

Georg-August Universität Göttingen

**Seed rain in remnant forests and an oil
palm plantation in Jambi province,
Sumatra**

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1 Summary

As part of the subproject B11, which belongs to the collaborative research project CRC 990, this study compared and analyzed seed rain between the oil palm plantation in Humusindo (B11 study site), a forest fragment close to Humusindo and Harapan rainforest, as well as along a distance gradient from the oil palm plantation to the forest fragment. Four randomly distributed seed traps were established within eight sampling plots in three systems: the rainforests, the forest fragment and in the oil palm plantation. At the distance gradient, seed traps were established on eight sampling plots, which are positioned along a transect on a logarithmic scale. All collected seeds were investigated and observed in the CRC lab at the University of Jambi.

During six seed collections many seed traps were destroyed probably by monkeys in the forest fragment. 3755 seeds of 59 species were discovered in 32 sampling plots. Five species were assigned to species level, 16 to genus level, 21 to family level and the 17 species were listed as Morpho-species. In the rainforest the species richness was higher (832 individuals; 39 spp.) than in forest fragment (66 individuals; 18 spp.), in the gradient (2708 individuals; 15 spp.) and in oil palm plantation (149 individuals; 4 spp.). The Kruskal-Wallis Test proved a highly significant difference (*Kruskal-Wallis Test* $P < 0.001$) of the number of species between each system and the gradient, but not for the abundance. Seven very abundant species with more than 100 seeds were encountered in the 32 sampling plots of the systems and the gradient. Three of these species (*Asystasia gangetica*, *Paspalum conjugatum*, *Clidemia hirta*) were invasive plants. All systems and the gradient showed steep rank abundance curves, which indicated the dominance of a few abundant species. The curve of the rainforest rank abundant plot merged in a long, shallow tail representing a high number of less abundant species (singletons). Furthermore, the species frequency in the rainforest was more evenly distributed as in other system or in the gradient. The non-metric multidimensional scaling (NMDS) ordination showed a wider scattering of rainforest sampling plots, indicating huge difference of their species within the rainforest, as in other systems and in the gradient. Furthermore, the large distances of the rainforests sampling plots to sampling plots of other systems and the gradient indicated the difference of the rainforests species to species in other systems and the gradient. The accumulation curve showed an increasing trend for each system and the gradient in following order: gradient, forest fragment and rainforest. The increasing trend of the curves indicated that the sampling effort was not sufficient in the systems and in the gradient. For the oil palm plantation the sampling effort was sufficient. The species estimators

Chao 1 and *Jackknife 2* confirm that the species richness was expected to be much higher in the rainforest and the forest fragment and a little higher in the gradient. Observed seeds indicated a small size between one and five millimeter (length/ width) and a very low weight (< 0.1 gram). The *Kruskal-Wallis Test* confirmed that the weight of the seeds differed significantly (*Kruskal-Wallis Test* $P=0.006$) and size differed highly significant (*Kruskal-Wallis Test* $P= >0.001$) between the systems and between the systems and the gradient.

In this study a significant difference of species richness between the rainforest and the oil palm plantation were determined. To discover more species and to get a data set, which represent the actual species richness, further research on seed rain in the systems and the gradient is recommended over a longer period.

2 Zusammenfassung

Als Teil der Subgruppe B11, welche dem transdisziplinären Kooperationsprojektes des Sonderforschungsbereich 990 (SFB 990) zwischen der Universität Göttingen zugehörig ist, vergleicht und analysiert diese Studie die Samenverbreitung zwischen der Ölpalmenplantage in Humusindo, einem nahegelegenen dem Waldfragment bei Humusindo, dem Regenwald in Harapan, sowie entlang eines Distanzgradienten zwischen der Ölpalmenplantage und dem Waldfragment. Vier zufällig verteilte Samenfallen wurden auf acht Sampling Plots im Regenwald, im Waldfragment und in der Ölpalmenplantage installiert. Auf dem Distanzgradienten wurden acht Sampling Plots entlang eines Transektes mit logarithmischen Abständen etabliert. Alle gesammelten Samen wurden im CRC Labor untersucht und bestimmt.

Während der sechs Datenaufnahmen wurden viele Samenfallen bei der Leerung zerstört aufgefunden. Die Zerstörung ist wahrscheinlich auf Affen zurückzuführen. 3755 Samen die 59 Arten zugehörig waren wurden in den 32 Sampling Plots entdeckt. Fünf Arten konnten bis zur Art bestimmt werden, 16 bis zur Gattung, 21 bis zur Familie und die übrigen Arten wurden als Morpho-Spezies klassifiziert. Im Regenwald wurde ein höherer Artenreichtum (832 Individuen; 39 Arten) festgestellt als im Waldfragment (66 Individuen; 18 Arten), sowie im Gradienten (2708 Individuen; 15 Arten) und in der Ölpalmenplantage (149 Individuen; 4 Arten). Der Kruskal-Wallis Test bestätigte einen signifikanten Unterschied (*Kruskal-Wallis Test* $P < 0.001$) zwischen den Systemen untereinander und den Systemen und dem Gradienten. Kein signifikanter Unterschied wurde bestätigt bei der Abundanz für die zuvor genannten Systeme und den Gradienten. Sieben sehr abundante Arten mit mehr als 100 Samen wurden in den 32 Sampling Plots der Systeme und im Gradienten gefunden. Drei dieser Arten (*Asystasia gangetica*, *Paspalum conjugatum*, *Clidemia hirta*) sind invasiven Pflanzen zu zuordnen. Alle Systeme und der Gradient zeigten steile Rang-Abundanz- Kurven, welche die Dominanz einiger abundanten Arten zeigen. Nur die Kurve des Regenwald-Rang-Abundanz Plots endete in einer langen, flachen Linie, welche Arten mit einer geringen Abundanz (Singletons bei einer Art mit einem Individuum) anzeigte. Außerdem war die Artenfrequenz im Regenwald gleichmäßig verteilter als in anderen Systemen und im Gradienten. Die Ordination mit einer nicht metrischen multidimensionalen Skalierung zeigte eine weite Streuung der Sampling Plots des Regenwaldes. Die Streuung deutete darauf hin, dass es größere Unterschiede in der Artenzusammensetzung innerhalb des Regenwaldes gab, als innerhalb anderer Systeme und im Gradienten. Die großen Distanzen der Regenwald Sampling Plots zu den Sampling Plots

anderer Systeme und des Gradienten zeigten den Unterschied der Arten zwischen dem Regenwald und der anderen Systeme und des Gradienten an. Die Akkumulationskurven zeigten einen Anstieg für die Systeme und des Gradienten in folgender Ordnung an: Gradient, Waldfragment und Regenwald. Der Anstieg der Akkumulationskurven gab an, dass mehr Arten in diesen Systemen und im Gradienten zu finden waren. Bei der Ölpalmenplantage war der Umfang der Datenaufnahmen ausreichend. Die Artenreichtumschätzer *Chao 1* und *Jackknife 2* bestätigten, dass der Artenreichtum viel höher in den Systemen und im Gradienten zu erwarten war. Die ermittelten Samen wiesen kleine Größen zwischen null und fünf Millimeter (Länge/ Breite) und ein sehr geringes Gewicht (< 0.1 Gramm) auf. Der *Kruskal-Wallis Test* bestätigte, dass das Gewicht der Samen signifikant (*Kruskal-Wallis Test* $P=0.006$) und die Länge und Breite sich hoch signifikant (*Kruskal-Wallis Test* $P= >0.001$) zwischen den Systemen und dem Gradienten unterschieden.

In dieser Studie wurde ein signifikanter Unterschied des Artenreichtums zwischen dem Regenwald und der Ölpalmenplantage festgestellt. Studien über einen längeren Zeitraum werden benötigt um bisher nicht entdeckte Arten zu ermitteln und somit einen Datensatz zu erhalten der das tatsächliche Artenvorkommen besser repräsentiert.

3 Introduction

3.1 Biodiversity Hotspot Sundaland

Tropical forests are globally the most diverse and most complex ecosystems (Myers, 1992), but the destruction of tropical habitats has become a serious threat to their biodiversity (Laurance, 1999). Southeast Asia, a region with high endemism and species richness, are highly endangered by deforestation and logging and additionally threatened by overexploitation of wildlife and anthropogenic fires (Wilcove et al., 2013).

Areas containing high rates of endemic plant species (0.5 % of the global plant species) and an ongoing loss of habitat are defined as biodiversity hotspots (Myers et al., 2000). Of 25 biodiversity hotspots in the world, there are two hotspots within Indonesia: Sundaland and Wallace (Sodhi et al., 2004). Both hotspots are separated through the Wallace Line between Bali and Borneo in the north and in the south between Lombok and Sulawesi. Geographically Sundaland is located on the southeast extension of the continental shelf of Southeast Asia. The Malay Peninsula Sumatra, Borneo, Java and Bali are included at the hotspot Sundaland (Sodhi et al., 2004).

Subsequently, I will focus on Sundaland, because Sumatra is the location of my two study sites, which contain three systems and the gradient. The remaining primary vegetation of Sundaland covers 7.8 % of its original vegetation (Sodhi et al., 2004). On Sundaland 5.0 % of the global endemic plants occur and 2.6 % of the endemic global vertebrate species (Myers et al., 2000). High species richness and endemism caused by the geological history of Sundaland as the tectonic shifting, fluctuation of the sea levels, which led to the isolation of islands (Sodhi et al., 2004).

3.2 Adverse effects of deforestation on tropical rainforest biodiversity of Sumatra (Southeast Asia)

Since the 1800's perennial crop such as rubber (*Hevea brasiliensis*), oil palm (*Elaeis guineensis*) and coconut (*Cocos nucifera*) was planted as a result of the agriculture expansion and the global need for rice (*Oryza sativa*) (Flint, 1994). A rise in demand for timber caused an increase of logging industry in Southeast Asia. During 1880 and 1980 an annual forest loss of three percent were documented (Flint, 1994). In 2010 approximately 70 % (773000 km²) of lowland

forests of Sundaland were deforested (Wilcove et al., 2013). Compared with to the global gross forest change, Indonesia had the highest rate of forest cover decline between 2000 to 2012 (Margono et al., 2014). A higher loss of primary forest was reported for Indonesia (0.84 Mha) than for Brazil (0.46 Mha) in 2012 (Margono et al., 2014). Indonesia's lowland forest are comparatively easy to access, which led to deforestation and subsequent conversion to plantations (Curran et al., 2004; Hansen et al., 2009; Margono et al., 2014).

The loss of forests in Indonesia has consequences for biodiversity conservation (Margono et al., 2014); many plant and animal will disappear (Wilcove et al., 2013). Sodhi et al. (2004) estimated that three quarters of primary forests and up to 42 % of its biodiversity will be lost in Southeast Asia by 2100. Wilcove & Koh (2010) argue that oil palm agriculture is the biggest threat to biodiversity in Southeast Asia due to a high conversion of forests. A single hectare of forest conversion to oil palm led to greater loss of biodiversity than logging in the same area (Wilcove & Koh, 2010). Logged over tropical forests are able to recover over time and contain fauna species of primary forests (Brühl & Eltz, 2010; Danielsen et al., 2009; Fitzherbert et al., 2008; Koh & Wilcove, 2007). When forests transformed to oil palm plantations approximately 75 % of bird species (Aratrakorn et al., 2006; Peh et al., 2006) and 80 % of butterflies (Dumbrell & Hill, 2005; Hamer et al., 2003), which inhabit forest habitats, are lost. To protect biodiversity in primary and secondary forests, clearing of forests and establishing new oil palm plantation must be stopped (Koh & Wilcove, 2007, 2008). Furthermore, to increase forest species in oil palm plantation forest patches and understory vegetation should be preserved (Koh, 2008). This design can result in isolated patches of forest on the landscape level within large areas of oil palm plantation (Wilcove & Koh, 2010). Designer landscapes are proposed to combine wildlife friendly farming with land sparing approaches for a sustainable oil palm production (Koh et al., 2009). Natural forests or forest fragments and other habitats with a high conservation value are surrounded by diverse agroforestry systems to serve as a buffer zone to crop plantations like oil palm (Koh et al., 2009).

3.3 Seed dispersal in tropical rainforests and fragmented habitats

Due to dispersal mechanisms seeds will be dispersed from their parent plants and colonize open areas, forests gaps or microsites (Howe & Miriti, 2004). There are different dispersal mechanisms: anemochory (wind dispersal), barochory (gravity dispersal), autochory (self-dispersed by explosion of the capsule) (Pakeman, 2001; Stoner & Henry, 2004). Zoochory is

standing for dispersal by animals and is differentiated to endozoochory, which means seeds are eaten and defecated by animals and exozoochory means seeds are attached to animal bodies (Pakeman, 2001; Stoner & Henry, 2004). Seed dispersal in diverse forests is very important, because it ensures the survival of distribution of species (Terborgh et al., 2008). Seed dispersal influences species turnover and the genetic structure by reducing gene flow between populations (Nathan & Muller-landau, 2000). Furthermore, seed dispersal occurs from the understory of vegetation to the canopy of high trees, by day and night and the spatial scale is ranging from a few centimeters to many kilometers (Corlett, 2009). Even within plant families dispersal mechanisms and dispersal range differ (Howe & Smallwood, 1982). However, many seeds disperse close to their parent plant (Corlett, 2009). The seed dispersal distance is very important for plant populations and community dynamics (Levin et al., 2003; Levine & Murrell, 2003), because it effects the survival of plants in human influenced areas (Ozinga et al., 2009) and the recovery of plants in degraded areas (Howe & Miriti, 2004). In many deforested areas forest species were absent (Sodhi et al., 2004; Wilcove et al., 2013). The recruitment of plants is limited by the number of seeds that occur and arrive at a site and the mortality of seeds (Martínez-Garza et al., 2009). Seeds that do not reach suitable establishment sites are considered dispersal limited (Norden et al., 2009). The number of seeds arriving and establishing on a site will influence the order of ecological succession (Martínez-Garza et al., 2009).

Corlett (2009) showed that the maximal dispersal distances of plants and their dispersal agents in Southeast Asia vary significantly. For example, he found members of the families Acanthaceae, Balsaminaceae, Euphorbiaceae, Fabaceae, Phyllanthaceae, Picrodendraceae, Urticaceae and Violaceae release their seeds mechanically by various mechanisms (e.g. when raindrops fell on a capsule) and disperse between 0- 10 m. Often these seeds disperse in a second phase by ants and rodents (Corlett, 2009). Winged fruits of Dipterocarpaceae and seeds other of plant families are wind displaced on 10 to 100 m from their parent plant. Wingless fruits and seeds often dispersed by rodents, which hoard seeds as their food storage for later consumption. Furthermore, Macaques (*Macaca spp.*) spread small intact seeds by swallowing and defecating (Corlett, 2009). Larger seeds (>4 mm diam.) fall directly from their mouth or they transport fruits away from their parent trees by storing the fruits inside of their cheek pouches (Corlett, 2009; Corlett & Lucas, 1990). On distances between 100 and 1000 m fruit bats, passerines and primates disperse seeds (Corlett, 2009). Old world fruit bats swallowed and defected seeds < 2- 3 cm diameter, while larger fruits transported to a feeding roost (Corlett, 1998). Forest passerines and primates swallowed and foraged seeds on their

daily ranges in their habitat (Corlett, 2009). Various animals can disperse seeds on a distance of 1- 10 km. Fruit bats spreads seeds on daily or seasonal flights between habitats. Also fruit eating carnivores such as civets, martens or bears (Grassman et al., 2005; Rabinowitz, 1991; S. Te Wong et al., 2004) and large herbivores such as elephants, tapir, orangutan or deer (Campos-Arceiz et al., 2008; Chanthorn & Brockelman, 2008; Singleton & Van Schaik, 2001) and large canopy birds as hornbills (Corlett, 2009) disperse seeds within their large home ranges. Small, light and wind dispersed seeds of the Asclepiadaceae, Asteraceae, Gesneriaceae or Orchidaceae family are able to spread over distances of more than 10 km (Corlett, 2009; Whittaker et al., 1997). Some fruit pigeons and hornbills disperse seeds on their daily or seasonal movements over 10 km, while rhinos and elephants do long distance movements on the ground (Corlett, 2009). For instance fruit pigeons do daily flights between the lowland rainforest and the upper montane rainforest (Symes & Marsden, 2007). People unintentionally spread seeds attached on cloth, shoes or on their vehicles (Von der Lippe & Kowarik, 2008). The maximum seed dispersal by people is unlimited worldwide, whereby people disperse invasive species accidentally (Corlett, 2009).

Seed dispersal in fragmented habitats

Fragmentation of tropical landscape is a limiting factor for seed dispersal and natural succession (Martínez-Garza et al., 2009) and may lead to a loss of biodiversity and genetic erosion. Seed dispersal is very variable among between habitat fragments dependent on plant and frugivorous persistence in the fragments and mobility of seeds between fragments (Brudvig et al., 2009; Cramer et al., 2007). Further seed dispersal between fragments is influenced by the surrounding habitats, frugivorous abundance and wind dynamics (Damschen et al., 2008; Prevedello & Vieira, 2010). There is a great difference between frugivorous species, which are able to move between fragments or show a tolerance to habitat degradation (Prevedello & Vieira, 2010). Seed dispersal especially by birds and bats is an important part for plant regeneration in degraded landscapes (Stoner & Henry, 2004). Birds and bats can be attracted by isolated trees, which are used for food and perch location (Galindo-gonzález et al., 2006). Decreasing habitat area and increasing isolation and reduces seed dispersal distance within and between fragments (Cordeiro et al., 2009; Kirika et al., 2008; Lehouck et al., 2009; Rodríguez-Cabal et al., 2007).

3.4 Context of the thesis

This Master thesis builds upon the doctoral research of Anne Gérard (Enrichment planting in oil palm plantations), from the Biodiversity, Macroecology, and Biogeography Group at the University of Goettingen (subproject B11 Biodiversity enrichment in oil palm plantations: ecological and socio-economic impacts on Sumatra (Indonesia)), which is part of the Collaborative Research Center (CRC 990). This long term research project is named “Ecological and socioeconomic function of tropical low land rainforest transformation systems” (EforTS) and was founded by the University of Goettingen in cooperation with Bogor Agriculture University (IPB), University of Jambi (UNJA) and the University of Tadulako (UNTAD). The project is funded by Deutsche Forschungsgemeinschaft (DFG) and aims investigation and protection of ecological functions and ecosystems services of tropical lowland rainforests as well as rainforest transformation systems as jungle rubber, rubber and oil palm plantation, while analysing socioeconomic functions and improving human welfare also important aspects. The CRC project is divided in project groups investigating different aspects of rainforest transformation: Project Group A analyse environmental processes, Project Group B investigate biota and ecosystem services and Project Group C studying human dimensions.

The research group B11 is a biodiversity enrichment experiment, where tree islands with six different species (*Parkia speciosa*, *Archidendron pauciflorum*, *Durio zibethinus*, *Dyera costulata*, *Peronema canescens*, *Shorea leprosula*) planted to promote biodiversity in a monocultural landscape. Humans and animals can use the fruit trees, and the native trees serve as a source for natural latex and timber. Studies of tree growth, plant dynamics and succession on the tree island were conducted. Further research is focused on seed dispersal as well as on ecological and successional dynamics of plant communities in gaps. Also interdisciplinary studies of ecological and economic aspects are planned.

3.5 Aim of the study

This study had been conducted to analyze and compare the species diversity, richness, abundance and turnover of collected seeds in three systems: a rainforest, forest fragment and an oil palm plantation. Forests distance gradient were investigated including the range in which a neighboring forest fragment affects the seed rain in an oil palm plantation. Further the effects of the transformation of rainforests to oil palm plantations on seed rain and dispersal

related seed traits were studied. All collected seeds were measured to analyze how their characteristics affecting seed rain.

From October 10th and December 23th 2014 seeds were collected in traps in the three systems and the gradient.

Plant species have a higher diversity in rainforests as in oil palm plantations (Drescher et al., 2016; Fitzherbert et al., 2008). Additionally, the species disperse their seeds close to the parent plant (Corlett, 2009), and there are not many seed dispersers occurring in rainforest and oil palm plantations (Fitzherbert et al., 2008). For this reason I hypothesize that **(H1) Species turnover and diversity of collected seeds will increase along a gradient from Harapan rainforest to the oil palm plantation in PT Humusindo.**

In connection with **(H1)** and the species impoverishment in oil palm plantations (Wilcove & Koh, 2010), I assumed that **(H1a) Proportion of seeds with specialized dispersal-related traits will increase from oil palm plantation to rainforest (Harapan rainforest) .**

Fragmentation of tropical landscape is a limiting factor for seed dispersal and natural succession (Martínez-Garza et al., 2009) and may lead to a loss of biodiversity and genetic erosion. Seed dispersal is very variable among between habitat fragments depending on plant and frugivorous persistence in the fragments and the mobility of seeds between fragments (Brudvig et al., 2009; Cramer et al., 2007). Due to the fact that fragmentation of tropical landscapes is a limiting factor for seed dispersal (Martínez-Garza et al., 2009) and on the other side forest fragments can harbor forest-dependent species (Edwards et al., 2010) I hypothesize that **(H2) Species turnover and diversity of collected seeds will increase along a forest-distance gradient from oil palm plantation to a neighboring forest fragment.**

4 Material and methods

4.1 Study area

The field work took place in Jambi province on Sumatra, Indonesia. With an area the size of 475,00km², Sumatra is the largest island of the country and the fifth largest in the world. Sumatra belongs to the Sunda Islands and is located in the Malay Archipelago (Laumonier, 1997). The coasts of Sumatra is surrounded by the Indian Ocean in the west, northwest and southwest, and the strait of Malacca borders in the and separates the island from Malaysia. In the South- east the Sunda Strait separates Sumatra and Java.

Approximately 70 million years ago, in the early Tertiary, the Indian and Asian continental plates collided with each other and started to shift under Asia (Laumonier, 1997). This tectonic activity is the main factor of the origin of the Barisan Mountains on Sumatra, which stretch out over the entire western part of the island. Tectonic shifting caused strong earthquakes. Finally, the present landscapes were created during the Quaternary glacial and inter glacial periods (Laumonier, 1997).

Sumatra is divided into five ecological zones: Western coast, Mountain and Piemont zone, Eastern Peneplain and Swamp lowlands (Murdiyarso et al., 2002). Sumatra belongs to the Malesian biogeographic region and the flora of Sumatra displays similarities to the Malay Peninsula and to Borneo (Laumonier, 1997). Dipterocarp rainforests characterize the native vegetation of Sumatra (Laumonier et al., 2010). More than 30 % of the canopy trees in the lowland rainforests are members of the Dipterocarp Family (Laumonier et al., 2010). In the eastern part of Sumatra and along the major rivers mainly hydromorphic or alluvial soils occur, whereas the swampy areas of south Sumatra are dominated by Organosols (Laumonier, 1997). Yellow podzolic or Acrisol soils are common in the lowlands of Jambi province (Drescher et al., 2016).

The equatorial island of Sumatra is characterized by frequent rainfalls that are well distributed over the whole year (Laumonier, 1997). Annual precipitation ranges from 6000 mm/ year in the mountains to less than 1500 mm in some lowland areas of the eastern parts of the island. The climate is influenced by the northeasterly monsoon from December till March and southwesterly monsoon between May and September. Mostly the highest amount of rain occurs between both monsoon periods (Whitten et al., 2000). The temperature varies monthly between 25 -27C° and shows daily thermic amplitudes of 7 to 32C°. From April till October the temperature reaches the maximum, because the sun is at its zenith (Laumonier, 1997).

Jambi province covers an area of 50160 km² (Badan Pusat Statistik, 2014 quoted in Drescher et al., 2016) and is located between the Barisan mountain range in the west and in the east southern Malacca Strait. The climate in the lowlands of Jambi province is tropical humid with a dryer period from July till August and with two rainy periods in around March and December (Drescher et al., 2016).

Due to the transmigration program of Indonesian Government, about 400,000 people moved from Java, a very dense populated island, to Jambi Province (Pemerintah Provinsi Jambi, 2008 quoted in Drescher et al., 2016) to start mainly cash crop production between 1967 to 2007. Consequently, the increasing population and the intensive agriculture use resulted in a land cover change: 55 % of land was replaced by agricultural landscape, 10 % of land was degraded and 30 % of rainforest remain in 2013 (Drescher et al., 2016).

The field work was conducted at two study sites: the oil palm plantation PT Humusindo with the surrounding area near Bungku village and Harapan rainforest (Figure 1).

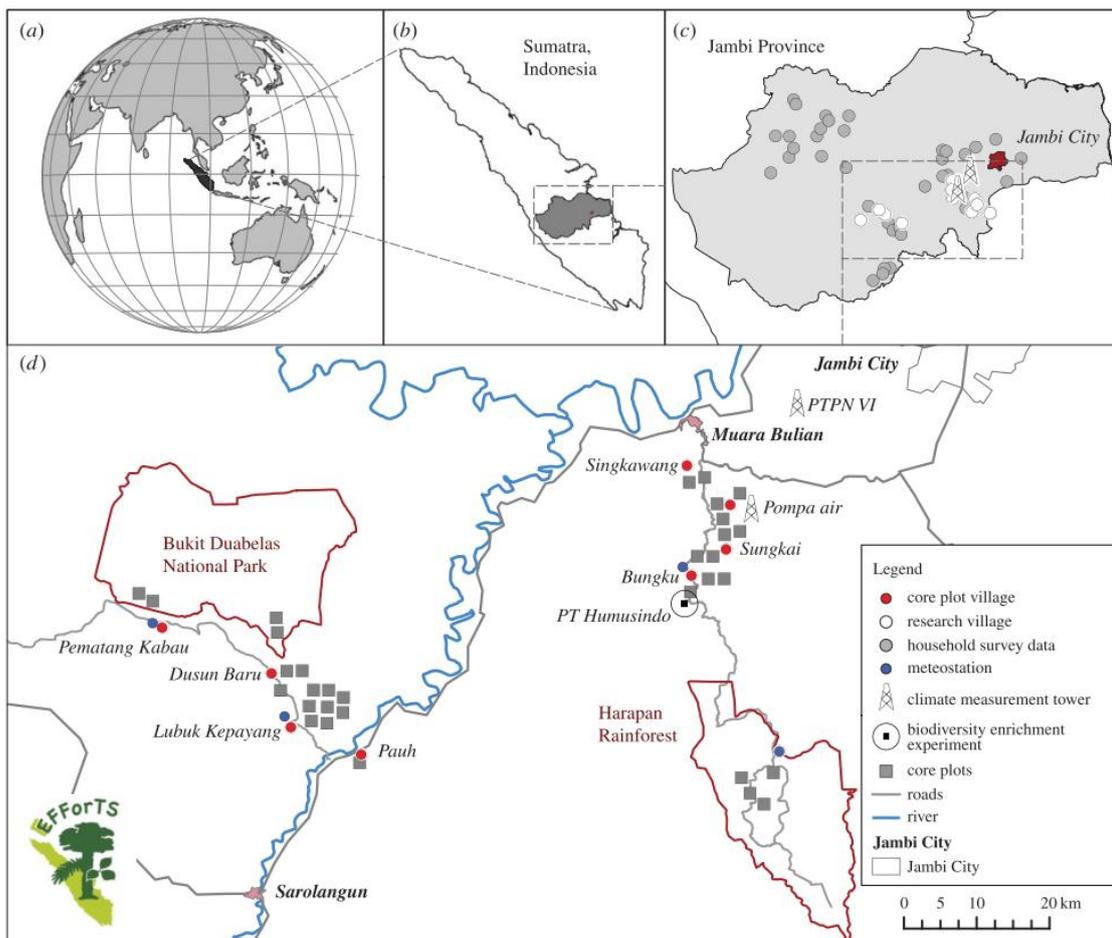


Figure 1: Location of Jambi Province on Sumatra (a, b, c), EFForTS study areas (c, d) and study sites of the master thesis (d). Source:(Drescher et al., 2016)

The B11 experiment is established in the plantation at PT Humsindo. Harapan rainforest is a restoration concession and managed PT Reki. The area covers 98,554 hectares of “primary degraded forest” (Drescher et al., 2016; Margono et al., 2014), which were logged mainly by immigrants outside of Jambi to convert the forest to oil palm plantations (Harapan rainforest, 2016). Besides the restoration of degraded forests PT Reki works together with local communities, NGOs cooperating together to protect the area, provide ecosystem services and livelihood opportunities for the local communities (Graudel, 2015; Harapan rainforest, 2016).

4.2 Study Design and data collection

Three different systems were investigated: tropical lowland rainforest, an oil palm plantation, and a neighboring small forest fragment. Additionally, the distance gradient between oil palm plantation and forest fragment were integrated in the study. The sampling plots of the tropical lowland rainforest were located in Harapan rainforest, the other two systems and the gradient were at the oil palm plantation PT Humusindo and in the surroundings (Figure 2).

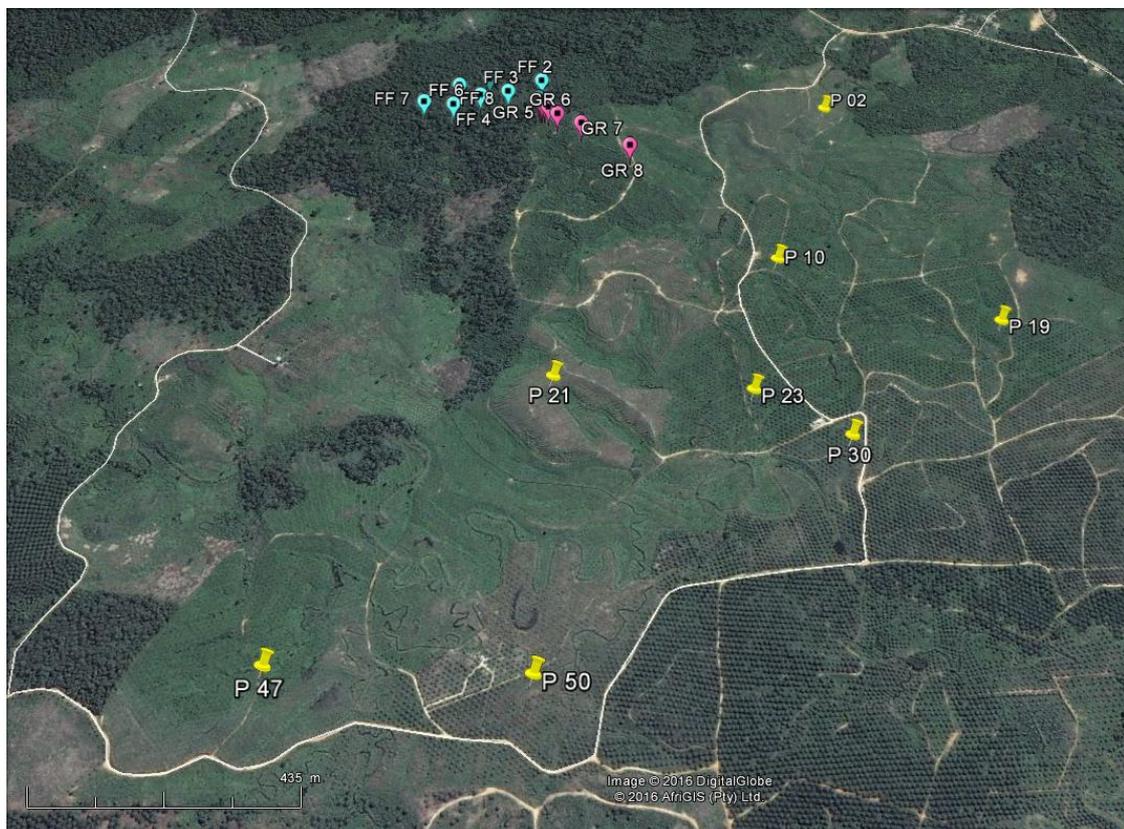


Figure 2: Sampling plots of the systems/gradient at the oil palm plantation and the surrounding area. Sampling sites of the forest fragment (FF) (green), the gradient (GR) (pink) and oil palm plantation (OP) (yellow) are shown. Source: Google Earth (2016), modified by the author.

The small holder oil palm plantation (OP) is the study site of the B11 experiment.

The forest fragment (FF) was isolated by the surrounding oil palm plantations and consisted of an abundance of lianas, rattans and a dense understory. Trees had an estimated size up to 30 m (Figure 3 b-c).

The areas of the gradient (GR) were cleared and planted with oil palms saplings. At the time of field work, the oil palms had an approximate size of up to 0.5 m. Furthermore various grasses and small shrubs were present in this area (Figure 3a).



Figure 3: Vegetation in the sampling plots: a) Shrubs and grass along the gradient. b) View of the forest fragment. c) Inside of the fragment. d) At the core plot in Harapan rainforest

In Harapan rainforests (RF) various plant and tree species of Southeast Asia e.g. species of the Dipterocarpaceae family can be found (Figure 3d). Furthermore, a high diversity of native

faunal species occurs in Harpan rainforest: various bird species, invertebrates, reptiles, amphibians and mammals e.g. the Sumatran Tiger (*Panthera tigris sumatrae*) and the Malayan Sun Bear (*Helarctos malayanus*) (Harapan rainforest, 2016).

In each system: rainforest, forest fragment and the oil palm plantation, eight sampling plots were established each consisting of four randomly grouped seed traps within the plots. Coordinates of all 32 sampling plot were located with a GPS device. The minimum distance between sampling plots was 65 m and the distance to the outer boundaries of the systems was a minimum of 10 m (Figure 4).

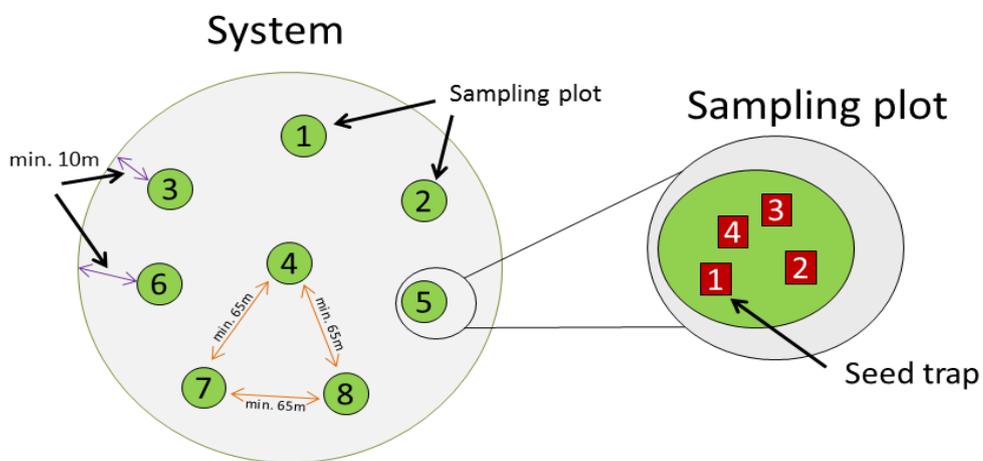


Figure 4: Study design: Experimental design of seed collection in the three systems: rainforest, forest fragment, oil palm plantation. The distance between sampling plots amount to at least 65 m. The distance between sampling plots and the boundary of a system amounts 10 m.

In the gradient, the sampling plots were positioned along a transect with intervals on a logarithmic scale. The start was at 2 m and the transect ended at 256 m in a southerly direction ($01^{\circ}56'S$ $103^{\circ}14'E$) (Figure 5).

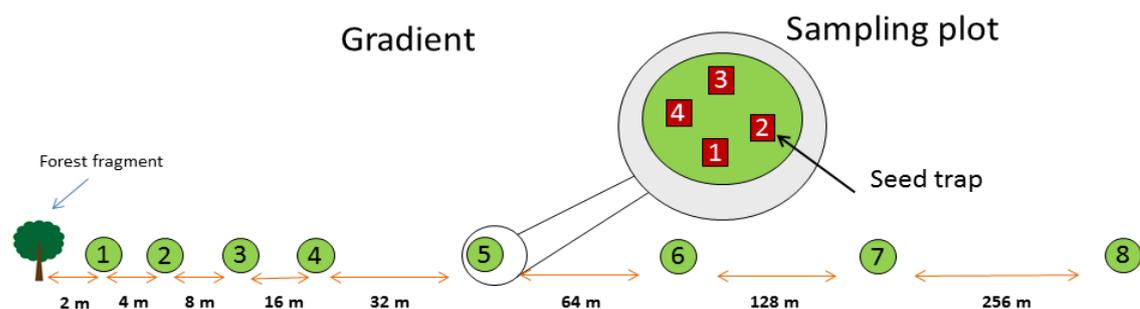


Figure 5: Study design: Experimental design of the seed collection in the gradient. The distance between sampling plots follows a logarithmic scale.

I chose a logarithmic scale for the transect of the gradient, because the distance from the forest fragment to the oil palm plantation was too short for eight sampling plots with a distance of 65 m from each other. To measure the projected distances between sampling plots in the gradient, an ultrasonic measuring device (*Haglöf[®] Vertex IV*) was used. At Harapan rainforest seed traps were established on the core plots of the EFForTS project with a size of 50 m x 50 m. Two sampling plots were installed in one core plot.

Seed traps were constructed from mosquito nets with 1x1 mm mesh size in a hanging inverted pyramid form and fixed with a frame of four 0.5 m wide plastic sticks, which were anchored to the bottom by four 0,8 m long plastic sticks (Figure 6). All holes for the seed traps were drilled with manually used auger. At the B11 study site, seed traps have already been established for a long-term observation in January 2014. Upon completion of the collection, all seed traps in Harapan rainforest, in the fragment and at the gradient were removed.



Figure 6: Seed traps in sampling plots: a) Forest fragment. b) Set up of the seed traps. c) Small section of the gradient. d) Harapan rainforest. f) Oil palm plantation.

4.3 Measurements and analyses of collected seeds

Between October 10 and December 23 2014, all seed traps were emptied in six collections within a rotation of two weeks. The complete content of four seed traps were taken from a sampling plot and stored together in paper envelopes. All samples were brought to the University of Jambi within 2 days after the collection.

The content of the seed traps was dried at 40°C in a drying oven at UNJA for several days. For species identification, all seed samples were observed with stereo microscope (Figure 7c). The identified seeds were assigned to Morpho-species and when possible to family or species level. In the case of finding seeds in faeces, they were stored in alcohol for several days to soften the material in preparation for the extraction of seeds from the fecal matter. Furthermore, all detected seed species were photographed with a camera on top stereo microscope (Figure 7c), and then counted. Seeds in photos were measured by the image processing program *ImageJ*. The seeds were measured in mm at the longest side (length) and at on the opposing side (width). A representative subsample of 10 individuals per species of a sampling plot was measured due to the high number of individuals of some species. I weighed all individuals per species per sampling plot together and calculated the mean weight per species in gram, because some individuals were too lightweight for the scales (Model, precision= 0.0001). After all analyses had been conducted, seeds per sampling plot were stored separately in an envelope. In addition, a seed herbarium was established, where each discovered and labeled species was stored in a glass bottle with a silica gel pad to serve as a reference for others or later seed identifications (Figure 7b). All samples and the seed herbarium were stored for later identification in the CRC lab at University of Jambi.

In this study I assign seeds to a relevant dispersal mechanism. If I couldn't identify the dispersal mechanism of a species, I assigned the seeds to dispersal mechanisms based on their appearance.



Figure 7: Lab work: a) Seeds identification of the content of a sampling plot. b) Labeled glass bottles of the Seed Herbarium. c) Stereo Microscope with camera on top and the connected PC with seed images. d) Image of a *Paspalum conjugatum* seed

4.4 Statistical analysis

Microsoft Excel Version 2010 was used to organize and combine the different data sets of the systems and the gradient. Statistical analyses and graphics were performed in the open source software *RStudio* Version 0.99.446.

4.4.1 Seed abundance and diversity

For each sampling plot, I pooled the six collections that I took from October 10th to December 23th together. An overview of the collected seeds with microscopic pictures per species can be found in the appendix table 1. The pooled data include individuals, species and seed characteristics (seed weight (g), seed length (mm), seed width (mm)) per sampling plot in the three system and gradient. For the seed characteristics I calculated an average value per species in the sampling plot, because not every single seed were measured. Six collections were chosen to get sufficient data set.

Boxplots (*box-and-whisker-plots*) were plotted to give an overview of the distribution of individuals and species in the different systems or gradient and to compare the data per system or in the gradient. The non-parametric *Kruskal–Wallis Test* was applied to analyze differences in species richness and abundance between the investigated systems and the gradient and a subsequent *Nemenyi Test* was used to indicate the statistical significance between the systems and the gradient (Kruskal & Wallis, 1952; Pohlert, 2016). The following codes for the significance were used: p- value < 0.001 (highly significant***), p- value > 0.05 (low significant *). The package *stats* version 3.2.1. (R Core Team, 2016), was used for the *Kruskal–Wallis Test*. To perform the *Nemenyi Test* the command *posthoc.kruskal.nemenyi.test* in the R package *PMCMR*, version 1.1 (Pohlert, 2016), was applied.

To give an overview of how many species within a system or in the gradient, and how many overlaps of species between the systems and the gradient were found, a Venn diagram was developed using the command *draw.quad.venn* in the package *VennDiagram* version 1.6.16 (Hanbo Chen, 2016).

For visualization of the observed species abundance distribution in the investigated systems or in the gradient a rank abundance plot was applied. The rank abundance plot is useful to identify if species were evenly distributed or dominated by few species (Magurran, 2004) in the systems or in the gradient. Along the x-axis species were ranked and plotted in order from the most to least abundant and the opposite y-axis displayed the abundance (Magurran, 2004). The rank abundance curve was plotted for each system and the gradient using the command *rankabundance* in the R package *BiodiversityR*, version 2.3-0 (Kindt & Coe, 2005). Based on the same method and commands, curves for the frequency were performed to show species frequency distribution in sampling plots of the system and in the gradient. The species frequency displays how many species were found in a sampling plot. Therefore, species frequency was ranked on the x axis, while the number of sampling plots was displayed on the y-axis.

To analyze similarities and dissimilarities of species between samplings plots of the systems and the gradient, a non-metric multidimensional scaling (NDMS) was applied. The NDMS is a rank-based ordination method which uses presence or absence data. The command *metaMDS* in the R package *vegan* (Oksanen et al., 2016) produced a NDMS, which placed all sampling plots on a two dimensional space using 100 random starts to find the most suitable distance between sampling plots (Oksanen, 2016). Coordinates were assigned to each sampling plots on two dimensions. Similar sampling plots are ordered closer to each other caused by similar

species, than dissimilar sampling plots. Finally, the ordination was displayed as a scatterplot and an ellipse with a standard deviation of 95% was plotted and placed around the center of the systems applied by the function *ordiellipse* (Oksanen, 2016).

A widely used method to determine whether the sampling effort for the recorded species was sufficient is the species accumulation curve (SAC). This curve plots the increasing number of recorded species (S) as a function of sampling effort (Colwell & Coddington, 1994), which in the context of this study is the cumulative number of sampling plots per system or of the gradient. Through continuous sampling, new species were added to the data set, which leads to an increase in slope of the accumulation curve. SACs were calculated using the command *specaccum* in the *vegan* package (Oksanen et al., 2016). In a random permutation of 100 times, sampling plots were added to the plot producing a line each time (Magurran, 2004). The final species accumulation curve illustrates the mean (centerline) and the standard deviation (shaded region around centerline) of the 100 permutations for each system and the gradient. If the accumulation curve displays a permanent increase more species per system or in the gradient are assumed with further sampling effort. When the SAC demonstrated a saturated development (asymptote) the species richness is nearly achieved (Colwell & Coddington, 1994).

Furthermore, species accumulation curves can provide an estimate of the total species richness of an assemblage by extrapolation, because samples do not directly display the total species richness (Magurran, 2004). To extrapolate species richness for a fixed number of sampling plots per system or in the gradient, two different non-parametric species estimators were applied: *Chao 1* and *Jackknife 2*. *Chao 1* is an abundance based estimator for the absolute number of species and considers the amount of rare species in an assemblage (Colwell & Coddington, 1994). The formula below follows (Chazdon et al., 1998):

$$S_{Chao\ 1} = S_{obs} + \frac{F_1^2}{2F_2}$$

Where S_{obs} is the number of observed species that occur in a sample, F_1 is the number of species, which is represented by only one individual (singletons) in a sample and F_2 is the number of species, which is represented by two individual (doubletons).

Jackknife 2 is based on incidence data instead of abundance data. The function calculates the number of species which are found in only one sample (Q_1) or two samples (Q_2). Jackknife 2

can be applied, if many singletons and doubletons in the assemblage (Colwell, 2005). The number of samples is indicated by m . The equation of *Jackknife 2* is displayed below:

$$S_{Jack\ 2} = S_{obs} + \left[\frac{Q_1(2m - 3)}{m} - \frac{Q_2(m - 2)^2}{m(m - 1)} \right]$$

The extrapolated species richness for the estimators *Chao 1* und *Jackknife 2* were executed with the function *poolaccum* of the *vegan* package (Oksanen et al., 2016). Two different species estimator were applied to compare the results of both methods.

An estimation curve with the estimated species on the y-axis and the sampling plots on the x-axis can be performed for both species estimators. If the curve shows an asymptote the sampling can be considered as complete at that point.

4.4.2 Seed characteristics

Seed characteristics were displayed in histograms, scatter plots and boxplots. Histograms show the distribution and the frequency of every seed trait variable per system and in the gradient. The relationship between the average length and width of the seeds was plotted as a scatterplot for all systems collectively and the gradient. Boxplots were also constructed to show the distribution of average seed trait values (weight, length and width) per species in each sampling plot. A non-parametric *Kruskal–Wallis test* and a subsequent *Nemenyi test* were also applied to investigate significant differences and contrasts of the three seed traits with their connected systems or the gradient.

5 Results

5.1 Seed abundance and diversity

During the six collections many seed traps were destroyed in the forest fragment compared to the other two systems and the gradient (Figure 8).

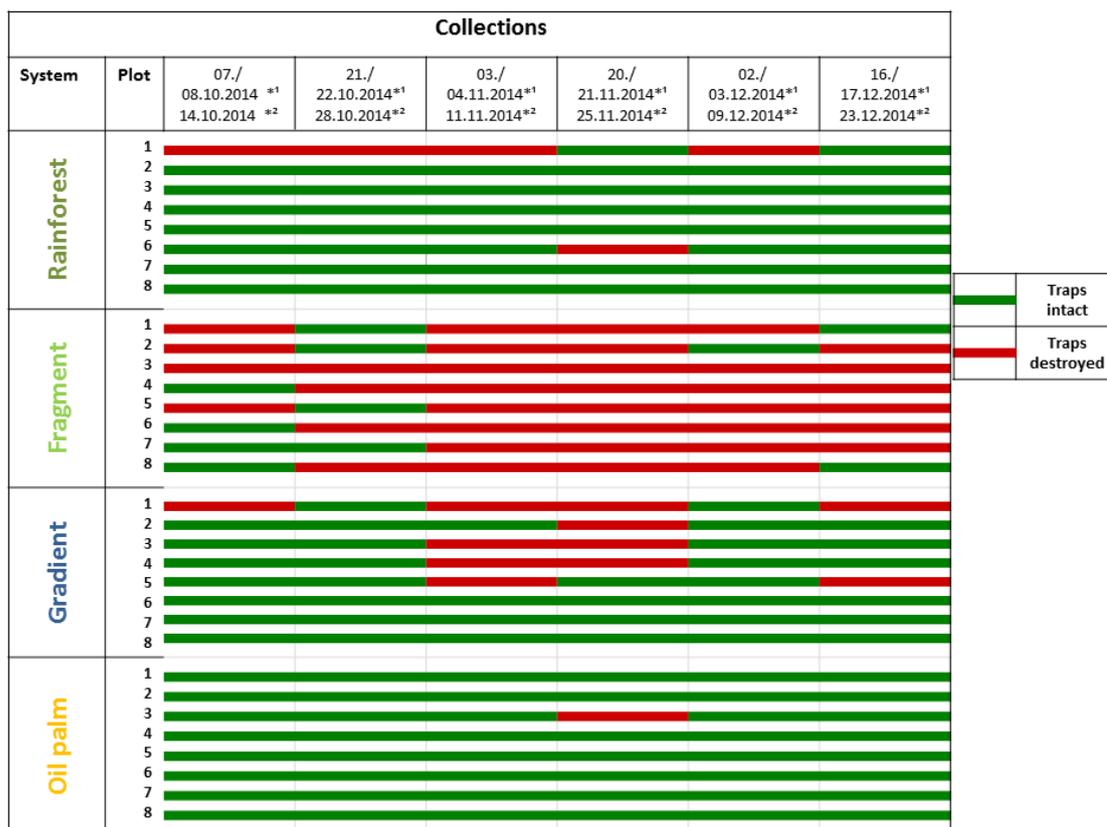


Figure 8: Seed collections: The intact and destroyed seed traps are shown in corresponding to their collection dates, systems, gradient and sampling plots. *1 = Seed Collection of the gradient, forest fragment, Harapan rainforest; *2 = Seed Collection in the oil palm plantation (PT Humusindo)

A total of 3755 seeds of 59 seed species were found in 32 sampling plots. Of the 59 species recorded, five were assigned to species level, 16 to genus level, 21 to family level and 17 were listed as Morpho-species. A complete species list with associated seed characteristics for all collections is found in the appendix (Table 1 & 2). In the gradient, seed abundance was highest, with a total of 2708 seed recorded. Sixty-six individuals seeds were collected in the forest fragment, 149 in the oil palm plantation, and 832 in the rainforest (Figure 9a). The Barplot showed that a higher species richness was found in the rainforest system than in the oil palm

plantation: 39 species were found in rainforest, 18 plant species in the forest fragment, 15 in the gradient and only 4 in the oil palm plantation (Figure 9b).

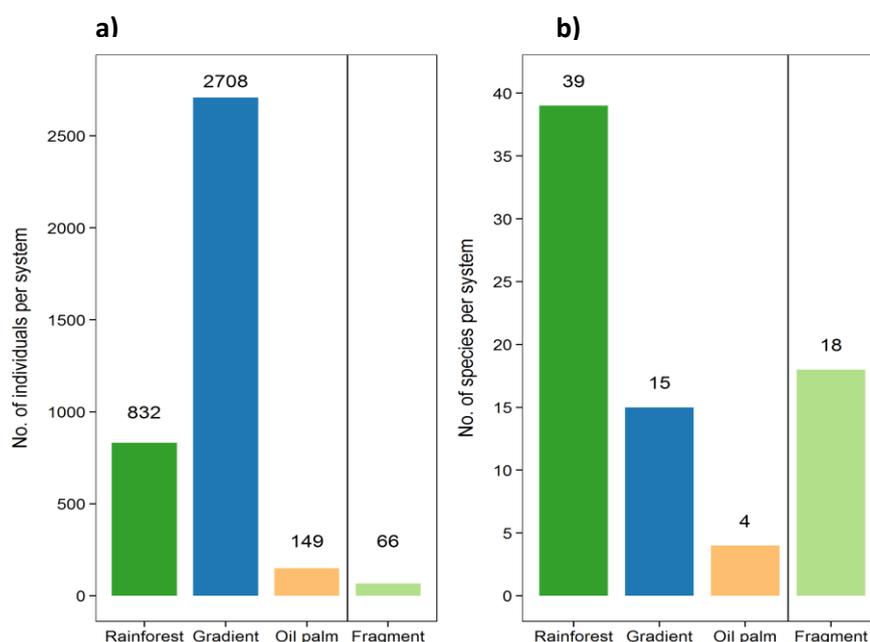


Figure 9: a) Abundance and b) Species richness per system or gradient: The forest fragment is shown separately, because of it contains insufficient data due to high amount of destroyed seed traps

Seven of the species were encountered with more than 100 seeds. These species were *Paspalum conjugatum*, *Pogostemon spec.*, *Hedyotis spec.*, *Lipocarpha spec.* and *Clidemia hirta* which were particularly abundant in the gradient, *Asystasia gangetica*, which occurred mostly in the oil palm plantation and *Ficus spec.*, which showed a high abundance in the rainforest (Table 1).

Table 1: Most abundant species. Abundance of species discovered in 32 sampling plots of the three systems and the gradient

Family	Species	No. individuals			
		Rainforest	Fragment	Gradient	Oil palm
<i>Acanthaceae</i>	<i>Asystasia gangetica</i>	-	-	9	121
<i>Poaceae</i>	<i>Paspalum conjugatum</i>	1	1	81	24
<i>Moraceae</i>	<i>Ficus spec.</i>	626	-	12	-
<i>Lamiaceae</i>	<i>Pogostemon spec.</i>	-	15	115	-
<i>Rubiaceae</i>	<i>Hedyotis spec.</i>	1	3	176	-
<i>Cyperaceae</i>	<i>Lipocarpha spec.</i>	-	-	502	-
<i>Melastomataceae</i>	<i>Clidemia hirta</i>	-	8	1742	-
Total		628	27	2637	145

Four species, *Asystasia gangetica*, a perennial creeper (Chew et al., 2012), *Paspalum conjugatum*, a perennial grass from South America (Hakim et al., 2006; Liu et al., 2006) and *Clidemia hirta*, a perennial bird dispersed shrub from tropical America (Peh, 2010) are invasive plants, and are often found in oil palm plantations and disturbed sites (Tjitrosoedirjo, 2007). Of the five discovered invasive species, *Ageratum conyzoides*, from tropical south America (Kohli et al., 2006), was the only one with two individuals and was only found in the rainforest.

Moreover, the species composition changed between and within the four systems: *P. conjugatum* and Asteraceae sp. 50 were discovered in all systems (Figure 10). Whereas the abundant species *Hedyotis* spec. was the only plant found in the rainforest, the forest fragment and the gradient. The very abundant species *C. hirta*, *Pogostemon* spec. and Morpho-species no. 35 occurred in the forest fragment and gradient. *Ficus* spec. and Morpho-species no. 52 were found in the gradient and rainforest. *Rhodemia* spec., *Melastoma* spec. and Lythraceae sp. 37 were rarely discovered in the rainforest and the forest fragment. The highly invasive and abundant species *A. gangetica* was the only species discovered in the oil palm plantation and gradient.

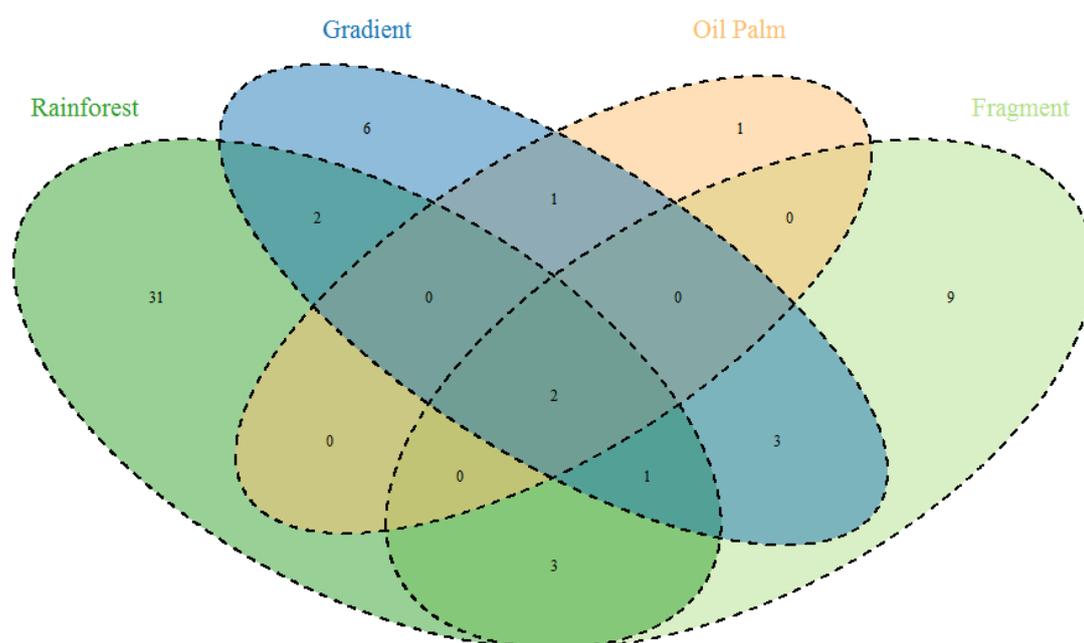


Figure 10: Venn diagram. Distribution of the amount of species in the investigated systems

A total of 20 families were recorded in all systems and in the gradient, shown in Table 2. The highest diversity of families (16 families) displayed in the rainforest followed by the forest fragment and gradient with 11 families. Only three families were discovered in the oil palm plantation.

Table 2. List of recorded families including number of observed individuals and species per system or in the gradient: Families which occurred in three systems and in the gradient are underlined. Families which were found in three systems or two systems and in the gradient are underlined by a dotted line.

Family	No. Individuals				No. species			
	RF	FF	GR	OP	RF	FF	GR	OP
<i>Acanthaceae</i>	-	-	9	121	-	-	1	1
<i>Areaceae</i>	41	-	-	-	1	-	-	-
<u><i>Asteraceae</i></u>	17	4	11	3	5	1	1	1
<i>Cannabaceae</i>	10	-	-	-	1	-	-	-
<i>Cucurbitaceae</i>	3	-	-	-	1	-	-	-
<i>Cyperaceae</i>	-	-	540	-	-	-	2	-
<i>Euphorbiaceae</i>	-	4	-	-	-	2	-	-
<u><i>Fabaceae</i></u>	1	4	1	-	1	2	1	-
<u><i>Lamiaceae</i></u>	4	15	115	-	1	1	1	-
<i>Lythraceae</i>	5	-	-	-	1	-	-	-
<u><i>Melastomataceae</i></u>	1	13	1742	-	1	2	1	-
<i>Moraceae</i>	626	-	12	-	1	-	1	-
<i>Myristicaceae</i>	2	-	-	-	1	-	-	-
<i>Myrtaceae</i>	3	2	-	-	2	1	-	-
<u><i>Phyllanthaceae</i></u>	8	2	15	-	1	1	1	-
<u><i>Poaceae</i></u>	7	1	82	24	2	1	2	1
<i>Rhamnaceae</i>	4	-	-	-	1	-	-	-
<u><i>Rubiaceae</i></u>	3	4	176	-	2	2	1	-
<i>Solanaceae</i>	1	6	-	-	1	1	-	-
<i>Sphenocleaceae</i>	4	-	-	-	1	-	-	-
Not identified	92	11	5	1	15	4	3	1
Total	832	66	2708	149	39	18	15	4

The gradient showed the highest median (338.8) compare with the three systems (Figure 11a): The median of the number of seeds collected from the rainforest was 104 and 18.65 in the oil palm plantation. In the forest fragment had the smallest median of 8.25 seeds. The highest range of seeds was observed in the gradient. Species abundance did not significantly differ between groups (*Kruskal-Wallis Test* $P > 0.05$). Due to the insufficient data of the forest fragment, this system was excluded from the other Boxplots and from the *Kruskal-Wallis Test*. For each species per sampling plot, the highest median of 8.5 were indicated by the rainforest and the second highest (6 species) by the gradient (Figure 11b). A lower median was shown by forest fragment (3 species) and by the oil palm plantation (1 species). The rainforest displayed the highest range of species. A highly significant difference between groups of species was found (*Kruskal-Wallis Test* $P < 0.001$). The *Nemenyi Tests* showed that the number of species in the rainforest and gradient differ significantly from the oil palm plantation.

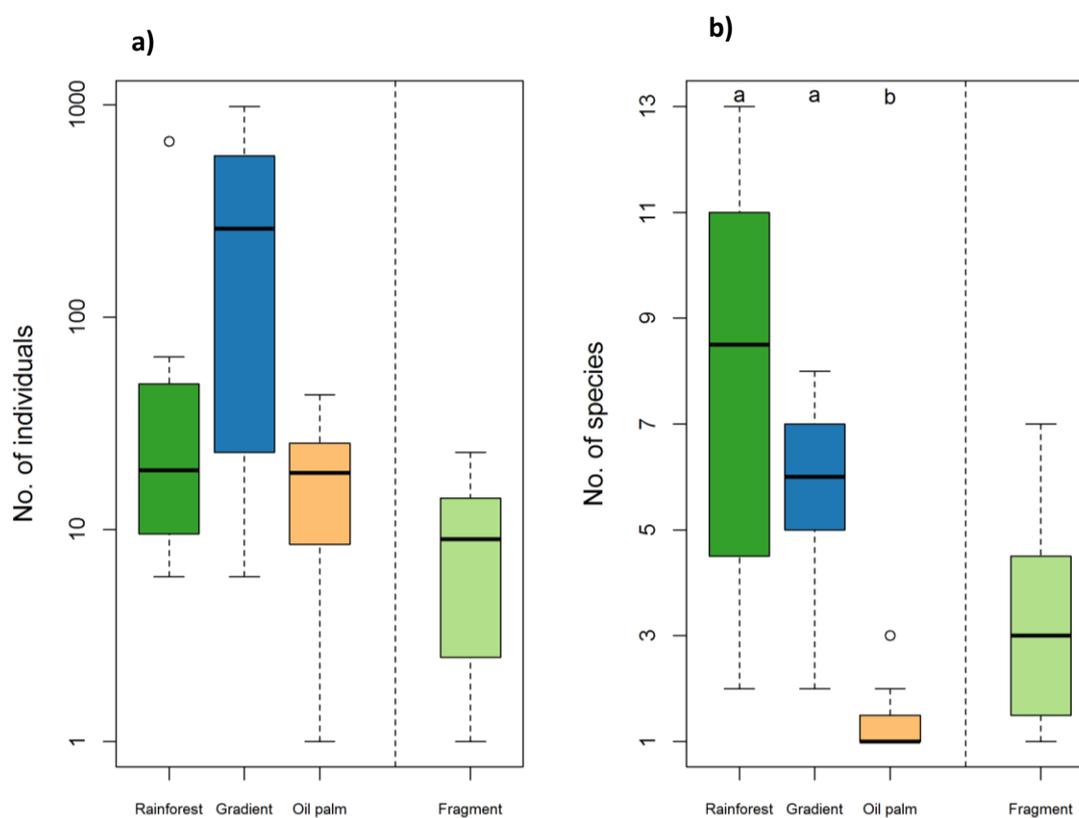


Figure 11: Box-Whisker Plots. a) Number of individuals per sampling plot and systems or in the gradient. The boxplots show the median, the percentiles, the upper and lower quartiles as well as outliers of individuals or species per sampling plots in their respective the system or gradient. The *Kruskal-Wallis Test* displays a p-value > 0.05 . b) Number of species per sampling plots and systems or in the gradient. The *Kruskal-Wallis Test* displays a p-value of < 0.001 (highly significant ***). The fragment was excluded from the *Kruskal-Wallis Test* for the individuals and the species due to insufficient data.

In rank abundance plots the absolute abundance is ranked in order to their species for the systems and the gradient (Figure 12). One species per system or gradient was very abundant. *Ficus spec.* and *Clidemia hirta*, which were found in faeces, displayed a very high abundance with 626 and 1742 individuals. In the rainforest the highest number of species with only one individual (16 singletons) were found. The second largest number of singletons (7 species) was observed in the forest fragment. Furthermore the abundance curve of the rainforest system showed a steep curve at the very beginning, which merged into a shallow straight tail, indicating a large number of singletons (Magurran, 2004). The rainforest, the forest fragment and gradient curves displayed steep slopes with a short a tail. A very steep slope without a tail was indicated by the oil palm plantation, where one dominant and three less abundant species were present. The curve of the gradient showed that a few less abundant species occur. This appearance was caused by the highly abundant species *C. hirta* (Table 1).

In the rainforest the species frequency was more evenly distributed as in other systems or in the gradient (Figure 13). Half of the recorded species such as *P. conjugatum*, *Pogostemon spec.*, *Lipocarpha spec.* were found several times in the gradient. In contrast, two and one species had a high occurrence in the forest fragment and oil palm plantation, respectively. *Asystasia. gangetica* was only species, which were found in every sampling plot of the oil palm plantation.

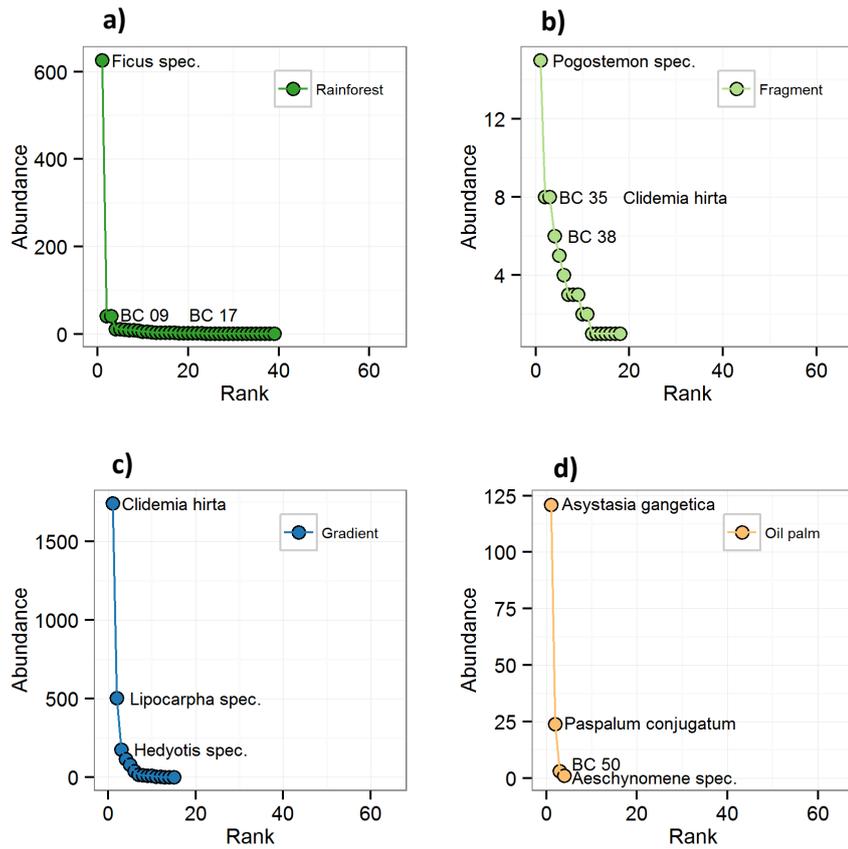


Figure 12: Rank abundance plot. Absolute abundance of species per system or in the gradient is shown in order to their ranking. The most abundant species are labeled.

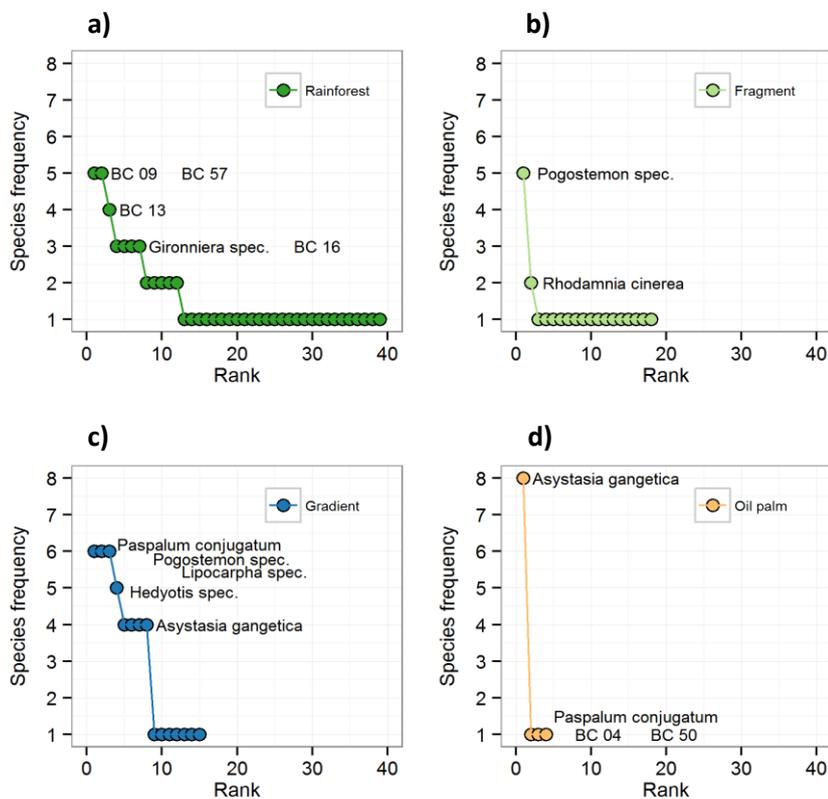


Figure 13: Rank frequency plots. Species per system or in the gradient are ranked in order of their frequency. High frequent species are labeled.

In the non-metric multidimensional scaling (NDMS) ordination each system and the gradient were formed separately as a group (Figure 14). The sampling plots of the rainforest displayed a larger confidence interval and expanded on a wider area than others, because their species composition varied. Sampling plots that contained the same species composition were stacked on top of each other). Through this effect only three sampling plots within the oil palm plantation were not visible in the ordination. A wide scattering was demonstrated for the rainforest sampling plots, where the most diverse species composition was found and a lower scattering for the other systems and the gradient. The sampling plots within the rainforest and oil palm plantation differed widely from each other across the distance matrix, whereas the forest fragment and gradient grouped closer together. This grouping showed that the forest fragment and the gradient shared several species. Additionally, one sampling plot of the oil palm plantation was close to the gradient.

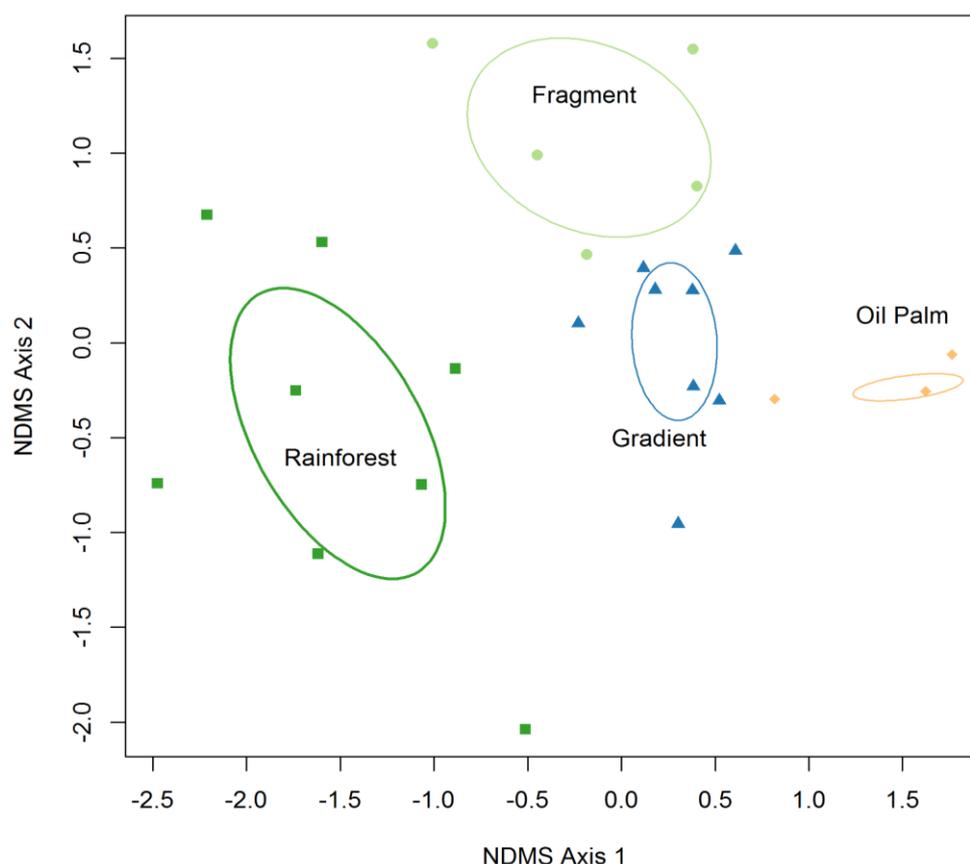


Figure 14: Non-metric multidimensional scaling (NDMS) ordination based on presence-absence data. The dots represent the species composition per sampling plots of the three systems and the gradient in a distance matrix. Around the centroids of the systems and the gradient 95 % confidence intervals are shown.

In the species accumulation curve the number of species was displayed on the y-axis, whereas the sampling plots were listed at the x-axis (Figure 15). The curve of the rainforest increased steeply and constantly, because new species were added to every sampling plot. The rate of species accumulation and the total number of species was very low and reached an asymptote almost immediately. Furthermore, the forest fragment overlapped with the thinner curve of the gradient, showing slight increase in the beginning and turned in a nearly saturated trend after four sampling plots. Similarly, the forest fragment showed a slight slope, but with a constant development along the sampling plots. This system showed the second highest slope after the rainforest.

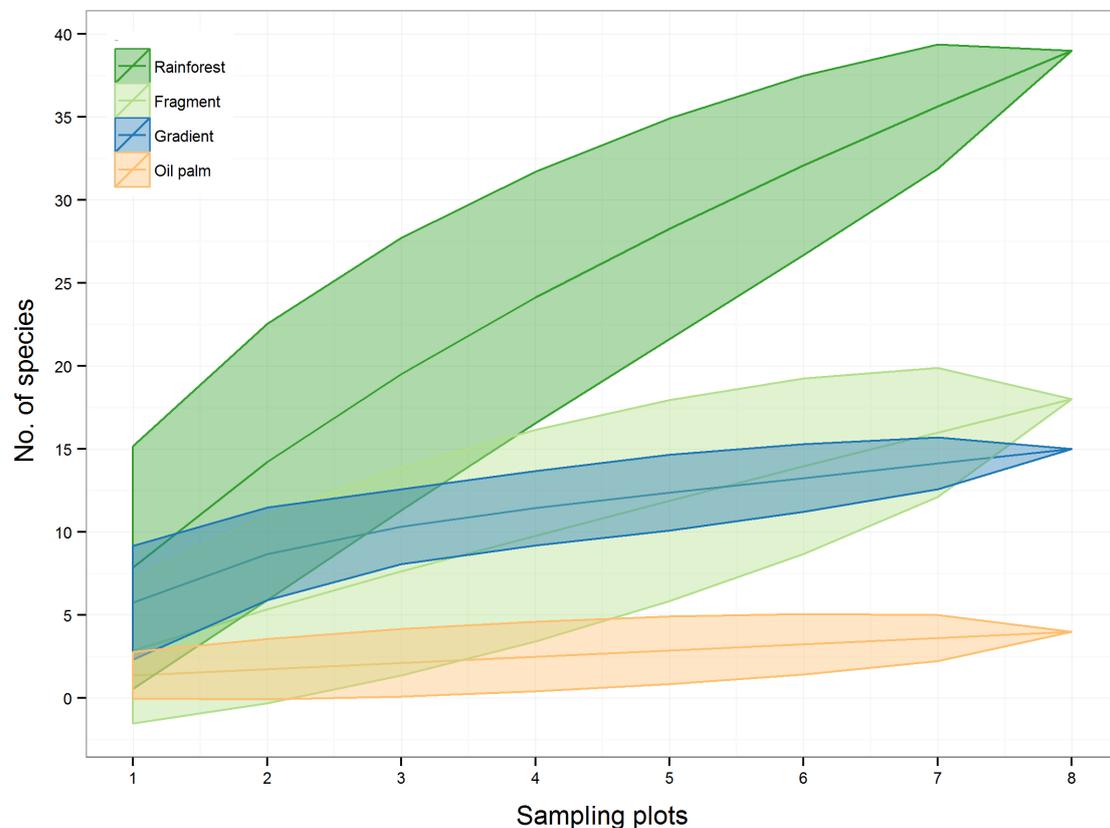


Figure 15: Species accumulation curve. Each system or gradient is represented by an accumulation curve. All curves demonstrate the mean and standard deviation in 100 permutations. The mean and standard deviation indicated by different curve shapes of the three systems and the gradient.

The estimated species richness per system or gradient and accumulation curve for both species estimator can be found in the appendix figure 1 and 2 and in appendix table 3 and 4. The abundance based estimator *Chao 1* estimated much higher species richness in the rainforest than *Jackknife 2*. *Chao 1* indicated 71 species at sampling plot three, which increased up to 180 species at sampling plot eight. Compared with the estimated species richness by *Chao 1* with total number of species in the assemblage, the estimated species were more than four times higher than in the assemblage. However *Jackknife 2* started with 34 species in the rainforest and ended up with 88 species at sampling plot eight. Compared with 39 species of the rainforest in the assemblage the estimated species by *Chao 1* were more than four times higher and more than two times higher for *Jackknife 2*. *Chao 1* calculated a very high species richness of 131 species for the forest fragment contrasting to the 18 species found in the data set, whereas *Jackknife 2* showed a two times higher species richness than in the assemblage. The curve of the gradient nearly reached an asymptote.

5.1.1 Seed characteristics

All species and their seed characteristics are listed in the appendix table 1. In the histograms the frequency on the y-axis showed the occurrence of a specified seed trait and on x-axis the seed characteristics were displayed. Histograms of the seed width and seed length (Figure 16 a-h) and Figure 17) displayed a wider distributed range of seed sizes especially in the rainforest and the forest fragment. Seeds up to 19.0 mm length and up to 13.0 mm width were found in the rainforest. Nevertheless, the largest proportion of the seeds was small, because the highest frequency of seed length and width was varying on a scale of 0.0 to 5.0 mm in all systems. The rainforest showed the most diverse frequencies for all seed characteristics followed by the forest fragment. Most of the seeds weight was below 0.1 g and only a few seeds in the rainforest showed values above 0.5g (Figure 16 (i-l)).

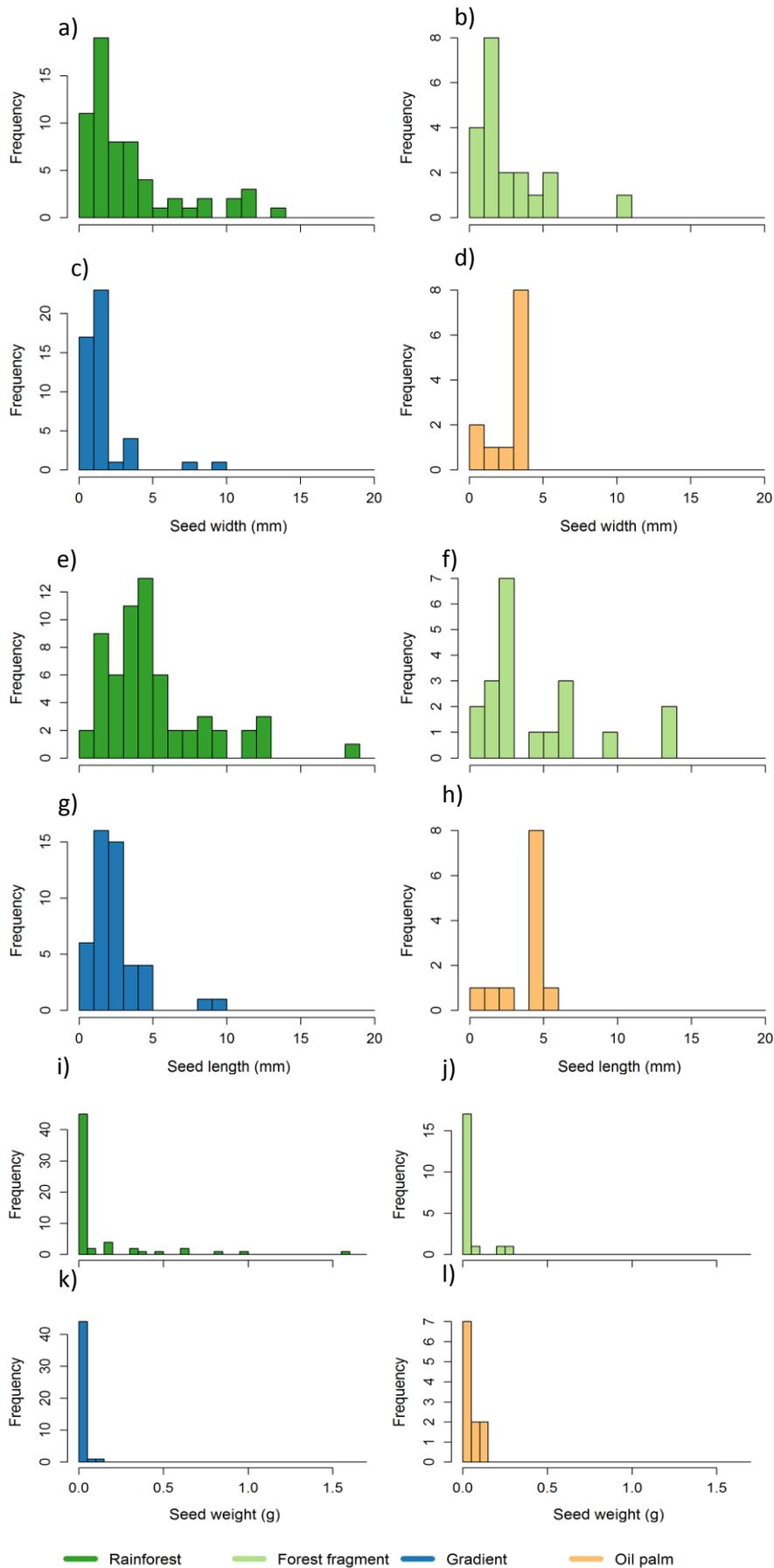


Figure 16: Histograms of seed characteristics. a) - d) Frequency of seed width (mm) per sampling plot. e) - h) Frequency of seed length (mm) per sampling plot. i) - l) Frequency of seed weight (g) per sampling plot

The largest seed, *Horsfieldia spec.* (Myristicaceae), was found only once and only in the rainforest (Figure 17). Conversely, the highly abundant species, *Clidemia hirta* (Melastomataceae) was the smallest and the lightest species, was showed, which was found in the forest fragment and in the gradient. Similarly, species with over 500 individuals per species such as *Ficus spec.* and *Lipocarpha spec.* also had a very small size (less than 2.00 mm) and very light weight (Appendix table 1). In contrast, the less abundant species *Horsfieldia spec.* and Morpho-species no. 57 indicated a higher weight (up to 0.7 g) and a larger size (> 10 mm; length/ width).

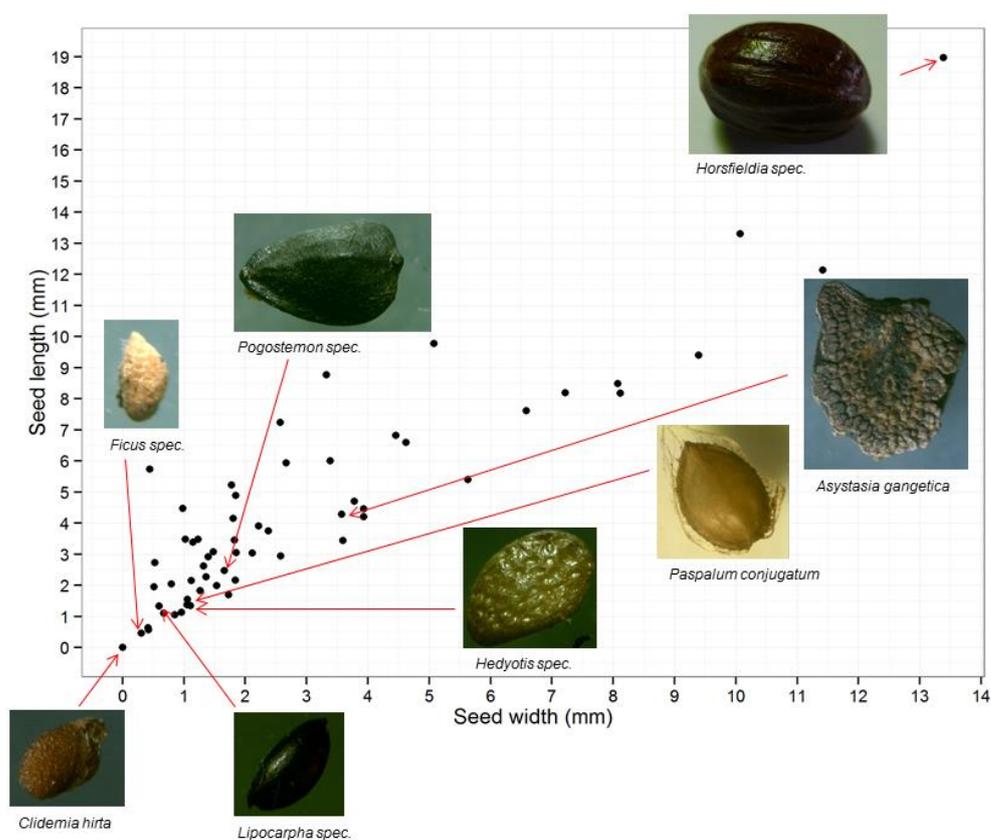


Figure 17: Relationship between seed length (mm) and seed width (mm). The average seed length (mm) and average seed width (mm) per species are plotted against each other. In addition microscopic pictures of the largest, smallest and most abundant species are shown in correspondence to their characteristics.

The range of seed trait values were at the highest for rainforests plants, and lowest for oil palm plantation plants (Figure 18). Seed weight significantly differed between the systems and the gradient (*Kruskal-Wallis Test* $P= 0.006$). Comparatively, seed length and seed width were indicated as highly significant between the groups (*Kruskal-Wallis Test* $P >0.001$). The subsequent Post-hoc tests after *Nemenyi Test* displayed a contrast between the rainforest and gradient as well as between the oil palm plantation and gradient for all seed trait variables.

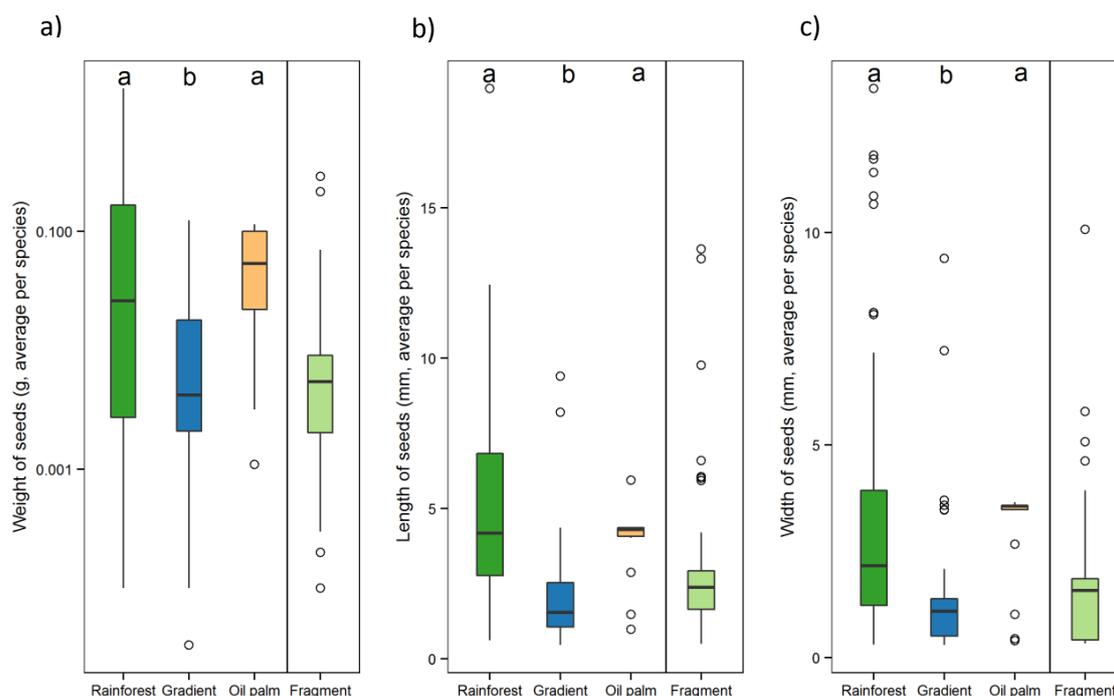


Figure 18: Box- Whisker Plots. a) Average weight per species and sampling plot of the systems and the gradient. The *Kruskal-Wallis Test* displays a p-value of 0.006. b) Average length per species and sampling plot of the systems and the gradient. The *Kruskal-Wallis Test* displays a p-value of < 0.001 (***) . c) Average width per species and sampling plot of the systems and the gradient. The *Kruskal-Wallis Test* displays a p-value of < 0.001 (***) . The forest fragment was shown separately in the boxplots of the seed individuals and species, because the sample contained insufficient data.

All seeds I identified to species level I could assign to a dispersal mechanism: *C. hirta* is a bird dispersed shrub (endozoochory) (Peh, 2010) , *P. conjugatum* is dispersed by exozoochory, while seeds adhering to animals or human (Sauer, 1988). *Asystasia gangetica* is a self-distributed plant by explosion of the capsule (autochory) (CRC for Australian Weed Management, 2003) or by rhizomes (Space et al., 2009). *Rhodamnia cinerea*, a small-canopy tree up to 15 m tall is dispersed by bats, birds, squirrels, and monkeys. (National Parks Board Singapore, 2013). *Ageratum conyzoides* is adapted for dispersion by wind and water (anemo- and hydrochorous) and *Ficus spec.*, a genus, which is distributed in various growth forms as trees, shrubs, climbers, epiphytes and hemiepiphytes are dispersed by birds and mammals via

endozoochory (Primack & Corlett, 2005). I assigned many of the seeds to animal dispersed species (endozoochory/exozoochory) based on their appearance. The assigned seed dispersal mechanisms can be viewed in the appendix table 1.

6 Discussion

6.1 Change in seed diversity, abundance and species composition between a rainforest and oil palm plantation

This is the first study to compare seed abundance, richness and species composition between a rainforest, a forest fragment, gradient and oil palm plantation. The results showed a significant difference of species richness between the investigated systems and the gradient. A high abundance of few species in the systems and the gradient and a difference in species composition between systems and the gradient were found.

One reason for the low species number in the forest fragment was that most of the seed traps were found destroyed (Figure 8). Occasionally, seed traps of the sampling plots in the gradient system close to the forest fragment were also destroyed. The broken seed traps could have a connection with local dense monkey populations in the forest fragment. High monkey population densities in forest fragments also occur in East Africa and South America (Addessi et al., 2007; Laurance et al., 2002; Wong & Sicotte, 2006). I assume that macaques (*Macaca spec.*) destroyed the seed traps, because I found lots of plastics sticks and mosquito net, which belonging to the seed traps in the entire forest fragment. I couldn't find any references that monkeys damage seed traps, but it is recorded that monkeys prey upon seed and fruits and play an important role in seed dispersal in the old world tropics and in the Neotropics (Galetti, 2001; Kunz & Linsenmair, 2010; Ruppert et al., 2014). For example in Malaysia the pig tailed macaques (*Macaca memestrina*) feed on *Ormosia venosia* seeds of the Fabaceae family on the forest floor (Miura et al., 1997). Seeds of the Fabaceae family were also found in the forest fragment. This suggests that the monkeys damage the seed traps on their search for food accidentally. Another assumption is that the monkeys played with the seed traps. This might be explained by the distributed sticks and nets in the entire forest fragment. It had to be questioned how to deal with data from damaged seed traps. The forest fragment is considered an important part along the gradient from the rainforest to the oil palm plantation; therefore I decided to retain the insufficient data of the forest fragment. This data is only an approach to get an impression of what can be expected under other conditions in the forest fragment. That's why the forest fragment was excluded from the *Kruskal-Wallis* Test.

The number of seed species in the oil palm plantation and in the rainforest showed the biggest difference in seed species richness of the data set: Only four species were discovered in the oil

palm plantation in contrary to the rainforest, which hosts 39 identified species. Similar species numbers were detected in the forest fragment (18 species) and in the gradient (15 species). Due to the insufficient data of the forest fragment the total species number is probably much higher. On the same core plots in the Harapan rainforest vascular plants were collected within five subplots and trees > 10cm DBH were counted. Nearly 300 species (average species number per plot) were recorded (Drescher et al., 2016). This number appears very high compared to an average of 8.5 species of seeds per sampling plot on the same core plots. The number of plants on CRC core plots in the surrounding oil palm plantation of Harapan rainforest were six times lower than in the rainforest (average number of plant species per plot) (Drescher et al., 2016). In my assemblage, the number of species was more than nine times lower in the oil palm plantation than in the rainforest. The *Kruskal-Wallis* rank sum test proofed a significant difference between the rainforest, gradient and oil palm plantation. The ordination visualized this difference of the systems and gradient by showing different distances of sampling plots based on NDMS coordinates, which were assigned to the species of sampling plot in the systems or gradient. The wide scattering of sampling plots in the rainforest explains the huge difference of their species within the system. Furthermore, the large distance between sampling plots of the rainforests and the other systems and the gradient showed the difference of rainforest species between species in other systems and in gradient. In contrary the very low scattering of sampling plots in the oil palm plantation showed the very poor species richness in this system. These arguments were also expressed by the confidence intervals of associated sampling plots each system.

The total number of the individuals was more than five times higher in the rainforest than in the oil palm plantation. Surprisingly, the total number of individuals in the gradient was by far higher than in any other system or gradient. In comparison to the neighboring oil palm plantation, which had the second lowest number of total individuals, the number of individuals was more than 18 times higher in gradient. Nevertheless, I could not confirm a significant difference between individuals per sampling plot between the rainforest, gradient and oil palm plantation.

The most abundant species of all systems and the gradient, *C. hirta*, an invasive, tiny, bird dispersed species, was mostly found in the gradient and seldom discovered in the forest fragment (Peh, 2010). The total number of individuals of this species counted to 1742 in the gradient, which is more than the half of all occurring individuals in this area. Two more invasive species (*A. gangetica* and *P. conjugatum*) were also found in the gradient, which belonging to

the very abundant species with more than 100 individuals (Chew et al., 2012; Liu et al., 2006). Surprisingly, the invasive species *A. conyzoides* was the only discovered in the rainforest. *Asystasia gangetica* was the most abundant and the most frequent species in the oil palm plantation and rarely found in the gradient. Not only abundant invasive species were found in the gradient: native abundant species such as *Hedyotis spec.*, *Lipocarpha spec.* and *Pogestemon spec.* were regularly found in the gradient. *Pogestemon spec.* belongs to a large genus with about 80 species and is distributed over Africa and Asia. This species is an essential native oil crop planted underneath of Teak (*Tectona grandis*) plantations and other agroforestry systems (Mahanta et al., 2007; Wilkinson & Elevitch, 2000). Due to the intensive use of *Pogestemon spec.* as a crop plant, this species dispersed accidentally and become a very abundant species. Furthermore, *Hedyotis spec.* also rarely located in the rainforest and forest fragment. Another example of an abundant native species is *Ficus spec.*, which occurred mostly in the rainforest and rarely in the gradient. Almost all of the seven highly abundant species were present in two or more systems and in the gradient with the exception of *Lipocarpha spec.*, which only occurred in the gradient (Table 1).

The high dominance of the a few very abundant species in the three systems and the gradient was clearly visible in the rank abundance curves. Additionally, this curve showed that two of highly abundant species belong to the invasive species, (e.g. *C. hirta* and *A. gangetica*), which were located on top of the steep curves in the forest fragment, gradient and oil palm plantation. Magurran (2004) showed that steep rank abundance curves are characteristic for a species poor assemblage with a high abundance of individuals. Only the rainforest accumulation curve, which displayed the highest species richness of the data set, merged in a shallow, long tail that represented the largest group of less abundant species (singeltons) of all systems and the gradient. In southeast Asia rare tree species are typical for lowland rainforests (Cannon, 1998; Fangliang et al., 1997). One reason for this is that diverse rainforests with a high number of endemic plant species occur in southeast Asia (Sodhi et al., 2004). In my assemblage most of the discovered seed species do not belong to trees species, but to grasses, herbs and shrubs. The species frequency corresponds to the rank abundance curve.

Based on the increasing slopes of the species accumulation curves in the following order, gradient, forest fragment, rainforest, the rainforest showed the highest expected species richness. This also indicates that sampling effort was at least sufficient in this system and more species could be found with an ongoing data collection compared to the two other systems and the gradient. It can be concluded that the real species richness was underestimated

particularly for the rainforest and the forest fragment. Only for the oil palm plantation the sampling effort was sufficient. A continuous sampling would cover more species. For instance, other studies on seed rain collected their samples over a longer period of one or two years (Cole et al., 2010; Howe et al., 2010). This time frame is too long for this master thesis; therefore further research would be preferable.

The two species estimators *Chao 1* and *Jackknife 2* confirm that the real species richness is expected to be much higher than in the observed assemblage. The species richness in the rainforest is more than four times higher estimated by *Chao 1* than in the data set. *Chao 1* indicates a higher number of species than *Jackknife 2* for all systems and the gradient. Chiarucci et al. (2003) found that the *Chao 1* approximation is close to real species number of perennial plant species in Australia. But the *Jackknife 2* estimator approached the real species richness quicker than other estimators. However, all species estimators were proofed to approach the real species number better than the observed number of species (Chiarucci et al., 2003).

Systems or the gradient with a high number of species also indicated a high number of plant families (Table 2). The Asteraceae, largest flowering plant family in the world (Bremer, 1987) and the Poaceae family, the grass family, were discovered in every system and in the gradient. However, the Asteraceae family displayed the highest frequency of species (10 species) in all systems and the gradient and second highest frequency of species showed the Poaceae family (6 species). Arecaceae, Moraceae, Rubiaceae, Euphorbiaceae, Myristicaceae were discovered families and belong to the typical members of tropical rainforests (Primack & Corlett, 2005). Arecaceae and Myristicaceae were only found in the rainforest and in the fragment, while Moraceae was also found also in the gradient. Rubiaceae was discovered in all system and in the gradient except the oil palm plantation and Euphorbiaceae, which family had its greatest diversity in Asian forests. The Fabaceae is also a component of Asian rainforest, but this family is predominant in Africa and the Neotropics (Primack & Corlett, 2005).

A large range of different sizes and weights of species were observed in the assemblage. Most of the seed species indicates small sizes, which vary between one and five millimeters and show very light weight < 0.1 gram. The rainforest, where the largest number of species was found, showed the most diverse sizes and weights. Compared with the oil palm plantation contained the least diverse species and the lowest variations in seed size and weight. The *Kruskal-Wallis Test* displayed a significant difference between seed length, seed width, and seed weight between the systems and the gradient. Surprisingly, the *Nemenyi Test* showed a

difference between the gradient and the rainforest, but no difference between the oil palm plantation and rainforest. An explanation for this could be that many small and light weight species were found in the gradient.

In regard to hypothesis H1 the species diversity and turnover increased from the rainforest to the oil palm plantation, because the number of species and their diversity steadily increased with increasing forest degradation. The species composition was very monotonous with four different species in the oil palm plantation comparing to 39 discovered species in the rainforest. Also occurring was a very low of number of shared species among the oil palm plantation. Additionally, the systems and the gradient concerning their species richness were significantly different. Due to all this arguments the hypothesis H1 can be proofed.

Only for five species, one genus and one family the dispersal mechanisms were determined. For the other 52 species the dispersal related seed traits can't seriously confirmed by studying the characteristics of the seed pods and the seed weight. By the reason of less information for a large proportion of seed species regarding their dispersal related traits, the hypotheses H1a cannot be proofed.

It is proofed that the turnover and diversity increase from the oil palm plantation to the neighboring forest fragment (H2). However a significant increase only applies to the total number of species and diversity. Along the sampling plots of gradient the number of species shows a slow increase by the reason that the total amount species start already with a high number of species at sampling plot 1.

6.2 Impacts of the (discovered) invasive species on ecosystems in Indonesia

This study shows that invasive species are dominant in landscapes with human impact as in the oil palm plantation, gradient or in the forest fragment but they also can be found in natural ecosystems as in Harpan rainforest.

(Rejmánek, 1996) points out that invasive species are able to displace and become a serious threat to native species. This invasion can result in a loss of biodiversity and to the extinction of endemic species or to the replacement of endemic species (Rejmánek, 1996). There are indirect effects of alien species to the local ecosystem (Peters, 2001; Phillips, 1997). Rejmánek

(1996) indicates that lower rates of alien species were discovered in the tropical rainforest than in temperate forests. Furthermore natural and anthropogenic disturbances may benefit from the entry of invasive species to tropical rainforests (Usher, 1988). For Indonesia 78 invasive plants are listed (13 shrubs, 11 trees, 9 herbs, 7 grass)(Peh, 2010). *Clidemia hirta*, a highly invasive perennial, bird dispersed shrub, originated from the Neotropics (Peh, 2010) and occur in Indonesia. This species is distributed in large variety in tropical forests in the world (Peters, 2001). The species is predominated on tropical islands for example on the Hawaiian Islands (DeWalt & Ickes, 2004) rather than on continental sites (Peters, 2001). Here and in Malaysia *C. hirta* established in the understory of primary rainforests (DeWalt & Ickes, 2004; Wester & Wood, 1977). Furthermore, *C. hirta* grows light gaps, gap edges of an undisturbed tropical rainforest in in Malaysia and secondary and primary forests in Singapore (Teo et al., 2003). In Malaysia, gaps with this species were significantly correlated with past disturbance of wild pigs (Peters, 2001). In this study *C. hirta* was found in the gradient, a cleared area with many weeds and some shrubs and in the forest fragment, where the canopy was opened through many gaps. In urban and rural areas *C. hirta* occurs also often. In this study this species were not found in the oil palm plantations. In other studies *C. hirta* was discovered as an epiphytic plant on oil palm trunks (Altenhövel, 2013; Krobbach, 2014). *Clidemia hirta* was always found in feces in this study. This means that seeds cannot fall through the net of the trap, because the feces I found were always bigger than the holes in the mosquito net. I cannot explain why *C. hirta* was not found in the oil palm planation. Could a secondary rainforest as Harapan forest a potential habitat for *C. hirta*? On the first stage of re-vegetation *C. hirta* occurred there, but this species cannot be found in Harapan rainforest today (Briggs et al., 2015). An explanation might be that many predators regulate the wild pig population, which was correlated with *C. hirta* in Malaysia.

The species *A. gangetica* is a rapidly growing perennial and native to tropical India, and Africa (Chew et al., 2012; Meyer & Lavergne, 2004) and was often found in the oil palm planation yet rarely discovered in the gradient. *Asystasia gangetica* was introduced as an ornamental flower to Malaysia and Indonesia at the beginning of the last century and become a serious threat to the local vegetation. *Asystasia gangetica* can form a dense ground cover by replacing the local flora or invade in plantations especially oil palm plantations (CRC for Australian Weed Management, 2003). That could explain why *A. gangetica* was found in every sampling plot in the oil palm plantation. Today, *A. gangetica* is distributed over large areas in Malaysia and Indonesia and often found at sites with human activities (e.g. in the gradient) (Chew et al., 2012).

Paspalum conjugatum, an endemic sour grass from tropical America, was discovered in all systems and the gradient. This perennial weed occurs very often in young oil palm and rubber plantation as well in fallow areas (Sahid, 1996). The seeds of *P. conjugatum* spread quickly by wind, birds and adhere to animals bodies (Sauer, 1988) or the root suckers of this species develops a thick vegetative mat (Agus et al., 1998). Around 1500 seeds produced by each plant. *P. conjugatum* is categorized as a shade tolerant species (King, 1966). This could be a reason why this species was found in the rainforest. Furthermore the rapid spread in combination with a high seed production could explain the occurrence of *P. conjugatum* in every system and in the gradient.

The fast growing species *Ageratum conyzoides* from tropical south Amerika invades cultivated areas, crop land and pastures. Surprisingly it was found in the rainforest and not in human influenced areas as the oil palm plantation or the gradient (Kohli et al., 2006).

6.3 Species loss in oil palm plantation comparing to forests

The high loss of forests due to logging activities to implement new monoculture plantations corresponds with a high loss of biodiversity (Margono et al., 2014; Wilcove et al., 2013; Wilcove & Koh, 2010).

Drescher et al. (2016) reported that six times as many vascular plant species in the rainforests as in monocultures in the same area of Jambi province, Sumatra. Further four times more epiphytic species were found in the rainforest as in the oil palm plantation (Altenhövel, 2013). Summarizing an average of 15 % of all taxonomic species in the rainforest were found in oil palm plantation worldwide (Fitzherbert et al., 2008). Faunal species in oil palm plantation were often abundant non-forest species, which belonging to generalists and invasive alien species (Aratrakorn et al., 2006; Chung et al., 2000; Danielsen et al., 2009). Furthermore, only a few abundant plant species, which belonging to generalists were present in the oil palm (Chung et al., 2000). Danielsen et al. (2007) investigated that the typical forest flora as forest trees, lianas, epiphytic orchids, and indigenous palms were not included in oil palm plantations in Indonesia. Compared to this study no typical forest species were found in seed traps in the oil palm plantation.

A decline of species richness of vascular plants along a transect of forests, juggle rubber (Rubber agroforestry) and rubber plantations was reported in Jambi province , Sumatra

(Beukema et al., 2007). Similar results were shown along the gradient of the system and the forest distance gradient in the study of this thesis. Fewer bat species, which are important for seed dispersal, occurred in smaller fragments, while the largest of fragments displayed a higher species richness due to higher number of generalists and edge-tolerant species (Struebig et al., 2011). Corresponding results were found in the rainforests with a higher species richness of plants compare with the forest fragment, where the invasive species *P. conjugatum* occurs, which is also a generalist.

Peh et al. (2006) investigated regarding to abundance and species richness, rubber plantations more important than oil palm plantations. For birds rubber plantations served as a location for moving and perching and the oil palm plantation for fogging (Peh et al., 2006). Many tropical seeds were dispersed by birds (Martínez-Garza et al., 2009). Twenty percent of primary forest avian fauna were discovered in oil palm in southern Malaysia (Peh et al., 2006). In Sumatra the bird diversity declined in the following order: Primary forests, jungle rubber and rubber plantation (Beukema et al., 2007). Due to the low bird diversity in oil palm plantations it has to be questioned if these habitats were barriers for seed dispersal. However, the bird diversity increased with the number of trees in oil palm plantation in Jambi province on Sumatra (Teuscher et al., 2015).

Seed dispersal differed significantly between habitats. A lower species richness was investigated in pastures than secondary and primary forest (Martínez-Garza et al., 2009). Fragments of forest close to degraded habitats showed a relatively high forest species richness of birds (Peh et al., 2006). This means a forest fragment can support biodiversity in degraded habitats. On the other hand fragmentation increases forest edge effects by which the vulnerability to wind and fire increase (Peh et al., 2006). In areas where forests were logged, jungle rubber and other agroforestry systems are important to provide habitat for intermediate level of fern biodiversity. But jungle rubber cannot substitute primary forests (Beukema & Van Noordwijk, 2004). Agroforestry systems with enrichment planting as the B11 biodiversity enrichment experiment can provide habitats for seed dispersing animals. An extensively managed oil plantation with a high number of trees increases the number of bird and leads to relatively high loss of revenue. On the other hand, an intensively managed oil palm plantation with the same properties results in a smaller loss of revenue despite an increase in bird species (Teuscher et al., 2015).

6.4 Conclusion

As part of the CRC 990 project and the subproject B11, this was the first study to investigate seed rain in an oil palm plantation, in a forest fragment, a distance gradient between the forest fragment and oil palm plantation and in a rainforest on Sumatra, Indonesia. Seed dispersal plays important role in ecosystem function especially in areas with ongoing deforestation and transformation of tropical lowland rainforest into monocultures such as in Jambi province, Sumatra. Due to seed dispersal plants are spread to new habitats, degraded areas or oil palm plantations, where they can establish or recover. Seed dispersal influences the genetic structure by increasing or decreasing gene flow of populations (Nathan & Muller-landau, 2000) and helps to overcome barriers such as an oil palm plantation (Peh et al., 2006).

I investigated in this master thesis that species richness and diversity of the discovered seeds were at the highest in the rainforest and decrease in following order: forest fragment, gradient and oil palm plantation. The significant difference between the systems and the gradient suggest a lack of forest specialists in the oil palm plantation and in the gradient. Instead, invasive species and generalists invaded these landscapes. Due to the lack of forests species the conservation value should be on high concern in monocultures as in the oil palm plantation and in transformed landscapes as in the gradient. Further research on seed rain in the systems and the gradient is recommended over a longer period to discover more species and to get a representative assemblage. Also the effects of flowering and fruiting trees in the B11 experiment on seed dispersal in the oil palm plantation in the future or to what extent these planted trees attract the seed disperser can be studied.

In summary, seed dispersal is influenced by the surrounding habitats (Damschen et al., 2008; Prevedello & Vieira, 2010) and species richness of plants and birds is higher in agroforestry systems as in monoculture plantations (Beukema et al., 2007). As such, designer landscapes, where diverse agroforestry serve as buffer zones between oil palm plantations and species rich landscape (Koh et al., 2009) are very important, and the experiment of the B11 subgroup in the CRC 990 project is an approach to maintain and promote seed dispersal and biodiversity in oil palm plantations.

7 References

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Table 1: Seed species and their characteristics

Microscopic picture	Seed No.	Morpho-Species	Family	Genus	Species	N	Average weight (g)	Average length (mm)	Average width (mm)	Dispersal mechanism
	1	-	<i>Acanthaceae</i>	<i>Asystasia</i>	<i>gangetica</i>	130	0.01010	4.29	3.57	Autochory (confirmed)
	2	-	<i>Poaceae</i>	<i>Paspalum</i>	<i>spec.</i>	1	0.00080	2.04	0.80	Exozoochory
	3	-	<i>Poaceae</i>	<i>Paspalum</i>	<i>conjugatum</i>	107	0.00034	1.55	1.06	Exozoochory (confirmed)
	4	-	<i>Fabaceae</i>	<i>Aeschynomene</i>	<i>spec.</i>	1	0.00450	5.94	2.67	Exozoochory/ Endozoochory

	5	-	<i>Moraceae</i>	<i>Ficus</i>	<i>spec.</i>	638	0.00012	0.64	0.42	Endozoochory (confirmed)
	6	-	<i>Asteraceae</i>	<i>Ageratum</i>	<i>conyzoides</i>	2	0.00051	5.73	0.44	Anemochory / Hydrochory (confirmed)
	7	-	<i>Myrtaceae</i>	<i>Rhodamnia</i>	<i>cinerea</i>	3	0.02947	5.40	5.63	Endozoochory (confirmed)
	8	BC.08				6	0.01605	3.44	3.59	-
	9	BC.09				41	0.00795	4.70	3.78	-

	10	BC.10				2	0.08653	6.82	4.46	-
	11	BC.16				1	0.00260	3.08	1.48	-
	12	-	<i>Cyperaceae</i>	<i>Fimbristyles</i>	<i>spec.</i>	38	0.00103	3.05	1.85	-
	13	-	<i>Rhamnaceae</i>			4	0.15675	8.49	8.07	Endozoochory (confirmed)
	14	-	<i>Myristicaceae</i>	<i>Horsfieldia</i>	<i>spec.</i>	2	0.79105	18.97	13.38	-

	15	-	<i>Cannabaceae</i>	<i>Gironniera</i>	<i>spec.</i>	10	0.11859	7.62	6.58	-
	16	-	<i>Solanaceae</i>			1	0.00050	1.06	0.85	-
	17	-	<i>Areaceae</i>	<i>Calamus</i>	<i>spec.</i>	41	0.00935	3.04	2.12	-
	18	-	<i>Poaceae</i>	<i>Brachiaria</i>	<i>spec.</i>	6	0.00163	3.75	2.37	-

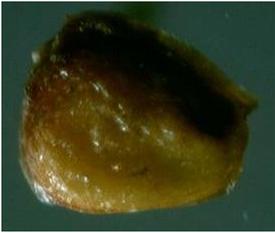
	19	-	<i>Cucurbitaceae</i>			3	0.00130	4.16	1.80	-
	20	-	<i>Lamiaceae</i>	<i>Pogostemon</i>	<i>spec.</i>	130	0.00164	2.48	1.66	-
	21	-	<i>Rubiaceae</i>	<i>Hedyotis</i>	<i>spec.</i>	180	0.00027	1.34	1.11	-
	22	-	<i>Cyperaceae</i>	<i>Lipocarpha</i>	<i>spec.</i>	502	0.00020	1.34	0.59	-
	23	-	<i>Rubiaceae</i>	<i>Psychotria</i>	<i>spec.</i>	1	0.01480	6.01	3.38	-

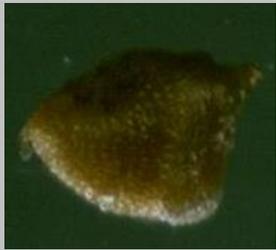
	24	-	<i>Euphorbiaceae</i>	3	0.071633	6.59	4.62	-
	25	-	<i>Phyllanthaceae</i>	2	0.001250	2.92	1.40	-
	26	-	<i>Fabaceae</i>	3	0.013033	13.64	2.43	-
	27	-	<i>Fabaceae</i>	1	0.04870	9.77	5.07	-
	28	-	<i>Asteraceae</i>	1	0.00040	3.48	1.02	-

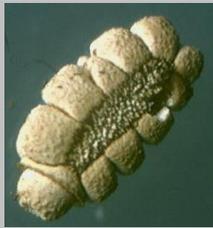
	29	-	<i>Phyllanthaceae</i>			8	0.00008	1.10	0.67	-
	30	-	<i>Asteraceae</i>			4	0.00120	3.39	1.15	-
	31	-	<i>Myrtaceae</i>			2	0.00210	1.69	1.73	-
	32	-	<i>Rubiaceae</i>			2	0.01590	4.46	3.93	-
	33	-	<i>Lamiaceae</i>	<i>Hyptis</i>	<i>spec.</i>	4	0.14380	1.99	1.54	-

	34	-	<i>Sphenocleaceae</i>		4	0.00748	2.94	2.58	-	
	35	-	<i>Phyllanthaceae</i>		23	0.00062	2.62	1.32	-	
	36	-	<i>Melastomataceae</i>	<i>Clidemia</i>	<i>hirta</i>	1750	0.00005	0.46	0.30	Endozoochory (confirmed)
	37	-	<i>Lythraceae</i>		6	0.04603	8.77	3.32	-	
	38	-	<i>Solanaceae</i>		6	0.00090	2.16	1.84	-	

	39	-	<i>Euphorbiaceae</i>	1	0.29050	13.31	10.07	-
	40	-	<i>Asteraceae</i>	1	0.00010	1.95	0.51	-
	41	BC.41		1	0.01790	5.23	1.78	-
	42	BC.42		2	0.00315	4.89	1.84	-
	43	BC.43		1	0.00972	4.21	3.93	-

	44	BC.44		1	0.00120	2.27	1.36	-
	45	-	<i>Asteraceae</i>	9	0.00019	3.49	1.23	-
	46	BC.46		1	0.00010	1.14	0.96	-
	47	BC.47		1	0.00130	7.24	2.57	-
	48	BC.48		1	0.00070	1.83	1.27	-

	49	BC.49		2	0.00045	0.57	0.42	-
	50	-	<i>Asteraceae</i>	19	0.00027	2.72	0.53	Anemochory/ Endozoochory/ Exozoochory
	51	-	<i>Fabaceae</i>	2	0.02385	9.40	9.39	-
	52	BC.52		10	0.00171	4.48	0.98	-

	53	BC.53			1	0.00130	3.45	1.82	-
	54	BC.54			1	0.00060	2.15	1.12	-
	55	-	<i>Fabaceae</i>	<i>Aeschynomene spec.</i>	1	0.00280	3.91	2.22	-
	56	BC.56			12	0.01555	8.19	8.12	-
	57	BC.57			12	0.47519	12.14	11.42	-

	58	-	<i>Melastomataceae</i>	<i>Melastoma</i>	<i>spec.</i>	6	0.01001	1.38	1.05	-
	59	-	<i>Fabaceae</i>	<i>Adenantha</i>	<i>spec.</i>	1	0.12330	8.20	7.22	-

Table 2: Species and Individuals per sampling site in the investigated systems

System	Sampling site	Morpho-Species	Family	Genus	Species	No. of individuals
Rainforest	rf 1	-	<i>Moraceae</i>	<i>Ficus</i>	<i>spec.</i>	622
Rainforest	rf 1	-	<i>Asteraceae</i>	<i>Ageratum</i>	<i>conyzoides</i>	1
Rainforest	rf 1	BC.08				2
Rainforest	rf 1	BC.09				36
Rainforest	rf 1	BC.10				2
Rainforest	rf 1	BC.11				1
Rainforest	rf 1	-	<i>Cannabaceae</i>	<i>Gironniera</i>	<i>spec.</i>	1
Rainforest	rf 1	-	<i>Poaceae</i>	<i>Brachiaria</i>	<i>spec.</i>	2
Rainforest	rf 1	BC.41				1
Rainforest	rf 1	BC.42				2
Rainforest	rf 1	BC.46				1
Rainforest	rf 1	-	<i>Fabaceae</i>	<i>Aeschynomene</i>		1
Rainforest	rf 2	-	<i>Myrtaceae</i>	<i>Rhodamnia</i>	<i>cinerea</i>	1
Rainforest	rf 2	BC.09				1
Rainforest	rf 2	-	<i>Arecaceae</i>	<i>Calamus</i>	<i>spec.</i>	2
Rainforest	rf 2	-	<i>Poaceae</i>	<i>Brachiaria</i>	<i>spec.</i>	1
Rainforest	rf 2	-	<i>Asteraceae</i>			1
Rainforest	rf 2	-	<i>Phyllanthaceae</i>			7
Rainforest	rf 2	BC.56				1
Rainforest	rf 2	BC.57				1
Rainforest	rf 3	BC.44				1
Rainforest	rf 3	BC. 52				6
Rainforest	rf 4	-	<i>Moraceae</i>	<i>Ficus</i>	<i>spec.</i>	4
Rainforest	rf 4	BC.08				2
Rainforest	rf 4	BC.09				1
Rainforest	rf 4	-	<i>Cannabaceae</i>	<i>Gironniera</i>	<i>spec.</i>	5
Rainforest	rf 4	-	<i>Arecaceae</i>	<i>Calamus</i>	<i>spec.</i>	38
Rainforest	rf 4	-	<i>Phyllanthaceae</i>			1
Rainforest	rf 4	-	<i>Asteraceae</i>			4

Rainforest	rf 4	-	<i>Asteraceae</i>			9
Rainforest	rf 4	BC.52				1
Rainforest	rf 5	BC.09				1
Rainforest	rf 5	-	<i>Rhamnaceae</i>			4
Rainforest	rf 5	-	<i>Myristicaceae</i>	<i>Horsfieldia</i>	<i>spec.</i>	2
Rainforest	rf 5	-	<i>Cannabaceae</i>	<i>Gironniera</i>	<i>spec.</i>	4
Rainforest	rf 5	-	<i>Solanaceae</i>			1
Rainforest	rf 5	-	<i>Areceaceae</i>	<i>Calamus</i>	<i>spec.</i>	1
Rainforest	rf 5	-	<i>Cucurbitaceae</i>			1
Rainforest	rf 5	BC.47				1
Rainforest	rf 5	-	<i>Asteraceae</i>			1
Rainforest	rf 5	BC.52				2
Rainforest	rf 5	BC.53				1
Rainforest	rf 5	BC.56				11
Rainforest	rf 5	BC.57				2
Rainforest	rf 6	BC.08				1
Rainforest	rf 6	-	<i>Lythraceae</i>			5
Rainforest	rf 6	BC.54				1
Rainforest	rf 6	BC.57				5
Rainforest	rf 7	-	<i>Poaceae</i>	<i>Paspalum</i>	<i>conjugatum</i>	1
Rainforest	rf 7	BC.09				2
Rainforest	rf 7	BC.48				1
Rainforest	rf 7	BC.57				1
Rainforest	rf 7	-	<i>Melastomataceae</i>	<i>Melastoma</i>	<i>spec.</i>	1
Rainforest	rf 8	-	<i>Asteraceae</i>	<i>Ageratum</i>	<i>conyzoides</i>	1
Rainforest	rf 8	BC.08				1
Rainforest	rf 8	-	<i>Poaceae</i>	<i>Brachiaria</i>	<i>spec.</i>	3
Rainforest	rf 8	-	<i>Cucurbitaceae</i>			2
Rainforest	rf 8	-	<i>Rubiaceae</i>	<i>Hedyotis</i>	<i>spec.</i>	1
Rainforest	rf 8	-	<i>Myrtaceae</i>			2
Rainforest	rf 8	-	<i>Rubiaceae</i>			2
Rainforest	rf 8	-	<i>Lamiaceae</i>	<i>Hyptis</i>	<i>spec.</i>	4
Rainforest	rf 8	-	<i>Sphenocleaceae</i>			4

Rainforest	rf 8	BC.57				3
Forest Fragment	ff 1	-	<i>Lamiaceae</i>	<i>Pogostemon</i>	<i>spec.</i>	5
Forest Fragment	ff 1	-	<i>Rubiaceae</i>	<i>Psychotria</i>	<i>spec.</i>	1
Forest Fragment	ff 1	-	<i>Melastomataceae</i>	<i>Clidemia</i>	<i>hirta</i>	8
Forest Fragment	ff 1	-	<i>Asteraceae</i>			4
Forest Fragment	ff 1	-	<i>Melastomataceae</i>	<i>Melastoma</i>	<i>spec.</i>	5
Forest Fragment	ff 2	-	<i>Poaceae</i>	<i>Paspalum</i>	<i>conjugatum</i>	1
Forest Fragment	ff 2	-	<i>Lamiaceae</i>	<i>Pogostemon</i>	<i>spec.</i>	3
Forest Fragment	ff 3	-	<i>Lamiaceae</i>	<i>Pogostemon</i>	<i>spec.</i>	2
Forest Fragment	ff 3	-	<i>Solanaceae</i>			6
Forest Fragment	ff 3	BC.43				1
Forest Fragment	ff 4	-	<i>Euphorbiaceae</i>			1
Forest Fragment	ff 5	-	<i>Myrtaceae</i>	<i>Rhodamnia</i>	<i>cinerea</i>	1
Forest Fragment	ff 5	-	<i>Euphorbiaceae</i>			3
Forest Fragment	ff 5	-	<i>Phyllanthaceae</i>			2
Forest Fragment	ff 5	-	<i>Fabaceae</i>			3
Forest Fragment	ff 5	-	<i>Fabaceae</i>			1
Forest Fragment	ff 5	BC.35				8
Forest Fragment	ff 5	BC.40				1
Forest Fragment	ff 7	-	<i>Myrtaceae</i>	<i>Rhodamnia</i>	<i>cinerea</i>	1
Forest Fragment	ff 7	-	<i>Lamiaceae</i>	<i>Pogostemon</i>	<i>spec.</i>	4
Forest Fragment	ff 7	-	<i>Rubiaceae</i>	<i>Hedyotis</i>	<i>spec.</i>	3
Forest Fragment	ff 7	BC.37				1
Forest Fragment	ff 8	-	<i>Lamiaceae</i>	<i>Pogostemon</i>	<i>spec.</i>	1
Gradient	gr 1	-	<i>Poaceae</i>	<i>Paspalum</i>	<i>conjugatum</i>	1
Gradient	gr 1	-	<i>Moraceae</i>	<i>Ficus</i>	<i>spec.</i>	12
Gradient	gr 1	-	<i>Lamiaceae</i>	<i>Pogostemon</i>	<i>spec.</i>	10
Gradient	gr 1	-	<i>Rubiaceae</i>	<i>Hedyotis</i>	<i>spec.</i>	4
Gradient	gr 1	-	<i>Cyperaceae</i>	<i>Lipocarpha</i>	<i>spec.</i>	4
Gradient	gr 1	-	<i>Phyllanthaceae</i>			3
Gradient	gr 1	-	<i>Fabaceae</i>	<i>Adenanthera</i>	<i>spec.</i>	1
Gradient	gr 2	-	<i>Poaceae</i>	<i>Paspalum</i>	<i>conjugatum</i>	19
Gradient	gr 2	-	<i>Lamiaceae</i>	<i>Pogostemon</i>	<i>spec.</i>	75

Gradient	gr 2	-	<i>Rubiaceae</i>	<i>Hedyotis</i>	<i>spec.</i>	51
Gradient	gr 2	-	<i>Phyllanthaceae</i>			9
Gradient	gr 2	-	<i>Melastomataceae</i>	<i>Clidemia</i>	<i>hirta</i>	826
Gradient	gr 2	-	<i>Asteraceae</i>			3
Gradient	gr 3	-	<i>Acanthaceae</i>	<i>Asystasia</i>	<i>gangetica</i>	1
Gradient	gr 3	-	<i>Poaceae</i>	<i>Paspalum</i>	<i>conjugatum</i>	5
Gradient	gr 3	-	<i>Lamiaceae</i>	<i>Pogostemon</i>	<i>spec.</i>	10
Gradient	gr 3	-	<i>Rubiaceae</i>	<i>Hedyotis</i>	<i>spec.</i>	4
Gradient	gr 3	-	<i>Melastomataceae</i>	<i>Clidemia</i>	<i>hirta</i>	243
Gradient	gr 3	-	<i>Asteraceae</i>			3
Gradient	gr 4	-	<i>Poaceae</i>	<i>Paspalum</i>	<i>conjugatum</i>	34
Gradient	gr 4	-	<i>Lamiaceae</i>	<i>Pogostemon</i>	<i>spec.</i>	3
Gradient	gr 4	-	<i>Rubiaceae</i>	<i>Hedyotis</i>	<i>spec.</i>	1
Gradient	gr 4	-	<i>Cyperaceae</i>	<i>Lipocarpha</i>	<i>spec.</i>	16
Gradient	gr 4	-	<i>Phyllanthaceae</i>			2
Gradient	gr 4	-	<i>Melastomataceae</i>	<i>Clidemia</i>	<i>hirta</i>	197
Gradient	gr 4	BC.49				2
Gradient	gr 4	BC.50				1
Gradient	gr 5	-	<i>Acanthaceae</i>	<i>Asystasia</i>	<i>gangetica</i>	3
Gradient	gr 5	-	<i>Poaceae</i>	<i>Paspalum</i>	<i>conjugatum</i>	21
Gradient	gr 5	-	<i>Cyperaceae</i>	<i>Fimbristyles</i>	<i>spec.</i>	38
Gradient	gr 5	-	<i>Cyperaceae</i>	<i>Lipocarpha</i>	<i>spec.</i>	341
Gradient	gr 5	-	<i>Phyllanthaceae</i>			1
Gradient	gr 6	-	<i>Cyperaceae</i>	<i>Lipocarpha</i>	<i>spec.</i>	2
Gradient	gr 6	-	<i>Asteraceae</i>			4
Gradient	gr 7	-	<i>Acanthaceae</i>	<i>Asystasia</i>	<i>gangetica</i>	2
Gradient	gr 7	-	<i>Poaceae</i>	<i>Paspalum</i>	<i>conjugatum</i>	1
Gradient	gr 7	-	<i>Lamiaceae</i>	<i>Pogostemon</i>	<i>spec.</i>	1
Gradient	gr 7	-	<i>Cyperaceae</i>	<i>Lipocarpha</i>	<i>spec.</i>	6
Gradient	gr 7	BC.52				1
Gradient	gr 8	-	<i>Acanthaceae</i>	<i>Asystasia</i>	<i>gangetica</i>	3
Gradient	gr 8	-	<i>Poaceae</i>	<i>Paspalum</i>	<i>spec.</i>	1
Gradient	gr 8	-	<i>Lamiaceae</i>	<i>Pogostemon</i>	<i>spec.</i>	16

Gradient	gr 8	-	<i>Rubiaceae</i>	<i>Hedyotis</i>	<i>spec.</i>	116
Gradient	gr 8	-	<i>Cyperaceae</i>	<i>Lipocarpha</i>	<i>spec.</i>	133
Gradient	gr 8	-	<i>Melastomataceae</i>	<i>Clidemia</i>	<i>hirta</i>	476
Gradient	gr 8	BC.51				2
Oil palm	op 1	-	<i>Acanthaceae</i>	<i>Asystasia</i>	<i>gangetica</i>	23
Oil palm	op 2	-	<i>Acanthaceae</i>	<i>Asystasia</i>	<i>gangetica</i>	43
Oil palm	op 3	-	<i>Acanthaceae</i>	<i>Asystasia</i>	<i>gangetica</i>	12
Oil palm	op 4	-	<i>Acanthaceae</i>	<i>Asystasia</i>	<i>gangetica</i>	15
Oil palm	op 4	-	<i>Fabaceae</i>	<i>Aeschynomene</i>	<i>spec.</i>	1
Oil palm	op 5	-	<i>Acanthaceae</i>	<i>Asystasia</i>	<i>gangetica</i>	21
Oil palm	op 6	-	<i>Acanthaceae</i>	<i>Asystasia</i>	<i>gangetica</i>	1
Oil palm	op 6	-	<i>Poaceae</i>	<i>Paspalum</i>	<i>conjugatum</i>	24
Oil palm	op 6	-	<i>Asteraceae</i>			3
Oil palm	op 7	-	<i>Acanthaceae</i>	<i>Asystasia</i>	<i>gangetica</i>	5
Oil palm	op 8	-	<i>Acanthaceae</i>	<i>Asystasia</i>	<i>gangetica</i>	1

Table 3: Species estimation of the abundance based species estimator *Chao 1*. Species per sampling site in the investigated systems were estimated.

Sampling site	Chao estimation: Rainforest	Chao estimation: Forest fragment	Chao estimation: Gradient	Chao estimation: Oil palm
3	65.8	22.6	17.2	4.0
4	82.8	37.7	17.1	4.7
5	103.4	55.3	18.6	5.2
6	119.5	77.8	23.2	5.7
7	139.9	101.1	33.6	6.5
8	180.1	131.0	44.0	7.6

Table 4: Species estimation incidence based species estimator *Jackknife 2*. Species per sampling site in the investigated systems were estimated.

Sampling site	Jackknife 2 estimation: Rainforest	Jackknife 2 estimation: Forest fragment	Jackknife 2 estimation: Gradient	Jackknife 2 estimation: Oil palm
3	34.7	14.7	15.7	4.3
4	46.3	20.6	18.5	5.4
5	56.9	27.7	20.2	6.4
6	67.6	33.4	22.6	7.6
7	78.4	38.2	25.5	8.8
8	88.4	44.4	28.4	9.9

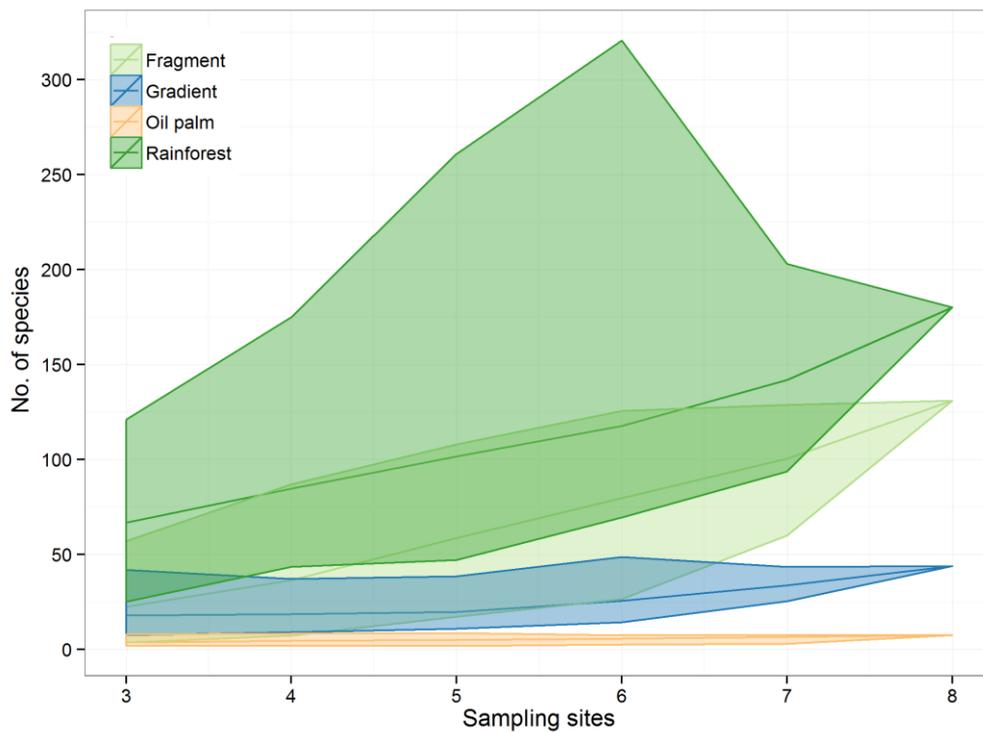


Figure 1: Species accumulation curve based on data of the Chao 1 estimator. The graph shows a simulation of estimated species per sampling site for all systems.

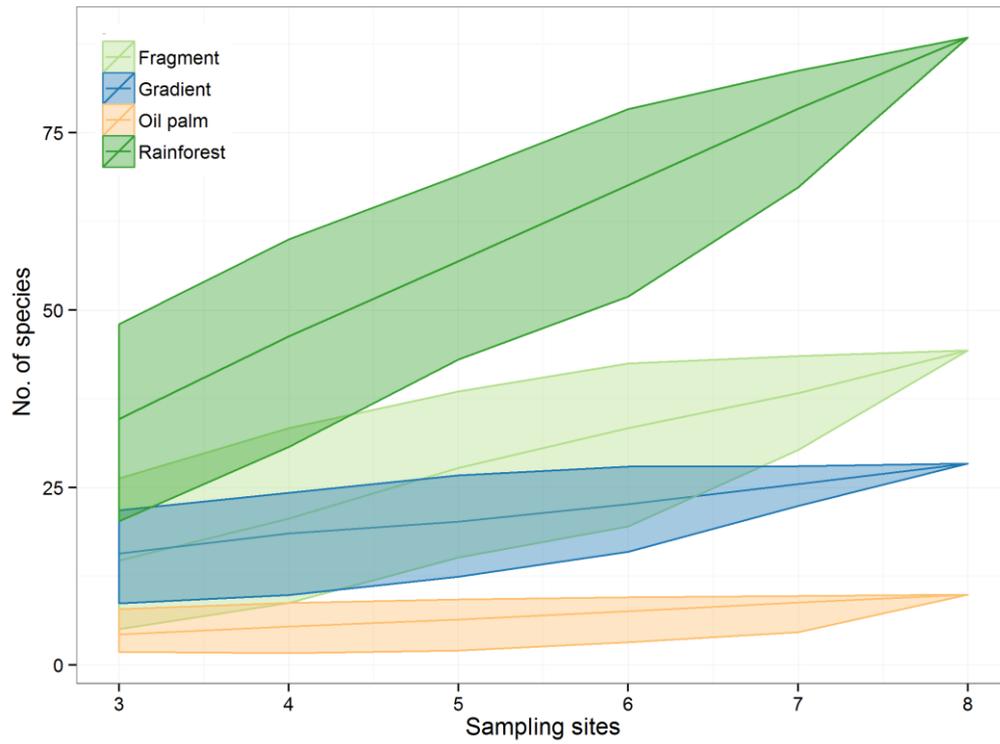


Figure 2: Species accumulation curve based on data of the Jackknife 2 estimator. The graph shows a simulation of estimated species per sampling site for all systems.

Selbständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Masterarbeit zum „Seed rain in remnant forests and an oil palm plantation in Jambi province, Sumatra“ selbständig und nur unter der Verwendung der angegebenen Hilfsmittel verfasst habe.

(Datum, Unterschrift)