feasibly explains the lower PSI in BD compared to HR.

Furthermore, the early effect of ENSO can be seen in the palynological richness of 2014 (Fig. 15, Fig. 16). The number of families in 2014 increased slightly (from 52 to 55 families), where the rarefaction curve is close to its saturation. Even though estimated counts are slightly higher than in 2013 the plateau is reached quickly, indicating that only little more families are to be expected in higher grain counts. This low  $\gamma$ -diversity in 2014 can also be explained by dry conditions advancing the ENSO event 2014 (LESTARI et al. 2018), which reduced pollen production and species diversity. Tropical forests under the influence of fire usually show a decrease in species richness (SYAUFINA & AINUDDIN 2011, YAEGER et al. 2003, HARRISON et al. 2016). The  $\alpha$ -diversity in 2014 decreased visibly, as seen in the Simpson index (Fig. 14a) and thus, shows the same trend as the PSI.

Nonetheless, forest plots show less palynological dissimilarity (Fig. 14b) amongst each other in their pollen and spore composition compared to other years. Usually taxa react equally to environmental disturbance amongst themselves. The same taxa might not flower or are getting disturbed in 2014 whilst other taxa can tolerate climatic disturbance and produce pollen anyways. This is reflected in the strong reduction of some families with mostly herbaceous taxa such as Asteraceae, Poaceae and Cyperaceae (appendix S1 Fig. 17). While other families such as Areaceae increased in 2014 as they are less affected by fire due to their vascular structure and resprouting ability above ground (VAN EIJK et al. 2009).

Afterwards, the pollen production increased in 2015, which could imply a higher overall flowering intensity at the community level that that might occur due to a synchronised GF episode, a unique phenological behaviour observed in the aseasonal Dipterocarpaceae-dominated rainforests (LH 2020). Thus, Dipterocarpaceae are expected to be well represented in pollen accumulation during ENSO events (VAN DER KAARS et al. 2000, 2010, SAKAI et al. 1999, ASHTON 1988).

Apart from dipterocarp behaviour, the pollen rain composition may also capture changes in flowering activity on the population and individual level along the years that might have been caused by the GF event. In this study, it is reflected in the influx of most dominant pollen and spore families which occurred every year such as Euphorbiaceae, Areaceae, and Rubiaceae, which show highest PSI values in 2015. However, considering Dipterocarpaceae to play a major role in mass

flowering (APPANAH 1985, 1993, SAKAI et al 1999) the PSI of the Dipterocarpaceae family was low (Fig. 13).

If GF occurred as suggested by the increase in annual pollen influx, the representation of the Dipterocarpaceae family could have been overshadowed by the general increase in flowering intensity. It is possible that dipterocarp pollen is under-represented compared to other families with species-rich palynological assemblages and therefore only shows a moderate representation (LH 2020) compared to families being known for accompanying GF during ENSO events such as Euphorbiaceae, Sapotaceae, Sapindaceae or Anacardiaceae (APPANAH 1985).

The study on GF in the rainforest system by LH (2020) resulted that the differences in palynological richness between 2015 (the year of ENSO) and 2014 were not significant. The pollen influx of the dipterocarp family increased noticeably during the GF event, although their representation was low compared to other dominant families. This suggests that even though a GF event occurred, the GF peak associated with the ENSO-drought phase (El Niño) was not prominent. Accordingly, other studies in the western peninsular Malaysia show that El Niño has only little impact on the occurrence of mass flowering. Instead, the mass flowering was correlated to La Niña events (ENSO cool phase; ASHTON et al. 1988, NUMATA et al. 2003, WICH & SCHAİK 2000, YASUDA et al. 1999). It is also possible that dipterocarps in both landscapes did not undergo strong mass flowering, whereby dipterocarps in other areas experienced a mass flowering, since a GF can reach from regional scales to local flowerings restricted to a certain area (APPANAH 1993). However, in general, an increase in pollen influx for the Dipterocarpaceae family was present in all investigated years with a peak in 2015.

In alignment with the GF, the  $\alpha$ -diversity also increased, driven by a higher offer in flowering taxa in the forest plots (Fig. 14a). Furthermore, the dissimilarities between plots are highest, as reflected in the  $\beta$ -diversity (Fig. 14b). A higher dissimilarity between plots could be caused by local flowering of certain families. Some families such as Myristicaceae, Sapindaceae or Dipterocarpaceae are usually underrepresented in plots due to low pollen production or aseasonal flowering rhythms (APPANAH 1993), even though they locally occur. With the occurrence of a mass flowering event, they now are present in the pollen and spore record and therefore increase the dissimilarity between different sites. Overall, the increasing representation of certain families due to the GF led to a significant increase of palynological richness in 2015 (from 55 to 63 families).

After the major increase in 2015, the PSI noticeably decreased in both landscapes especially in HR (Fig. 11, Fig. 12b). This might be related to the after-effect of a long dry period and/or a fire season and the distance between plots additionally (see chapter 7.1). In particular, the forest plots in HR are located close to each other at the forest margin, and therefore such disturbance might affect

the overall pollen and spore accumulation. The PSI started to decline in 2014 due to the early effect of drought related to ENSO but increased in 2015 through the GF event. However, the vegetation still suffers the effects of stress and disturbance and has been reduced due to higher mortality, which all was reflected in a low pollen production.

The changes in diversity in 2016 were pronounced by a strong decline in  $\alpha$ -diversity (Fig. 14a), caused by the dominance of pioneer taxa, which suppressed other taxa with lower abundance and partially excluded them from the pollen or spore count. However, the  $\beta$ -diversity is lower than in 2015 (Fig. 14b). This suggests a reduced representation of various families in different plots due to the GF event. The general changes in diversity are reflected in the palynological richness, where the number of families was significantly reduced right after the major ENSO event, which includes a phase of GF (from 63 to 52 families).

In the following year 2017, changes could be determined between both landscapes. The PSI in BD is lower than in HR. This can be explained by the strong dominance of the Urticaceae and Cannabaceae family in some plots of HR (Table 1), which include many anemophilous pollen taxa which are high pollen producers (REDDI & REDDI 1986). The differences in total pollen and spore accumulation are also noticeable between years and per landscape. In BF, the PSI continued to decrease while in HF, the PSI greatly increased. Again, the disturbance might influence the differences in PSI. The forest plots in BD, as discussed above are located closer to the forest margin and other land-use forms. Therefore, disturbance might lead to the decrease in influx in BD. On the other hand, forest plots in HR plots are more isolated. Thus, disturbance might not have much influence on the vegetation.

In this year, the  $\alpha$ -diversity index was higher compared to the previous year. This suggests an increase in species richness per plot. The palynological dissimilarities also increased, which might be influenced by an increase in landscape disturbance and forest fragmentation over time. On the other hand, palynological richness shows the highest estimated family number of all years with 67 families.

## 8. Conclusion

Modern pollen rain studies are essential to investigate plant phenological responses to climatic and environmental variability (e.g. occurrences of ENSO events vs normal years).

This study focuses on the after-effect of ENSO on pollen production and palynological diversity in different rainforest and land-use transformation systems in Sumatra for two consecutive years (2016 and 2017). Furthermore, a synthesis with previous studies has been done to complete a five-year data set (2013-2017) and to provide a better understanding of the long-term effects of climatic events such as ENSO on the vegetation's reproductive success and diversity patterns.

The palynological composition after the ENSO event in both investigated years (2016 and 2017) shows a change in the pollen and spore composition of major families and pollen accumulation between land-use systems and per year. The pollen and spore composition in 2016 shows that both landscapes, Harapan (HR) and Bukit Duabelas (BD), are dominated by families which include pioneer species such as Cannabaceae, Combretaceae/Melastomataceae and Elaeocarpaceae with dominant taxa including *Trema*, *Elaeocarpus* and *Nephrolepis*. However, there is a change in pollen and spore composition in the following year. In 2017, the dominant secondary forest components shift towards an increasing admixture of primary forest such as *Endospermum*, *Syzygium* or *Canarium*. This suggests that competition plays an important role after climatic disturbance, where taxa of secondary forest and succession are outcompeted against primary forest taxa with better adaptations to more stable climatic conditions.

Interestingly, the same dominant families occurred in both, forest and transformation systems. This suggests that distance between plots is an important factor, besides the differences in pollen and spore production, dispersal strategies or land-use types (forest, rubber jungle, rubber plantation and oil palm plantation).

The variation in palynological composition can also be observed through changes in the total pollen and spore accumulation (PSI). In the first year after ENSO, the PSI generally increased, driven by a constant pollen production of pioneer taxa and secondary forest taxa. In the second year after ENSO, pollen composition induces a certain degree of recovery towards a more stable forest ecosystem with a higher presence of functional primary forest taxa and higher diversity. Therefore, the PSI decreased noticeably with the retreat of secondary forest and rehabilitation of natural forest.

In most years, the PSI in BD is higher than in HR. In BD, the forest plots and land-use plots are located close to each other and forest plots are more prone to disturbance due to their location at the forest margin. Therefore, the dominance of secondary forest elements elevated the PSI. While

in HR the forest plots and land-use plots are isolated from each other and do not share contact to frequently disturbed secondary forest.

Diversity patterns between different land-use systems after the ENSO phenomenon are mostly influenced by the degree of management. However, slight changes between years are visible, especially in rainforest: 2016 shows lower  $\alpha$ - and  $\beta$ - diversity in forest plots, caused by the overall dominance of few pioneer taxa, suppressing less abundant taxa and causing a higher similarity between plots. The overall species richness is the lowest in all investigated years, indicating a low  $\gamma$ -diversity on a landscape-scale. Anyhow, changes between land-use forms are most prominent with a decrease in  $\alpha$ -diversity in oil palm plantations and slightly increasing dissimilarity in managed sites from 2016 to 2017, perhaps through increasing landscape fragmentation.

Considering the examined inter-annual changes over five years in rainforest plots, it is clear that various impact factors, triggered by ENSO alter modern pollen and spore influx and diversity. Here it is noticeable that both landscapes react slightly different, as forest plots in BD are more exposed to disturbance, being located closer to the forest margin.

An intensive dry period in 2014 (initiation of the ENSO) accompanied by fire and increasing haze may have caused a strong reduction in the PSI, the number and abundance of species ( $\alpha$ -diversity), palynological dissimilarity between plots ( $\beta$ -diversity) and palynological richness ( $\gamma$ -diversity). A general flowering event in 2015, triggered by the ongoing ENSO event increased  $\alpha$ -  $\beta$ - and  $\gamma$ -diversity and PSI significantly, in comparison to the year before. 2016 stands out as a year of natural succession, showing the after-effect of ENSO. Here the palynological composition changes towards the dominance of secondary forest components, which increased the PSI by a higher pollen production.  $\alpha$ - $\beta$ - and  $\gamma$ -diversity have been reduced again, through the reduction of more diverse primary forest components. 2017 offers a reinstatement to stable conditions and rehabilitation of natural primary forest vegetation. The PSI decreases slightly, caused by a reduced dominance of secondary forest taxa.  $\alpha$ - $\beta$ - and  $\gamma$ -diversity increase compared to the year before due to diverse primary forest vegetation.

In conclusion, palynological composition and PSI change in reaction to climatic changes. However, changes are most prominent in landscapes without constant disturbance. Furthermore, the location of plots needs to be considered to compare changes in palynological composition and PSI between plots, respectively. Land-use transformation systems do not reflect climatic disturbance, as anthropogenic disturbance is too high and always present. Four phases of change can be distinguished in the modern pollen and spore rain of rainforest systems: 1) A phase of climatic disturbance through drought or fire with the beginning of ENSO; 2) A phase of GF as an aseasonal phenological phenomenon in SE Asia; 3) A phase of succession and competition of secondary

forest against disturbed primary forest; and 4) A phase of recovery with the reestablishment of primary forest components.

This pattern could offer important information for the interpretation of environmental archives. Furthermore, it shows the strong phenological reaction of vegetation to aseasonal climatic changes. Land-use transformation systems on the other hand, show a strong decline in palynological diversity and richness with increasing management. In the long-term, diversity seemingly decreases from 2015, the first year monitored to year 2017. This can be the impact of continuous management and depletion of landscapes. With pollen and spores forming the key component of the vegetations reproduction and genetic diversity, this indicates a major decrease in landscape diversity. Anyhow, more years need to be investigated to determine clearly distinguishable trends.

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# Appendix Supplement 1

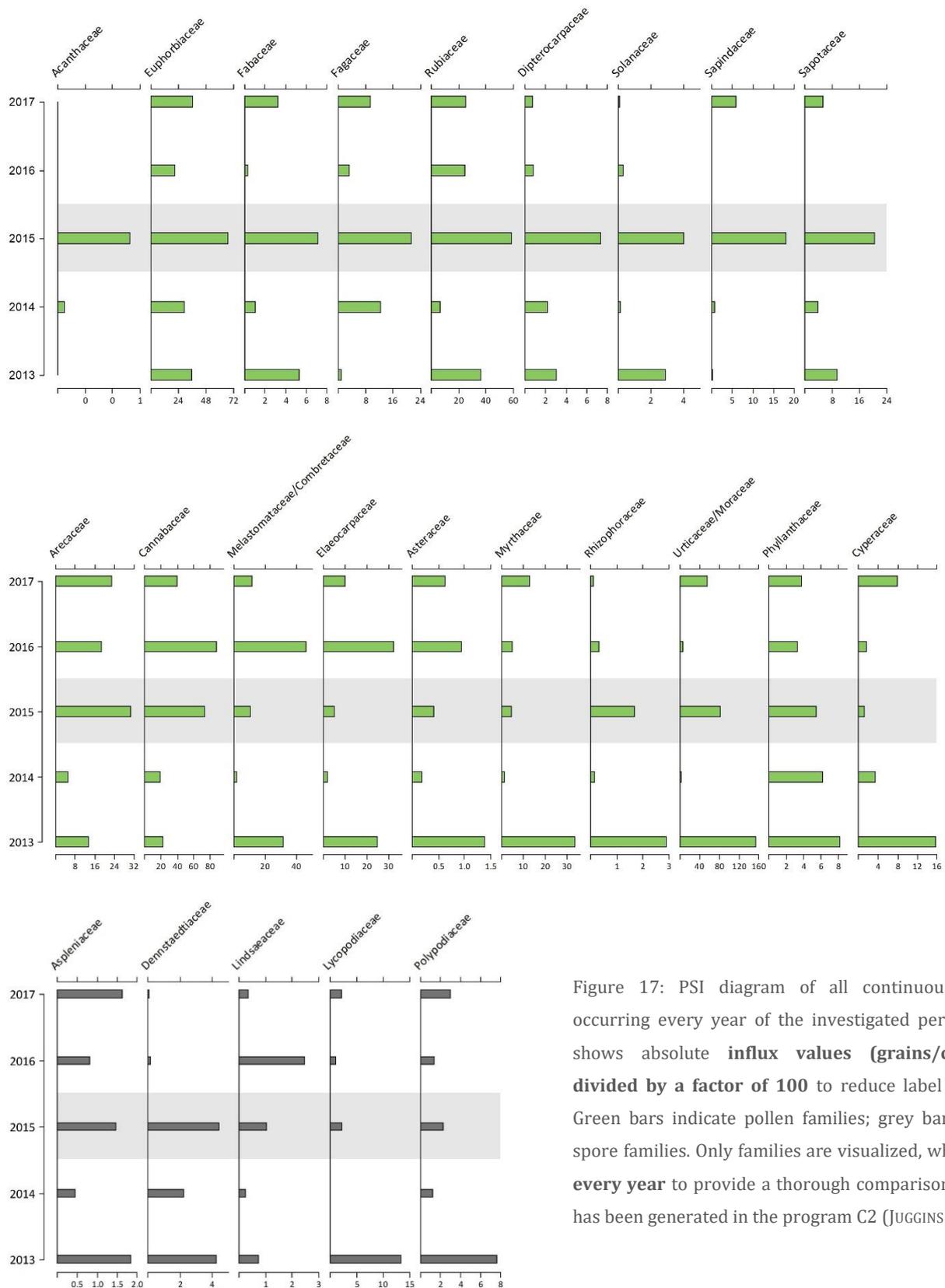
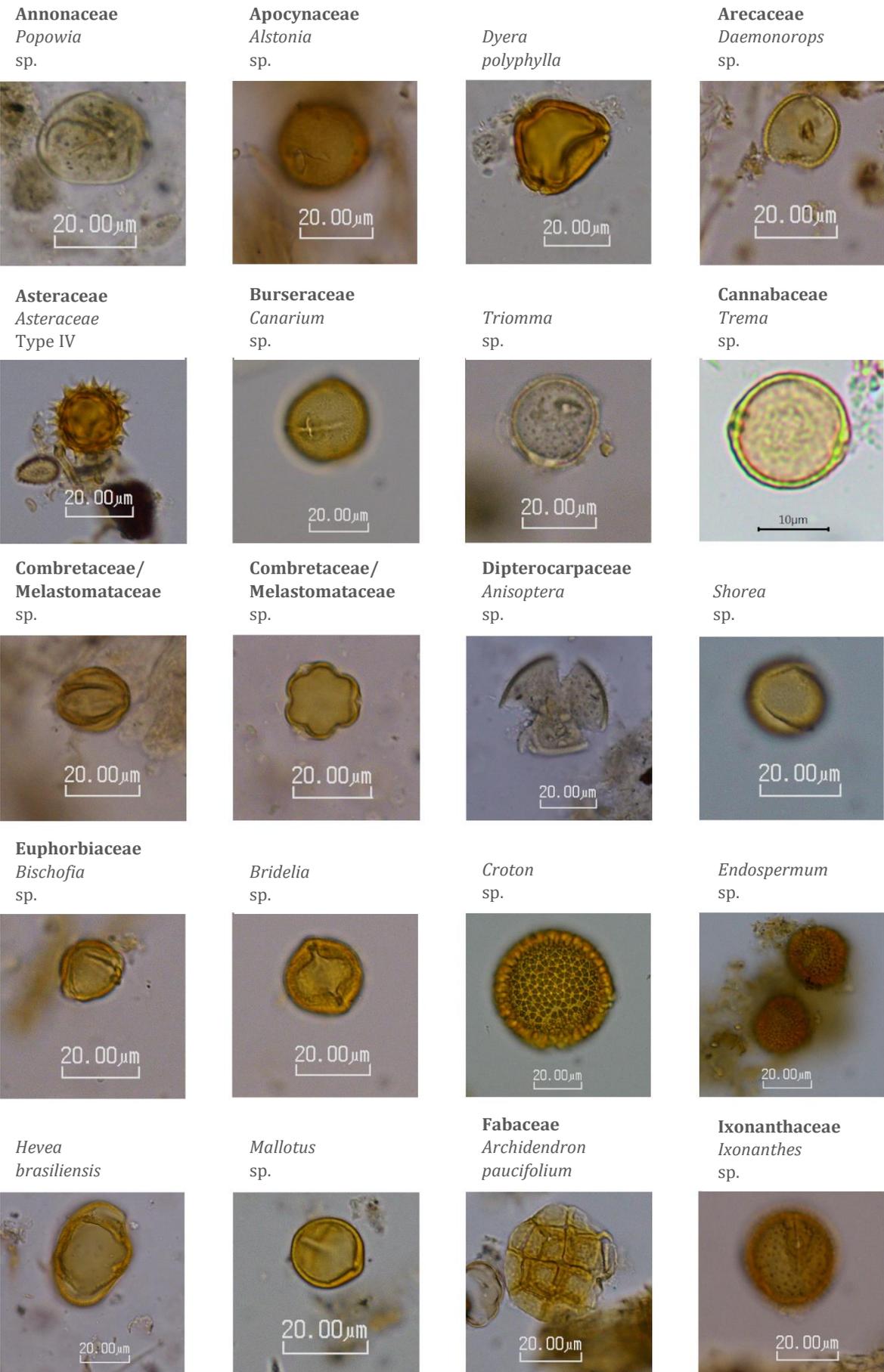


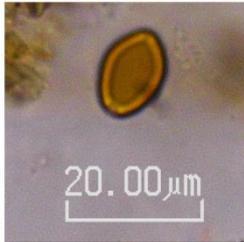
Figure 17: PSI diagram of all continuous families occurring every year of the investigated period. x-axis shows absolute **influx values (grains/cm<sup>2</sup>/year)** divided by a factor of 100 to reduce label crowding. Green bars indicate pollen families; grey bars indicate spore families. Only families are visualized, which **occur every year** to provide a thorough comparison. Diagram has been generated in the program C2 (JUGGINS 2016).

## Supplement 2

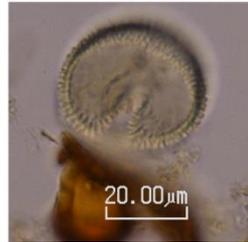
Figure 18: Pictures of various pollen and spore types of 2017.



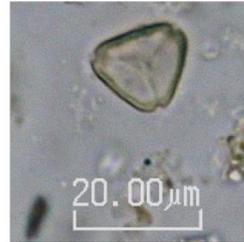
**Moraceae**  
*Ficus*  
sp.



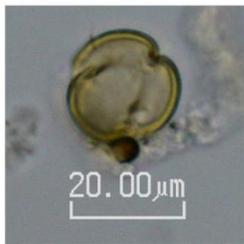
**Myristicaceae**  
*Knema*  
sp.



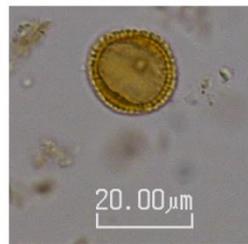
**Myrtaceae**  
*Syzygium*  
sp.



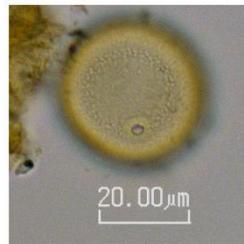
**Phyllanthaceae**  
*Baccaurea*  
sp.



*Phyllanthus oxyphyllus*



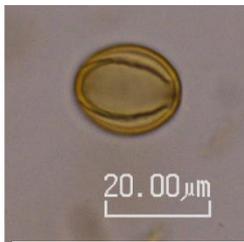
**Poaceae**  
sp.



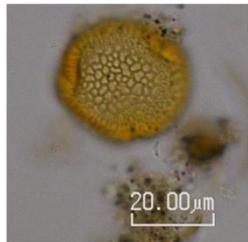
**Podocarpaceae**  
*Nageia nagi*



**Rubiaceae**  
*Coffea*  
sp.



*Eurycoma*  
sp.



*Nauclea and Elaeis guineensis*  
(Arecaceae)



*Porterandia*  
sp.



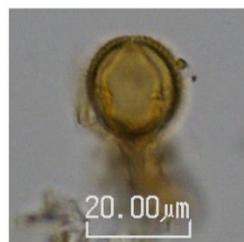
*Timonius*  
sp.



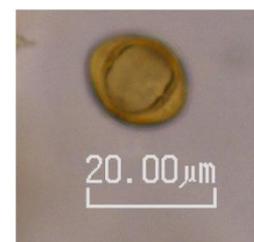
**Rutaceae**  
*Cleome*  
sp.



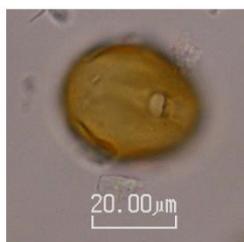
*Clausena*  
sp.



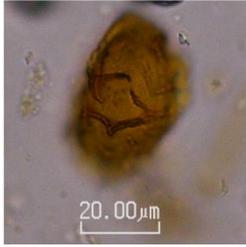
**Sapindaceae**  
*Mischocarpus*  
sp.



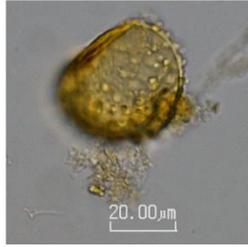
**Sapotaceae**  
*Palaquium*  
sp.



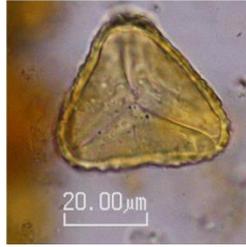
**Aspleniaceae**  
*Asplenium*  
Type II



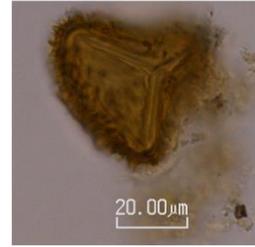
**Blechnaceae**  
*Stenochlaena*  
*palustris*



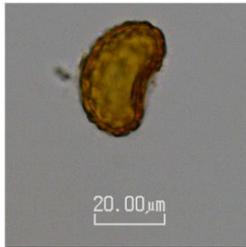
**Cyatheaceae**  
Type II



**Cyatheaceae**  
*Cyathea*  
*biformis*



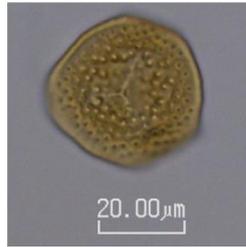
**Davalliaceae**  
*Davallia*  
Type IV



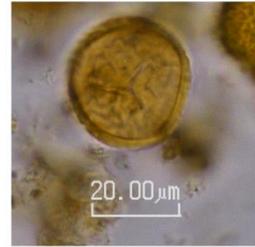
**Lindsaeaceae**  
*Lindsaea*  
Type I



**Lycopodiaceae**  
*Huperzia*  
Type II



*Lycopodiella*  
sp.



**Polypodiaceae**  
*Goniophlebium*  
sp.



*Pecluma*  
sp.



*Polypodium*  
sp.



**Pteridaceae**  
*Pteris*  
*excelsa*



## Declaration of authorship

Name: Ms Svea Lina Jahnk

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## Declaration

I hereby declare that I have produced this work independently and without outside assistance and have used only the sources and tools stated.

I have clearly identified the sources of any sections from other works that I have quoted or given in essence.

I have complied with the guidelines on good academic practice at the University of Göttingen.

If a digital version has been submitted, it is identical to the written one.

I am aware that failure to comply with these principles will result in the examination being graded "nicht bestanden", i.e. failed.

Göttingen, 3rd November 2020

Svea Lina Jahnk