Floral Composition and Regeneration in the Sabangau Peat Swamp Forest

Bachelor-Thesis

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Appendix
Abstract
The Sabangau Peat swamp forest, Central Kalimantan, Borneo, contains the largest Orangutan and Southern Bornean Gibbon population left in the wild and as a carbon sink is of quintessential importance in the fight against climate change. In this study I analysed structure, floristic composition and regeneration of this forest, so as to recognise possible edge effects and finding indicator species for vegetation changes. Since logging and palm oil companies are fragmenting the forest at frightening speed these basic information gains even more importance. The study was carried out in a grid of 700x700m starting from the forest edge moving into the interior. In 225 plots the DBH, BD, height and species of all trees were identified, as well as the diameter and species composition and abundance of lianas, figs, pitcher plants, Pandanaceae and terrestrial orchids. Abundance of tree saplings and seedlings was also recorded. The data analysis showed four different forest compositions, with various indicator species respectively. There were also clear indications for the presence of forest edge effects and different successional stages of the forest were found up to 100m into the interior. They most likely represent recolonization of a previously burned area. Clear trends were observed when moving into the forest interior, like a substantial increase in the alpha diversity of trees and lianas. A drop in abundance and change of species composition for Pandanaceae, Pitcher plants, lianas and terrestrial orchids when moving into the interior could be recognised. Tree species showed a clear pattern in tree height variation becoming more varied when moving in while the species composition gained diversity, with the edge being dominated by a few pioneer species like Tristaniopsis sp. and Calophyllum sp.
1. Introduction

1.1 Tropical rain forests of Borneo

Borneo is the third largest island on the planet and has until recently been left nearly completely untouched by industrialisation (if not otherwise indicated all following information in this chapter origins from Rautner et al. 2005). Unfortunately the island underwent a tremendous transition in the 1980s when large parts of the pristine rainforest were being cut down by industrialised nations like Japan and the United States. While there was still 73.7% of primary forest left in 1985 only 25 years later barely 44.4% of primary forest remained. Since there is no indication of the deforestation rates slowing down, the impact habitat fragmentation is having on the forest is becoming more and more important. It was therefore the aim of this study to quantify the effects on vegetation caused by edge effects, ascertaining different forest compositions near the edge and identifying indicator species for each composition for easy identification.

Borneo harbours an incredible floral diversity that is irreplaceable in the world, since its unique geological and climatic record allowed the development of such a plentiful diversity. There are over 15,000 different flowering plants in Borneo and over 3000 tree species, of which many are endemic to the island. A reason for this huge species abundance is the distinct ecosystems, such as the various types of forest, that can be found across Borneo.

Mangrove forests can be found in coastal regions were shallow areas of land meet the sea. The floral species there have developed ingenious adaptations that make them cope with the unique challenges a mangrove forest poses, like loose soil and high salt concentrations. Mangroves are also one of the only true viviparous plant species, having the seed germinate on top of the parent plant. Unfortunately Mangrove forests are being

Figure 1. The Sabangau peat swamp rainforest in Central Kalimantan, Borneo shrouded in morning mist.
destroyed at a frightening rate, less than 50% of its former glory remains and half of it is already degraded by anthropogenic actions (Upadhyay et al. 2002).

Dipterocarp forests are the most biodiverse and at the same time the most threatened forests in Borneo, 68% of which have been cleared in Kalimantan alone. This is due to the fact that the often huge trees, which frequently exceed 45m in height, offer excellent wood for timber companies. This logging activity though has taken a heavy toll on this ecosystem, which seems to be breaking down.

The montane forests of Borneo can be found at elevations between 1000 and 3300m. They are characterised by a much lower canopy height, a decrease in biomass and smaller leaves. These high altitude “islands” harbour many endemic species, which derived from Asian and Australasian families, which make them one of the most diverse montane habitats on earth.

Heath forests occur on well-drained, sandy soil that is very nutrient poor. As a consequence these forests are characterised by tree species that are tolerant of these hostile conditions (Ghazoul & Sheil 2010). Heath forests are also much less biodiverse than other tropical ecosystems. Since these forests rarely recover and fire risk is extremely high it is believed that within the next decade this ecosystem will have gone extinct.

This study focuses on peat swamp forest. These ecosystems are characterised by thick layers of peat that form on the ground. Lowland tropical peat consists mainly of decomposed trunks, branches and roots of trees, which is complemented by structureless organic material (Page et al. 1999). Peat thickness varies from site to site and is generally between 0.5-10m thick (Page et al. 1999). The reason why peat exists in these places and does not decompose like in more temperate regions is due to a combination of factors. When rainfall is high and the topography is conductive to poor drainage, permanent waterlogging and substrate acidification occurs. This is the cause for dead plant material accumulating on the ground faster than it decomposes and thereby forms the thick peat layer characteristic for this ecosystem (Page et al. 1999). This accumulation of dead plant matter made these forests huge carbon sinks. It is estimated that tropical peat land forests in South East Asia contain over 70 Giga-tonnes of Carbon (Miettinen et al. 2012). Peat forests are hence not only interesting to biologists for their incredible biodiversity but are also pivotal in the fight against climate
change. More and more peat swamp forests are being modified or destroyed by humans for the construction of industrial plantations, for palm oil or pulpwood (Miettinen et al. 2012). This leads to degraded forests with lower water levels, which are a lot more susceptible to fire (Wösten et al. 2008). In 1997 the amount of carbon released from peat and forest fires, caused by a continuing drought, the El Niño event, led to the largest annual increase in atmospheric CO₂ concentration until then (Page et al. 2002). About 0.81-2.57 giga-tonnes of carbon were released, which is equivalent to 13-40% of mean global carbon emissions per year from fossil fuels in the world (Page et al. 2002). In times of increasing fragmentation of peat swamp forests and greater land clearance (Miettinen et al. 2012) it becomes of quintessential importance to understand the effects this is having on this ecosystem and the biodiversity within it.

The Sabangau peat swamp forest, in which the study was carried out, is of particular importance because it is inhabited by the largest Bornean Orangutan (Pongo pygmaeus) (Morrogh-Bernard et al. 2003) and Southern Bornean Gibbon (Hylobates albibarbis) populations (Cheyne et al. 2007) left in the world, making the survival of the forest of quintessential importance for the conservation of these charismatic ape species and many other endemic flora and fauna species, which evolved to survive in the challenging conditions of a peat swamp forest.

Figure 2. An orangutan female with its infant moving through the diverse canopy of the Sabangau Forest.
1.2 Forest edge effects and fragmentation

The size of a natural landscape correlates directly with the species richness of a habitat. Because of this, habitat loss and fragmentation are two of the major threats to biodiversity (Andrén 1994). The more habitat loss a certain landscape suffers the greater the degree of fragmentation and the more isolated the left over forest patches are from one another (Andrén 1994). Greater fragmentation also leads to more forest areas being exposed to the edge, making edge effects more and more significant as fragmentation increases. Edge effects can affect up to 56% of the habitat even when 80% of the landscape is still classified as natural habitat (Harper et al. 2005). Forest edge effects contribute to forest degradation and a loss of biodiversity in the affected area (Saunders et al. 1991).

The distance and magnitude of edge influence in any particular ecosystem is controlled by various factors. Assuming that edge influence is monotonic and linear allows us to generalise the effects on edges. They can then range from having a large magnitude over a small distance to a small magnitude over a large distance (Harper et al. 2005) (see fig.3). In other words magnitude and distance don’t have to correlate with each other and could be affected differently by the same factors (Harper et al. 2005). Forest edges always experience an exchange of material, energy and organisms across the boundary (Cadenasso et al. 2003). Other effects include alterations in ecosystem composition and alterations in biophysical processes (Harper et al. 2005). Direct effects that can be observed include physical disturbance of vegetation, abiotic gradients (such as wind, moisture or light) and an increased access for materials like pollen or seeds, organisms and energy (Harper et al. 2005) (see fig. 3). Edge effects can be classified in primary and secondary categories. Primary effects are direct results from effects created by the edge like damage to vegetation, disruption of the forest floor, changes in evapotranspiration and decomposition (Harper et al. 2005) (see fig.3). Secondary effects, like regeneration, growth, reproduction and mortality are caused by the primary effects and change the species composition and forest structure near the edge (Harper et al. 2005) (see fig. 3). Secondary effects are often observed to reach further into the forest compared to primary effects, most likely because secondary responses arise due to primary effects and therefore could start later and affect areas that are not directly at the edge.
1.3 Regeneration

Forest landscapes are subject to constant change. The assumption that if left alone rain forests are changeless and exist in a state of equilibrium is wrong and misleading (Ghazoul & Sheil 2011). Natural processes build, sustain and transform tropical rain forests; many species even rely on these changes, like pioneer species. So in order to understand regeneration patterns of tropical rain forests one has to look first at the two principal elements of forest dynamics, which are disturbance and succession (Ghazoul & Sheil 2011).
Disturbance is defined as a reduction in population density, thereby creating a rapid release of resources, which organisms can then exploit (White & Jentsch 2001). There are various types of disturbance which all have different effects on the ecological functioning and diversity of rain forests. They can range from small gaps created by tree falls allowing new light resources to be taken in by undergrowth vegetation all the way to devastating forest fires, which leave miles of forest destroyed. The most devastating disturbance that affected the Sabangau forest in the last century was most likely the forest fires in the 1950s. These fires completely burned down the riverine forest and created a hostile environment for most of the vegetation. The reason why fires have such a devastating effect on peat swamp forests is because they are unnatural in undisturbed forest habitat. Since the Sabangau forest had been exploited by various logging companies it had become a lot more susceptible to fire for two major reasons. Logging companies fell a lot of trees exposing the ground to direct sunlight, this would not be a problem if the water level was just underneath or over the peat surface as is the natural condition. The problem however arised by the habit to drain the peat from its water reserves to ease forest work. This dried out large areas of the forest floor. Farmers also like to create controlled forest fires to clear their lands from vegetation, but during a drought and in heavily disturbed forests, these fires can grow out of control burning down the forest and the peat layer they grow on (Page 1997).

The forest edge has shifted since then, reclaiming the once burned areas slowly and thereby showing regeneration and succession. Succession is defined as a long-term directional change in community composition, structure and function following a disturbance event (Ghazoul & Sheil 2011). The magnitude and speed of succession is greatly influenced by the devastation that occurred during the disturbance (Ghazoul & Sheil 2011). Great disturbances like the one experienced in the Sabangau forest tend to lead towards a very slow succession. Distance from remnant forest patches or seed trees can significantly affect the recovery of the habitat due to poor seed dispersal. Succession nevertheless normally follows a relatively clear pattern. The first arrivals in a recently cleared forest patch are usually ferns, herbs, shrubs and climbers (Finegan 1996). In the case of the Sabangau forest this are pandanaceae and some liana species (Page et al. 1999). The initial ground cover renders the environment less hostile and allows more species to inhabit the habitat like pioneer tree species, which quickly become dominant (Chazdon 2008). Pioneer tree species are able to inhabit the environment faster from
either seed rain, seed banks in the ground or even resprouts (Mulkey et al. 1996)). These pioneer tree species create the first forest canopy and often dominate the landscape for various years (Finegan 1996). They are then slowly replaced by secondary forest species, with taller canopy and longer longevity. This successional stage can last for more than a century (Finegan 1996) until shade tolerant species, common in primary forest, slowly start to establish themselves in the habitat and eventually begin to reach the canopy (Ghazoul & Sheil 2011) and give the forest its characteristic primary undisturbed habitat. In the end and if given the chance, rain forests will recover from even severe disturbances, but this can take a very long time, a luxury that conservationists don’t have any more (Meijaard et al. 2012).

1.4 Flora of the mixed peat swamp forest of Sabangau

Tropical Rain forests show an immense diversity of trees in a very small area and peat swamp forests are no exception. It is a true miracle of evolution to see so many tree species coexist next to each other. The tropics offer not only more favourable conditions than temperate regions but also more constant climatic conditions throughout the year. This allowed the creation of countless niches over thousands of years, which were all filled by specialised species (Turner 2001). Another reason for the diversity of tree species could be recruitment limitation within a species, in other words a species is not able to establish itself in all the sites it might potentially occupy and therefore leaves room for other species to fill the same ecological niche (Hubbell et al. 1999). This led to various different survival strategies for different tree species. Since this study focused on all life forms their main characteristic shall briefly be described in the following section.

Pioneer tree species are most commonly found in areas that were recently cleared, since there is a lack of trees and therefore competition, pioneer species developed methods to be the fastest to colonise these areas, which often occur naturally through tree falls. This strategy has some key characteristics, which apply to most of these species (after Turner 2001). The seeds are generally rather small and abundant in the soil seed bank. This allows the seeds to immediately fill the gap when one arises. They generally have a rapid growth rate with a high juvenile mortality. The rapid growth rate is fuelled by a high photosynthetic and respiration rate and short-lived leaves with a high turnover. These
tree species are often also short lived and are in later stages of succession replaced by interior forest species. These general characteristics of pioneer species make them excellent indicator species for disturbance within a forest, since they should occur in high densities in these areas and are therefore also strongly positively affected by edge effects.

Within the forest interior climax species are dominant. These species generally germinate, establish and persist below canopy shade and can live for various years within the shaded understorey of a forest (Ghazoul & Sheil 2011). These slow growing strongly shade-tolerant species are characterised by large seeds, which can provide them with the necessary nutrients to survive under poor light conditions, and dense crowns with long-lived well defended leaves (Ghazoul & Sheil 2011). Some of these tree species have developed a different strategy though, they quickly grow above the majority of the canopy and establish a dense canopy that can be used to catch most of the light emitted by the sun, unblocked by leaves of neighbouring trees (Ghazoul & Sheil 2011), these species are often also referred to as canopy trees (see fig. 4).

Of course these different survival strategies are pronounced with different intensities depending on the species leading to an incredibly diverse forest interior.

Figs are a type of tree that has developed some unique survival strategies, which are worth taking a closer look at. They all belong to the genus Ficus and show a huge diversity of form, some are small shrubs and some develop to become huge trees and stranglers. A true marvel of coevolution is the fact that every tropical fig has its own obligate pollinating wasp species (Turner 2001). These fig wasps are very effective long-distance pollinators. Since they rely for pollination on an insect species with a relatively short life-cycle and short adult lives, figs are constantly flowering which leads to a regular fruit supply (Turner 2001). This makes figs keystone species in tropical
rainforests on which frugivore species, like orang-utans, can rely upon in times of food shortages (Turner 2001). The syconium, which is the typical form of inflorescence for figs, is also rich on calcium giving it even more nutritional importance.

Lianas are woody climbers with a stem that is flexible in compression but strong in tension (Turner 2001). They can be incredibly abundant in lowland tropical forest and can account for a quarter of woody stems and species in forests and therefore can affect an ecosystem substantially (Turner 2001). Lianas and climbers in general thrive in heavily disturbed forests making them quite good indicators for forest edge effects and anthropogenic disturbance (Kokou et al. 2002, Letcher & Chazdon 2012). Lianas are increasing in abundance and biomass in tropical forests (Letcher & Chazdon 2012); this could have a significant impact on forest dynamics and composition making it more and more important to understand their ecology. Just like trees lianas have developed different ecological strategies for survival and distribution, which are generally based on dispersal mode, seed mass and leaf traits (Letcher & Chazdon 2012). This led to some liana species being better pioneer species in disturbed habitat and other species being more dominant in undisturbed forest interior. Many liana species are obligate climbers from the start and need support to thrive. Since support availability is higher in young forests compared to interior forests it can be a major factor in the establishment of a liana species in a habitat (Letcher & Chazdon 2012). Lianas that climb with hooks, spines and tendrils require smaller diameter supports and are therefore more abundant in early succession stages of a forest (Letcher & Chazdon 2012) and thereby good indicators of the current state of the habitat.

Pandanaceae are old world tropical monocots, which generally are palm like trees with long, rigid spirally arranged leaves and prop roots (see fig. 5). Its unusual growth forms, leading from evergreen trees to woody lianas and shrubs, and their dioecious breeding system make them botanically very interesting (Nadaf & Zanan 2012). The family pandanaceae contains four genera of which two are present in the mixed swamp forest of Sabangau, with

Figure 5. Pandanaceae dominate the ecosystem next to the Sabangau river appearing in great abundance.
three species of the genera *Pandanus* and one *Freycinetia* species. All four species are ecologically more like shrubs inhabiting the forest floor and contribute fundamentally on the structure and physiognomy of the vegetation.

Carnivorous plant species are normally a minor, ecologically fascinating component of forest vegetation. They have adapted to compensate the lack of nutrients on nutrient poor ground by “hunting” animal prey, which is rich in nitrogen (Ghazoul & Sheil 2011). On Borneo one type of carnivorous plant has evolved, the *Nepenthes*, commonly known as pitcher plants. Pitcher plants have adapted to attract prey to their big pitchers by using high contrast markings, sometimes even providing nectar (Ghazoul & Sheil 2011). Since the surface of the pitchers is extremely smooth and humid it prevents adhesion by arthropod footpads, making them slide into the pitcher plant were they fall into digestive fluids that slowly decompose them (Ghazoul & Sheil 2011). In the Sabangau mixed peat swamp forest three species of *Nepenthes* have been identified, each with unique ecological needs. *Nepenthes ampullaria* is a very unique type of *Nepenthes*, because it doesn’t feed on animals but on dead plant material that fall into its open pitcher (see fig.6) (Clarke 1997). They are commonly distributed on flat terrain in undisturbed forest interior, since they rely on a constant fall of dead plant material like leaves. *Nepenthes gracilis* is most commonly found on wet open areas on virtually any soil type and can grow up to 6m tall, it is widespread with high densities in secondary forests (Clarke 1997). *Nepenth es rafflesiana* also prefers open, sandy, wet areas and is particularly abundant in boundaries and elevated areas (Clarke 1997). These very different ecological needs for the different species make them excellent candidates as indicator species for different forest compositions.

Orchids (Orchidaceae) comprise one of the largest families in the plant kingdom with over 18500 species. Ecologically orchids are fascinating species, their complex life cycle, involving countless pollination mechanisms and their obligate interactions with mycorrhizal fungi led to quite unique niche occupations (Kindlmann et. al. 2006). Many
orchids in the tropics are epiphytes, they live their whole life on top of other plants, mostly trees, and gain all their nutrients from rain that falls on them and the debris lying around them. The Orchids looked at in this study were all terrestrial. Terrestrial Orchids need free moisture to survive and therefore areas near watercourses were mesic conditions predominate are preferred. Areas in which inundation occurs are also preferred by most Orchid species. Orchids can grow on quite unfertile soil making them good colonisers of peat. Orchid abundance are known to be lower in areas with rainshadow, like the forest interior, since they heavily rely on nutrients and water supply from the rain (Kindlmann et. al. 2006, Whitman & Ackerman 2012).

1.5 Study Questions

The general aims of this study were to analyse the forest composition near the edge and to see if forest edge effects were present. With the current rates of deforestation forest edges will become more important over time in Kalimantan and the effects of these edge effects could affect results of various monitoring projects meant to detect disturbance in interior forest rather than edge effects, like butterfly monitoring and vegetation plots.

The questions that were tackled by this thesis were therefore: (1) Are there different forest compositions in the Sabangau forest? (2) If so what indicator species are there? (3) Are there forest edge effects present and if so how far do they reach? (4) Do we find forest regeneration and different successional stages?
2. Material & Methods

2.1 Field site & plot layout

The Sabangau Forest is located in the Indonesian part of Borneo in the province of Central Kalimantan centred on the Sabangau River (see fig.7). It covers an area of approximately 9,000 km² of which 6,300 km² are still forested. Peat land covers most of the lowland river plains in southern Borneo and the Sabangau Forest is the biggest area of lowland peat swamp rainforest remaining in Borneo (Outrop, 2012).

The Sabangau peat swamp forest is ombrogenous (Page et al. 1999), this means it gains its water and nutrient supply only from aerial depositions and maintains a water table close or above the peat surface throughout the year.

This particular peat swamp forest is characterised by four main zones. The riverine forest is intermediate between freshwater swamp forest and peat swamp forests and is located close to the river (Page et al. 1999). A mixed swamp forest is classified by peat 2-6m thick and the forest is relatively tall and stratified with a canopy height of about 35m (Page et al. 1999). Going further into the interior of the forest one finds a low pole forest, which grows on a thicker layer of peat between 7-10m and the water table is permanently high with an uneven forest floor (Page et al. 1999). The tall interior forest occupies most of the elevated part of
the peat land dome, the water table is below the surface throughout the year and the trees are significantly taller with a canopy height of 45m (Page et al. 1999).

The study focused on the mixed swamp forest, since it was located directly at the forest edge. The riverine forest that used to reach the Sabangau River was completely burned down during fires in the 1950s, which had a 100% mortality rate on the vegetation, this left the first 1-2km from the river to the new forest edge as a very hostile environment covered in low growing Pandanaceae species. The mixed swamp forest extends up to 4km from the rivers edge with increasing peat depth from 2-6m moving in (Page et al. 1999). The mean pH of the peat water is 3.9 ± 0.5, with surface peat samples having a pH of 2.9 ± 0.3.

In 1996 a Natural Laboratory of Peat Swamp Forest (NLPSF) was created inside the Sabangau forest. It is 50.000 hectares big and located in the north of the Sabangau River (see fig. 8). It is managed by the Centre for the International Cooperation in Sustainable Management of Tropical Peat lands (CIMTROP) which conducts vital research in conservation related questions. It is also within this natural laboratory that the NLPSF base camp is situated, which conducts long-term behavioural studies on Orangutans, Gibbons and Red Langurs (Outrop, 2012).

The study was carried out between September and November 2012. A survey grid was developed, over an area of 700m x 700m perpendicular to the forest edge (see fig. 9), starting 800m West from the Field Station and facing inwards into the forest. The plots were located at 50m intervals, due to a nonlinear forest edge five more plots had to be located 50m in front of the survey grid to allocate them at the forest edge. The plots were all positioned blindly and do not follow any transect patterns.

**Figure 9.** Survey grid of the study area with the 225 plots indicated as blue pins. The light blue lines are the transects used by the NLPSF base camp, which is marked as a yellow pin.
2.2 Plot and measurements

A plot consisted of a 10m x 10m quadrat. In its middle a 2m x 2m interior plot was located and a 1m x 1m subplot was placed in the centre of it. The boundaries of the plot were marked using ropes that had knots on the equivalent distance needed for each plot size to indicate the corners. Within the 10m x 10m plot we measured the diameter at breast height (DBH), the basal diameter (BD) the height and the species of all the trees that had a higher DBH than 6 cm. BD was measured directly above any stilt/buttress roots that protruded from the ground while DBH was measured 1.3m above that point. Tree height was estimated in 5m intervals (1-5m, 6-10m, etc.).

Non-tree flora was also recorded, this included: lianas, figs, pitcher plants, Pandanaceae and terrestrial orchids. For all the lianas and figs the diameter was measured and categorised in four different diameter classes (<0.5cm, 0.5-1cm, 1-3cm, >3cm), the species was also identified. The species for the pitcher plants and Pandanaceae was identified and the abundance in each plot was recorded. Orchids could only be identified to the family level Orchidaceae, since they were only present in the vegetative state during the study period, and their abundance was recorded in each plot.

Within the 2m x 2m interior plot the sapling abundance was measured. A sapling was classified as a tree taller than 1.3m but with a DBH lower than 6 cm. Inside the 1m x 1m subplot the seedling abundance was quantified, a seedling was classified as any tree smaller than 1m with a DBH lower than 6 cm.

All floral species were identified by local botanists with high field experience in the forest area.
2.3 Statistical analysis

For the statistical analysis RStudio (version 0.95.265) © 2009-2011 RStudio, Inc. was used. The DBH and BD values of all the trees were used to identify different forest compositions. A Shapiro-Wilks test was used to see whether the data was parametric (p>0.05 for normal distribution). Since this was not the case a Kruskal-Wallis test was used to see if different forest compositions were present. A Wilcoxon rank sum test with Bonferroni correction was used for post hoc analysis to identify different forest compositions. To calculate the mean tree height and liana diameter a weighted middle was used for the height classes and diameter classes respectively.

To identify indicator species the IndVal method was used (Dufrene & Legendre, 1997). Since there were over 146 tree species within the grid, the 5 most abundant tree species within each forest composition were used to look at their indicator values.

For quantifying the liana and tree biodiversity within each group a Shannon Wiener Index was used followed by an Evenness test to look at the species abundance distribution within each group. The different groups were then tested on the similarity of their species composition by using the Sørensen similarity index.

The biomass in %0 refers to the area occupied by the trees BD within a 10m x 10m plot, which was calculated by using the formula:

\[
\left(\frac{\sum_{i=1}^{d} d_i^2 \times \pi \div 4}{100m^2 \times n}\right) \times 1000
\]

(1)

\(d\): The diameter of each tree within the group in m²
\(t\): total amount of trees in the group
\(n\): the amount of plots within the group
3. Results

3.1 Forest composition

3.1.1 Tree Diameter at Breast Height (DBH)

The analysis of the DBH values resulted in four significantly different forest groups at different distances from the edge. Since there was a highly significant difference in the DBH between the plots within the grid (Kruskal-Wallis: chi-squared = 299.2, df = 224, p-value = 0.001) a post hoc analysis was necessary to identify the different compositions. All plots did not show any significant differences within their groups respectively and their values could therefore be pooled together (Kruskal-Wallis test: Plots at forest edge chi-squared = 12.1, df = 14, p-value = 0.601; plots 50m from the edge: chi-squared = 10.0, df = 13, p-value = 0.695; plots 100m from the edge: chi-squared = 13.6, df = 14, p-value = 0.480, plots in the forest interior 150-700m: = 200.2, df = 179, p-value = 0.133).

The DBH values of the four recognised groups differed significantly from one another (see fig. 11) (Wilcoxon rank sum test with Bonferroni correction: Forest edge to 50m: W = 30796.5, p-value = 0.005; Forest edge to 100m: W = 24783, p-value = 9.23e-11; Forest edge to 150-700m: W = 325856.5, p-value = 4.58e-10; 50m to 100m: W = 28513.5, p-value = 0.001629; 50m to 150-700m: W = 363265, p-value = 0.063; 100m to 150-700m: W = 434441, p-value = 0.014).

The outliers were excluded in figure 3 since they made comparing the different boxplots difficult due to their high values. The outliers do show a clear pattern though to higher DBH values further in the forest (see Appendix A).

Single tree species followed a similar pattern with their DBH values (see Appendix B).

Figure 11. Boxplot for the average DBH of the four recognised forest compositions. DBH is the Diameter at breast height measured on trees. Boxplots with different letters show a significant difference. (notch=Median, upper and lower extend of the box indicate 25-75% percentile; whiskers: 1.5 times interquartile range)
3.1.2 Tree Basal Diameter (BD)

For the analysis of the BD the same approach was used as with the DBH. When looking at the BD of the whole grid there was again a clear significant difference (Kruskal-Wallis: chi-squared = 340.3, df = 224, p-value = 8.44e-07). When separating the grid to identify different forest compositions the same four groups crystallised themselves out of the data with no significant differences within each of them concerning BD (Kruskal Wallis: Forest edge: chi-squared = 13.76, df = 14, p-value = 0.468; 50m from edge: chi-squared = 8.6815, df = 13, p-value = 0.797; 100m from edge: chi-squared = 15.32, df = 14, p-value = 0.357; 150-700m from edge: chi-squared = 205.9, df = 176, p-value = 0.061). At the distance 50m the same plot as for the DBH had to be excluded from the group and within the group 150-700m 3 plots had to be excluded.

The Post hoc test showed even clearer significant differences between the four groups (see fig. 12) (Wilcoxon rank sum test with Bonferroni correction: Forest edge to 50m: W = 23123.5, p-value = 7.08e-07; Forest edge to 100m: W = 23366, p-value = 3.91e-13; Forest edge to 150-700m: W = 306502, p-value = 6.20e-14; 50m to 100m: W = 28377.5, p-value = 0.001; 50m to 150-700m: W = 360598.5, p-value = 0.041; 100m to 150-700m: W = 432987.5, p-value = 0.018).

As was the case with the DBH values the outliers had to be excluded in figure 4 because it made comparing the boxplots to difficult due to the high values of the outliers. The outliers do show though the higher amount of high values found further in the forest compared to the edge (see Appendix C).

![Figure 12](image.png)

**Figure 12.** Boxplot for the average BD of the four recognised forest compositions. BD is the basal diameter of the trees. Boxplots with different letters show a significant difference. (notch=Median, upper and lower extend of the box indicate 25-75% percentile; whiskers: 1.5 times interquartile range)
3.1.3 Tree height

Trees of the height class 6-10m clearly dominated the landscape at the edge and decreased going in (see fig. 13). The higher height classes increased in dominance going further in, the tallest trees were more abundant in the forest interior (150-700m).

![Figure 13](image_url)

**Figure 13.** The percentage of each height class for each of the four forest compositions (Forest edge, 50m from edge, 100m from edge and 150-700m from edge).

3.1.4 Plant abundance

The liana, pitcher plant, Pandanaceae and terrestrial orchid abundance clearly dropped towards the forest interior, showing very high abundances at the edge (see fig. 14). The tree abundance was slightly higher at the edge and then quickly stabilised for the rest of the study area. Figs showed a very low abundance throughout the study area, none were found at the forest edge though.
3.1.5 Pandanaceae dominance

There was a clear dominance of *Pandanus* sp.2 and *Pandanus* sp.3 at the forest edge, which was later on replaced with a dominance of *Pandanus* sp.1 and *Freycinetia* sp. at about 300m. Note how the dominance patterns of *Pandanus* sp.1 and *Freycinetia* sp. seemed to have complemented each other (see fig. 15). For the local Indonesian names of all the floral species see Appendix D.

**Figure 14.** Abundances of different plant types compared for the four different groups (forest edge, 50m from edge, 100m from edge and 150-700m from edge).

**Figure 15.** Dominance Pattern of the four different Pandanaceae at different distances from the forest edge to the interior.
3.1.6 Pitcher Plant dominance

*Nepenthes gracilis* and *N. rafflesiana* clearly dominated at the forest edge decreasing rapidly in their abundance moving in (see fig. 16). *Nepenthes ampullaria* on the other hand started to appear further in the forest at about 200m; the high amount of fluctuation observed with *N. ampullaria* can best be explained by the small sample size and clumped distribution.

![Figure 16. Dominance pattern of the three different pitcher plant species moving into the forest at 50m intervals.](image)

3.1.7 Liana abundance and diameter

Lianas of the diameter class 0-0.5cm were much more abundant at the forest edge compared to the inside (see fig. 17). In the forest interior (150-700m) the diameter classes seemed to be more evenly distributed. Note that the diameter class 1-3cm can be misleading, since it encompassed a much wider spectrum. Hence more lianas are bound to be found in this class, which led to higher percentages in this diameter class.
3.1.8 Orchid abundance

There were significantly more terrestrial orchids at the forest edge compared to the interior (see tab. 1) (Wilcoxon rank sum test: forest edge to 50m: $W = 164.5$, p-value = 0.030; forest edge to 100m: $W = 186$, p-value = 0.001; forest edge to 150-700m: $W = 2293$, p-value = 1.27e-07).

Table 1. Mean abundance of orchids per 100m$^2$ found in the four different groups.

<table>
<thead>
<tr>
<th>Distance</th>
<th>Orchid abundance [100m$^2$]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest edge</td>
<td>9.2</td>
</tr>
<tr>
<td>50 m in</td>
<td>3.7</td>
</tr>
<tr>
<td>100 m in</td>
<td>1.4</td>
</tr>
<tr>
<td>Forest interior</td>
<td>0.9</td>
</tr>
</tbody>
</table>

3.1.9 Fig abundance

There appeared to be no figs present at the forest edge, the abundance seems to stabilise quite quickly between 0.5 and 1 fig every 100m$^2$ (see tab. 2). Since the sample size for figs was very low the high fig abundance at 100m is most likely affected by it.
Table 2. Mean abundance of figs per 100m$^2$ found in the four different groups.

<table>
<thead>
<tr>
<th>Distance</th>
<th>Fig abundance [100m$^2$]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest edge</td>
<td>0.00</td>
</tr>
<tr>
<td>50 m in</td>
<td>0.53</td>
</tr>
<tr>
<td>100 m in</td>
<td>1.07</td>
</tr>
<tr>
<td>Forest interior</td>
<td>0.57</td>
</tr>
</tbody>
</table>

3.2 Indicator species

3.2.1 Trees

There were clear indicator species present for all four identified forest compositions (see tab. 3). Since there was a total of at least 146 tree species, the species chosen for this method were decided by taking the 5 most abundant tree species in each group (see Appendix E).

Table 3. Indicator values for different tree species at four different distances from the forest edge.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>0m</th>
<th>50m</th>
<th>100m</th>
<th>150-700m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Myrtaceae <em>Tristaniopsis</em> sp.</td>
<td>70.9</td>
<td>9.3</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Hypericaceae <em>Cratoxylon glaucum</em></td>
<td>38.6</td>
<td>9.4</td>
<td>2.5</td>
<td>0.9</td>
</tr>
<tr>
<td>Clusiaceae <em>Calophyllum</em> sp.</td>
<td>67.3</td>
<td>0.2</td>
<td>0.2</td>
<td>&lt;0.1%</td>
</tr>
<tr>
<td>Chrysobalanaceae <em>Licania splendens</em></td>
<td>17.5</td>
<td>48.5</td>
<td>2.8</td>
<td>&lt;0.1%</td>
</tr>
<tr>
<td>Anisophyllaceae <em>Combretocarpus rotundatus</em></td>
<td>39.8</td>
<td>8.8</td>
<td>2</td>
<td>0.2</td>
</tr>
<tr>
<td>Myrtaceae <em>Syzygium</em> sp.</td>
<td>17</td>
<td>17.8</td>
<td>18.8</td>
<td>7.8</td>
</tr>
<tr>
<td>Elaeocarpaceae <em>Elaeocarpus mastersii</em></td>
<td>0</td>
<td>18.8</td>
<td>9.2</td>
<td>16.8</td>
</tr>
<tr>
<td>Sapotaceae <em>Palaquium cochlearifolium</em></td>
<td>0</td>
<td>6.6</td>
<td><strong>39.5</strong></td>
<td>10.3</td>
</tr>
<tr>
<td>Sapotaceae <em>Palaquium</em> sp.</td>
<td>0</td>
<td>7.0</td>
<td><strong>20.5</strong></td>
<td>10.2</td>
</tr>
<tr>
<td>Dipterocarpaceae <em>Shorea teysmanniana</em></td>
<td>0</td>
<td>3.7</td>
<td>14.8</td>
<td><strong>17.9</strong></td>
</tr>
<tr>
<td>Rutaceae <em>Tetractomia tetrandra</em></td>
<td>0</td>
<td>0</td>
<td>0.5</td>
<td><strong>37.3</strong></td>
</tr>
<tr>
<td>Euphorbiaceae <em>Neoscornechinia kingii</em></td>
<td>0</td>
<td>0</td>
<td>2.1</td>
<td><strong>42.2</strong></td>
</tr>
<tr>
<td>Clusiaceae <em>Mesua</em> sp.</td>
<td>0</td>
<td>3.9</td>
<td>7.7</td>
<td><strong>23.9</strong></td>
</tr>
</tbody>
</table>

3.2.2. Lianas

The *Rubiaceae Lucinea* sp. clearly crystallised itself as an edge species, while most other liana species seemed to be better indicators for the forest interior rather than for the groups at distances 50m and 100m from the edge (see tab. 4). The five most abundant liana species over the whole study area were chosen to be tested as indicator species (see Appendix F). Note that *Fragrea* sp. could sometimes have been wrongly identified as *Fibraurea tinctoria* leading to an incorrect distribution of this species.
Table 4. Indicator values for different liana species at four different distances from the forest edge.

<table>
<thead>
<tr>
<th>Liana species</th>
<th>0m</th>
<th>50m</th>
<th>100m</th>
<th>150-700m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rubiaceae <em>Lucinea</em> sp.</td>
<td>86.2</td>
<td>6.9</td>
<td>0.8</td>
<td>&lt;0.1%</td>
</tr>
<tr>
<td><em>Fibraurea tinctoria</em></td>
<td>0</td>
<td>3.5</td>
<td>14.2</td>
<td>40.7</td>
</tr>
<tr>
<td>Annonaceae <em>Artobotrys</em> cf. <em>roseus</em></td>
<td>0</td>
<td>8.6</td>
<td>24.6</td>
<td>25.3</td>
</tr>
<tr>
<td>Rubiaceae <em>Uncaria</em> sp.</td>
<td>0</td>
<td>0</td>
<td>3.2</td>
<td>50.3</td>
</tr>
<tr>
<td>Apocynaceae <em>Willughbeia</em> sp.</td>
<td>0</td>
<td>1.3</td>
<td>12.9</td>
<td>17.3</td>
</tr>
<tr>
<td>Annonaceae <em>Artobotrys suaveolins</em></td>
<td>0</td>
<td>1.2</td>
<td>7.9</td>
<td>11.7</td>
</tr>
</tbody>
</table>

3.2.3 Pitcher plants

While *N. gracilis* and *N. rafflesiana* showed a clear preference towards the edge and were nearly absent in the interior, *N. ampullaria* thrives in the interior of the forest and was completely absent in the other three groups (see tab.5).

Table 5. Indicator values for the three different *Nepenthes* species found in the study area at four different distances from the forest edge.

<table>
<thead>
<tr>
<th>Pitcher plant species (<em>Nepenthaceae</em>)</th>
<th>0m</th>
<th>50m</th>
<th>100m</th>
<th>150-700m</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nepenthes ampullaria</em></td>
<td>0</td>
<td>0.6</td>
<td>0</td>
<td>15.6</td>
</tr>
<tr>
<td><em>Nepenthes gracilis</em></td>
<td>53.2</td>
<td>23.3</td>
<td>15.5</td>
<td>0.7</td>
</tr>
<tr>
<td><em>Nepenthes rafflesiana</em></td>
<td>35.5</td>
<td>26.9</td>
<td>9.9</td>
<td>1.6</td>
</tr>
</tbody>
</table>

3.2.4 Pandanaceae

*Pandanus* sp.2 and sp.3 showed clear edge preference and are good indicator species for it (see tab. 6). *Pandanus* sp.1 and *Freycinetia* sp. on the other hand are better indicators for the forest interior; *Freycinetia sp.* was almost exclusively found there (see tab. 6).

Table 6. Indicator values for the four different Pandanaceae species found in the study area at four different distances from the forest edge.

<table>
<thead>
<tr>
<th>Pandanaceae species</th>
<th>0m</th>
<th>50m</th>
<th>100m</th>
<th>150-700m</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pandanus</em> sp. 1</td>
<td>0</td>
<td>1.1</td>
<td>13.5</td>
<td>76.0</td>
</tr>
<tr>
<td><em>Pandanus</em> sp. 2</td>
<td>64.4</td>
<td>14.5</td>
<td>16.6</td>
<td>1.0</td>
</tr>
<tr>
<td><em>Pandanus</em> sp. 3</td>
<td>74.3</td>
<td>8</td>
<td>4.8</td>
<td>8.6</td>
</tr>
<tr>
<td><em>Freycinetia</em> sp.</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>55.3</td>
</tr>
</tbody>
</table>

3.2.5 Orchids

*Orchidaceae* crystallises itself to be an edge family that gets less characteristic for the different distances when moving into the forest (see tab. 7). The amount of species present in this forest could not be determined, since all terrestrial orchids were only present in their vegetative state during the study period.
Table 7. Indicator value for Orchidaceae at four different distances from the forest edge

<table>
<thead>
<tr>
<th>Family</th>
<th>0m</th>
<th>50m</th>
<th>100m</th>
<th>150-700m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orchidaceae</td>
<td>52.6</td>
<td>14.7</td>
<td>2.5</td>
<td>1.7</td>
</tr>
</tbody>
</table>

3.3 Diversity

3.3.1 Shannon Wiener Index and Evenness

The alpha diversity of trees clearly increased when moving further into the forest, the species distribution was also higher in the forest interior compared to the edge (see tab. 8).

Table 8. Shannon Wiener Index and Evenness of tree species composition in the four forest groups.

<table>
<thead>
<tr>
<th>Distance</th>
<th>Shannon Wiener Index</th>
<th>Evenness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest edge</td>
<td>2.45</td>
<td>0.78</td>
</tr>
<tr>
<td>50 m in</td>
<td>3.3</td>
<td>0.84</td>
</tr>
<tr>
<td>100 m in</td>
<td>3.85</td>
<td>0.91</td>
</tr>
<tr>
<td>Forest interior</td>
<td>4.17</td>
<td>0.86</td>
</tr>
</tbody>
</table>

Liana diversity also increased drastically when moving away from the edge and stabilised itself quicker compared to the trees (see tab. 8 and tab.9). The species were also much more evenly distributed further in the forest (see tab.9).

Table 9. Shannon Wiener Index and Evenness of liana species composition in the four forest groups.

<table>
<thead>
<tr>
<th>Distance</th>
<th>Shannon Wiener Index</th>
<th>Evenness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest edge</td>
<td>0.18</td>
<td>0.16</td>
</tr>
<tr>
<td>50 m in</td>
<td>1.63</td>
<td>0.66</td>
</tr>
<tr>
<td>100 m in</td>
<td>2</td>
<td>0.83</td>
</tr>
<tr>
<td>Forest interior</td>
<td>1.9</td>
<td>0.67</td>
</tr>
</tbody>
</table>

3.3.2 Sørensen Similarity Index

The tree composition of the four forest groups differed significantly. The groups farther inside (50m to interior) clustered more together compared to the forest edge, which was the most dissimilar (see fig. 17) (for the values calculated with the Sørensen Similarity Index see Appendix G).

Figure 18. The tree species similarity index by Sørensen for the four groups (for the values see Appendix G).
3.4 Regeneration

3.4.1 Seedling and Sapling abundance

The Seedling abundance decreases significantly when moving into the forest interior (see fig. 19) (Kruskal-Wallis chi-squared = 20.7294, df = 3, p-value = 0.0001). The three groups closer to the forest edge show a significantly higher abundance of seedlings compared to the forest interior. (Wilcoxon rank sum test with Bonferroni correction: Forest edge to 50m: W = 120.5, p-value = 0.76; Forest edge to 100m: W = 134, p-value = 0.38; Forest edge to 150-700m: W = 1961, p-value = 0.003; 50m to 100m: W = 116.5, p-value = 0.88; 50m to 150-700m: W = 1855.5, p-value = 0.016; 100m to 150-700m: W = 2001, p-value = 0.001).

There was no clear pattern to be observed with sapling abundance showing relatively constant values throughout the study area (see fig. 19) (Kruskal-Wallis chi-squared = 5.5231, df = 3, p-value = 0.137).

![Figure 19. Abundance of Seedlings and Saplings for the four forest groups.](image)

3.4.2 Tree abundance and Biomass

The biomass increased when moving further into the forest while the tree abundance decreased at the same time. This indicates that thin trees in high numbers are more characteristic of the forest edge, while a smaller amount of thick trees is characteristic for the forest interior (see fig. 20). The biomass was obtained by calculating the % of area covered by the BD of the tree species in 100m².
3.4.3 Tree and Liana mean DBH

The mean DBH for both lianas and trees increased when moving into the forest interior (see fig. 21), the mean DBH was considerably lower at the forest edge.

**Figure 20.** Tree abundance and Biomass for the four forest groups.

**Figure 21.** Mean Liana and Tree DBH for the four forest compositions.
3.5 Group Composition

There are clear different characteristics and indicator species for each of the four forest compositions identified in the study area (see fig. 22).

**Forest Edge**

**Trees:**
- Shannon Wiener Index: 2.45
- Evenness: 0.78
- Species: 23
- Biomass: 2.3 %

- Mean DBH: 10.1 ± 5.1
- Mean BD: 11.3 ± 5.5
- Mean height: 9.3 ± 2.5

- Seedlings [per 100m²]: 1630
- Saplings [per 100m²]: 277.5

**Lianas:**
- Shannon Wiener Index: 0.18
- Evenness: 0.16
- Species: 3
- Mean Diameter: 0.41

**Plant abundances Per 100m²:**

- Orchids, 9.2
- Trees, 18.5
- Lianas, 28.2
- Pitcher Plants, 29.9
- Sedges, 163

**Indicator species**

**Trees:** Tristaniopsis sp., Cratoxylon glaucum, Calophyllum sp., Combretocarpus rotundatus,

**Others:** Orchidaceae, Nepenthes gracilis, Nepenthes rafflesiana, Lucinea sp., Pandanus sp.2 (Rasau Kelep), Pandanus sp.3 (Rasau Kecil).

**50 m from edge**

**Trees:**
- Shannon Wiener Index: 3.30
- Evenness: 0.84
- Species: 50
- Biomass: 3.2 %

- Mean DBH: 12.0 ± 6.6
- Mean BD: 13.7 ± 7.4
- Mean height: 10.4 ± 3.8

- Seedlings [per 100m²]: 1500
- Saplings [per 100m²]: 335

**Lianas:**
- Shannon Wiener Index: 1.63
- Evenness: 0.66
- Species: 12
- Mean Diameter: 1.01

**Plant abundances Per 100m²:**

- Orchids, 3.7
- Figs, 0.53
- Trees, 17.2
- Sedges, 29.6
- Lianas, 9.3
- Pitcher Plants, 15.4

**Indicator species**

**Trees:** Licania splendens

**Others:** Lack or significant abundance drop of all indicator species present at forest edge like Tristaniopsis sp.
Figure 22. Information cards with some key characteristics of each forest distance.
4. Discussion

4.1 Forest compositions

This study revealed four clearly distinguishable forest compositions in the mixed swamp zone of the Sabangau forest. They were characterised by floristic composition, basal (BD) and breast diameter (DBH) of the trees. Indicator species were found for each composition respectively and regeneration at the edge seemed to occur in greater magnitude compared to the inside. The significant increase in diameter when moving into the forest suggests different stages of succession, forest edge effects or a change in abiotic factors.

Since the fires in the 1950s (Outrop 2012) it is known that the forest has started to recolonize the burned habitat. The increasing DBH of the trees could therefore also be an indication for older trees in the interior of the forest; this is also supported when looking at the outliers, since there are a lot more trees with a high DBH in the forest interior. There still remains the possibility though that the greater DBH in the forest interior is due to abiotic factors like deeper peat, peat water levels and flooding duration during the rainy season, which are not affected by forest edge effects.

A number of characteristics support the hypothesis that the forest edge (0-50m) was in a stage of early succession. The great dominance of trees in the height class 6-10m being one of them, since the lack of variance in tree height is an indicator for a strong dominance of pioneer tree species (Finegan 1996). This is further supported by the indicator species in this area. All of the species most abundant at the forest edge are nearly completely absent in the forest interior. This indicates that these species specialize in recolonizing gaps that are created through disturbance in the forest, a characteristic of pioneer species (Ghazoul & Sheil 2010). The tree composition seems to be dominated by a few species that created one canopy level. Other supporting characteristics are a high abundance of Pandanaceae and lianas in this area, since these species normally are the first arrivals in a recently cleared forest patch (Finegan 1996). The forest edge is also clearly dominated by the liana species Lucinea sp., as shown by the very low Shannon Wiener Index, Evenness and high Indicator value. Similar to the tree species I therefore suspect a specialisation of this species in disturbed habitats, either due to an ecological niche or spreading by animal species that are restricted to edge habitat. Nearly all of the lianas were in the diameter class <0.5 cm. This suggests
that there was not enough time yet for lianas to gain diameter and therefore supports the idea of a young forest edge, although the possibility that this species has a natural small diameter cannot be excluded. The pitcher plants *N. gracilis* and *N. rafflesiana* were also very abundant at the forest edge and clear indicator species. The ecology of both species favours open areas, secondary forest and boundaries (Clarke 1997) indicating that this area is either being affected by edge effects or at least suffering under disturbance. The low densities further in of these *Nepenthes* species also suggest an absence of these species in relatively undisturbed forest. The higher abundance of terrestrial orchids at the edge could have various reasons. Since the drop of orchid abundance is quite fast, one could argue that abiotic gradients moving into the forest like the water table or peat thickness may be excluded. Light and rain availability I believe is the driving factor for the higher abundance.

The forest area 50m from the edge still shows some indications of succession and edge effects. The first successional stage seems to be over in this part of the forest, lacking the very high abundance of Pandanaceae, lianas, pitcher plants and orchids, although it is still not quite as low as further in the forest. The tree heights also seem to be gaining in variance and the characteristic species of the forest edge have become rare, suggesting that pioneer species no longer dominate this forest area but are instead replaced by species of later successional stages (Finegan 1996), like *Licania splendens* seems to be. The higher alpha diversity and evenness of both liana and tree species also indicate the presence of a forest further on in succession where the few pioneer species are being replaced by a variety of shade-tolerant species. Lianas and trees of greater diameter also start to become more present in this area, suggesting the possibility of an older forest.

The difference between the areas 50m and 100m from the edge are subtler but still present. Pitcher plants, Pandanaceae and orchids keep following the trend of becoming less abundant moving in although the difference is not comparable to the significant abundance drop between the edge and the 50m area. This slowing down could be interpreted as decreasing forest edge effects. Another possible explanation could be that the area 100m from the edge was part of the forest edge 50 years ago and therefore represents unburned forest that still suffered some kind of damage, either through fire or edge effects and therefore differs from the forest interior. The continuously increasing alpha diversity of both trees and lianas also seem to suggest a positive correlation with the distance from the edge. The increasing abundance of higher trees
also appears to indicate the presence of canopy trees in this area that could only have developed over a longer period. *Combretocarpus rotundatus* for example, even though an indicator species for the forest edge, appears in this area with very high and wide trees supporting the hypotheses that this forest area survived the fires at least partly. My results show a greater similarity of tree composition between the 50m and 100m area compared to the interior, suggesting that a large component of regeneration and succession still seems to occur 100m from the forest edge.

In the forest interior one can find most canopy trees, according to the tree heights. This indicates a less disturbed habitat, although the values are still lower than the ones described as being characteristic for mixed peat swamp in 1999 (Page et al. 1999). Pitcher plant abundance also suffers a significant drop compared to the area 100m from the edge. This is a good indicator for a change in the ecological composition of the forest in the interior since the drop in abundance occurs at the same time when *N. ampullaria* becomes more dominant compared to the other two Nepenthes species, which virtually disappear. The fact that *N. ampullaria* is most commonly found in undisturbed forest habitat (Clarke 1997) supports the hypotheses that edge effects and succession don’t affect the forest at a distance 150m from the edge. The greater variance of diameter classes within lianas and the higher abundance of lianas with a diameter greater than 3 cm also indicate an older more stable forest area. Since this forest composition stays relatively stable throughout the 550m it encompasses it strengthens the hypothesis of referring to it as interior forest.

Unfortunately there were too few figs for robust statistical testing. Fig abundance seem to stabilise at 50m into the forest. At the edge no figs were found, which supports the hypotheses of a young regenerating forest. Since figs are epiphytes at the beginning of their lifecycle they need the support of big trees to flourish, which are not present in the early stages of succession.

Pandanaceae show a very interesting dominance pattern when moving into the forest. *Pandanus* sp.2 and sp.3 were the only Pandanaceae species present at the forest edge with an incredibly high abundance. The immediate drop after only 50m indicates that these species thrive under edge conditions and are most likely the first species to recolonize an uninhabited forest patch. The increasing dominance of *Pandanus* sp. 1 and *Freycinetia* sp. when moving in can only partly be explained by succession and edge
effects since the abundance of these species seem to stabilize quite far in the forest. It could be that other abiotic factors are ecologically more important for these species, like the water table, the height and duration of flooding during the rainy season, which is known to decrease going in, or the increasing peat depth (Page et al. 1999). An interesting phenomenon seen in the data is the alternating dominance with distance between Freycinetia sp. and Pandanaus sp. 1, which could mean that they stand in direct competition for a very similar ecological niche and that minor changes in biotic or abiotic factors could affect their abundance, like light availability. In other words it could be that one species favours areas with an open canopy, maybe due to tree falls, while the other one prefers areas with a more closed canopy.

Other studies within the NLPSF support the results from this study. The alpha diversity, evenness and mean height measured within the mixed swamp forest correlate with our results of the composition of the forest interior (Hamard 2008). Deviating results in tree DBH are most likely due to different definitions on what DBH encompasses. This study showed a significant higher DBH most likely because it only measured trees with a DBH greater than 10cm (Hamard 2008). The study also supports the hypotheses that the forest interior is preferred by Gibbons, since our results of the forest interior correlate most with what is defined as suitable Gibbon habitat (Hamard 2008).

Another study also observed an increase in biomass when moving towards the forest interior (Mrimanto 2010). In that study it was argued that this could be related to distance from the river, since flooding decreases primary biomass productivity (Mrimanto 2010). I disagree with this hypotheses due to the steep increase in biomass over a very short distance, compared to the distance of the forest edge to the river, which in my opinion indicates other factors like peat depth, micro topography and disturbance as more relevant factors in biomass accumulation. Also the higher density shown in that study is most likely due to a different definition on trees, since trees were included in this study starting with a DBH of 4.8cm (Mrimanto 2010). The much lower diversity recorded in the present study could maybe be explained by a less accurate identification of species leading to an underrepresentation of total species richness.

A similar study carried out 2 month prior to the present study supports most of the hypotheses on forest composition and succession previously stated (Chetina 2013). The Liana diameter classes showed similar abundance patterns when moving towards the
interior of the forest, having larger proportions of thinner lianas in disturbed habitat and near the edge, which is a pattern also observed in other ecosystems (van der Heijden & Philips 2009, Schnitzer & Bongers 2002). Since most floral species in that study that were found at the forest edge were also found in disturbed habitats, including pitcher plants and pandanaceae (Chetina 2013). This could indicate a correlation between edge effects and disturbance (Chetina 2013).

4.2 Forest regeneration

The higher seedling abundance at the edge, which drops linearly when moving into the interior, supports the hypotheses that regeneration is being observed in the first 100m of the forest, which is a key factor of succession (Finegan 1996). Sapling abundance on the other hand does not indicate any signs of succession or greater regeneration at the edge since numbers stay constant throughout the study area, an identification of sapling species might have shown a difference in the species composition within saplings but was not possible during the study period.

The higher tree abundance with less biomass at the edge is also a clear indication for the dominance of many thin/young trees at the edge and since the biomass increases while the abundance drops when moving further in one can assume that a few thick/old trees dominate the tree composition in the interior. The presence of a lot of thin and therefore young trees at the edge also indicates succession (Finegan 1996). The increasing mean DBH of trees and lianas when moving further into the forest also further supports this hypothesis.

4.3 Forest edge effects

There are many abiotic and biotic factors that may potentially influence the forest composition near the edge and it is unfortunately impossible to make assumptions without exact measurements of these variables. Factors that most likely could affect the edge are wind, humidity, peat depth, peat water level and the frequency or duration of flooding, light, competition from light-loving and wind desiccation resistant species, availability of seed dispersers and pollinators (Harper et al. 2005). Even though the
reason for edge effects will be difficult to pinpoint with the current data one can safely assume that edge effects are present. The magnitude and distance these edge effects reach seem to differ depending on the factor. While data on the abiotic and biotic factors hasn’t been collected directly we can make assumptions from floral compositions. The fast drop in terrestrial orchid and Pandanaceae abundance, when moving into the interior, suggests an edge effect for light and rain availability on the ground that doesn’t reach very far into the forest. The Pandanaceae species show a change in composition at a much later stage suggesting edge effects reaching much further in, or at least a change in abiotic conditions in general. *Nepenthes ampullaria* only occurs in the forest interior, which could be linked to ground topography (Clarke 1997). In other words the different ecologically limiting factors for each species distribution indicate that different edge effects affect the forest at different distances with different magnitudes.

4.4 Conclusion

In conclusion the study revealed clear different forest compositions near the edge, which are most likely linked to different successional stages. The relatively slow recolonization of burned habitat of maybe 100m stresses the importance of conservation of these habitats before disturbance since regeneration of once lost habitat occurs naturally at a very slow rate. The clear indicator species for each forest composition ease identification of different successional stages or disturbance in the field and allow quick assessments of forest condition in unknown areas. Edge effects are clearly present and make the importance of an unfragmented landscape even greater, so as to minimise edge effects. The edge also shows a very monotonous species composition, which most likely does not favour a great variety of animal species. Typical orang-utan and gibbon feeding trees are also a lot more abundant in the forest interior (Morrogh-Bernard et al. 2006, Cheyne & Sinta 2006), although interestingly two indicator species of the 100m area, *Palaquium* sp. and *P. cochlearifolium*, were among the most frequently used feeding trees (4.91% for orang-utans and 12.47% for gibbons) (Morrogh-Bernard et al. 2006, Cheyne & Sinta 2006) while none of the most abundant trees found at the forest edge were used as feeding trees by either orang-utans or gibbons, which showed similar feeding preferences (Morrogh-Bernard et al. 2006, Cheyne & Sinta 2006).
5. References


- Chetina N. 2013. Establishing the impact of forest disturbance on non-tree flora in Bornean peat swamps. FHS in biological sciences, undergraduate project report, University of Oxford.


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Appendix

A. Boxplot for the DBH of the four recognised forest compositions with outliers. DBH is the Diameter at breast height measured on trees. (notch=Median, upper and lower extend of the box indicate 25-75% percentile; whiskers: 1.5 times interquartile range)

B. Mean DBH values for four different indicator tree species that had a relatively high abundance in the four forest compositions.
C. Boxplot for the BD of the four recognised forest compositions with outliers. BD is the Diameter at breast height measured on trees. (notch=Median, upper and lower extend of the box indicate 25–75% percentile; whiskers: 1.5 times interquartile range)

D. The Local names for the different species used during this study.

<table>
<thead>
<tr>
<th>Latin species name</th>
<th>Local name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Myrtaceae Tristaniopsis sp.</td>
<td>Blawan merah</td>
</tr>
<tr>
<td>Hypericaceae Cratoxylon glaucum</td>
<td>Geronggang</td>
</tr>
<tr>
<td>Clusiaceae Calophyllum sp.</td>
<td>Mahadingan</td>
</tr>
<tr>
<td>Chrysobalanaceae Licania splendens</td>
<td>Bintan</td>
</tr>
<tr>
<td>Anisophyllaceae Combretocarpus rotundatus</td>
<td>Tumih</td>
</tr>
<tr>
<td>Myrtaceae Syzygium sp.</td>
<td>Jambu Jambu</td>
</tr>
<tr>
<td>Elaeocarpacae Elaeocarpus mastersii</td>
<td>Manginang</td>
</tr>
<tr>
<td>Sapotaceae Palaquium Cochlearifolium</td>
<td>Nyatoh Gagas</td>
</tr>
<tr>
<td>Sapotaceae Palaquium sp.</td>
<td>Nyatoh Burung</td>
</tr>
<tr>
<td>Dipterocarpacae Shorea Teysmanniana</td>
<td>Meranti Semut</td>
</tr>
<tr>
<td>Rutaceae Tectarotia tetandra</td>
<td>Rambangun</td>
</tr>
<tr>
<td>Euphorbiaceae Neoscortechinia kingii</td>
<td>Pupuh Palanduk</td>
</tr>
<tr>
<td>Clusiaceae Mesua sp.</td>
<td>Tabaras akar tinggi</td>
</tr>
<tr>
<td>Rubiaceae Lucinea sp.</td>
<td>Liana Tabari</td>
</tr>
<tr>
<td>Fibraurea tinctoria maybe Fragrea sp.</td>
<td>Liana Kuning</td>
</tr>
<tr>
<td>Annonaceae Artobotrys cf. roseus</td>
<td>Kalalawit Hitam</td>
</tr>
<tr>
<td>Rubiaceae Uncaria sp.</td>
<td>Kalalawit Merah</td>
</tr>
<tr>
<td>Apocynaceae Willughbeia sp.</td>
<td>Willughbeia</td>
</tr>
<tr>
<td>Annonaceae Artobotrys suaveolins</td>
<td>Balayn</td>
</tr>
<tr>
<td>Pandanaceae Pandanus sp. 1</td>
<td>Pandan</td>
</tr>
<tr>
<td>Pandanaceae Pandanus sp. 2</td>
<td>Rasau Kelep</td>
</tr>
<tr>
<td>Pandanaceae Pandanus sp. 3</td>
<td>Rasau Kecil</td>
</tr>
<tr>
<td>Pandanaceae Freycinetia sp.</td>
<td>Akar Gerising</td>
</tr>
</tbody>
</table>
E. Abundance of the five most common tree species found in the four forest compositions and the total quantity of that species found throughout the study area.

<table>
<thead>
<tr>
<th>Group</th>
<th>Tree species</th>
<th>Abundance</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest edge</td>
<td>Blawan merah</td>
<td>64</td>
<td>101</td>
</tr>
<tr>
<td>Forest edge</td>
<td>Geronggang</td>
<td>52</td>
<td>126</td>
</tr>
<tr>
<td>Forest edge</td>
<td>Mahadingan</td>
<td>27</td>
<td>34</td>
</tr>
<tr>
<td>Forest edge</td>
<td>Bintan</td>
<td>25</td>
<td>88</td>
</tr>
<tr>
<td>Forest edge</td>
<td>Tumih</td>
<td>18</td>
<td>43</td>
</tr>
<tr>
<td>Forest edge</td>
<td>Jambu Jambu</td>
<td>18</td>
<td>182</td>
</tr>
<tr>
<td>50m from edge</td>
<td>Bintan</td>
<td>50</td>
<td>88</td>
</tr>
<tr>
<td>50m from edge</td>
<td>Geronggang</td>
<td>19</td>
<td>126</td>
</tr>
<tr>
<td>50m from edge</td>
<td>Jambu Jambu</td>
<td>17</td>
<td>182</td>
</tr>
<tr>
<td>50m from edge</td>
<td>Blawan merah</td>
<td>17</td>
<td>101</td>
</tr>
<tr>
<td>50m from edge</td>
<td>Mangkinang</td>
<td>14</td>
<td>201</td>
</tr>
<tr>
<td>100m from edge</td>
<td>Nyatoh gagas</td>
<td>24</td>
<td>134</td>
</tr>
<tr>
<td>100m from edge</td>
<td>Jambu jambu</td>
<td>18</td>
<td>182</td>
</tr>
<tr>
<td>100m from edge</td>
<td>Meranti Semut</td>
<td>12</td>
<td>137</td>
</tr>
<tr>
<td>100m from edge</td>
<td>Mangkinang</td>
<td>11</td>
<td>201</td>
</tr>
<tr>
<td>100m from edge</td>
<td>Nyatoh burung</td>
<td>10</td>
<td>97</td>
</tr>
<tr>
<td>Forest interior</td>
<td>Mangkinang</td>
<td>176</td>
<td>201</td>
</tr>
<tr>
<td>Forest interior</td>
<td>Rambangun</td>
<td>136</td>
<td>137</td>
</tr>
<tr>
<td>Forest interior</td>
<td>Pupuh Palanduk</td>
<td>129</td>
<td>131</td>
</tr>
<tr>
<td>Forest interior</td>
<td>Tabaras akar tinggi</td>
<td>129</td>
<td>139</td>
</tr>
<tr>
<td>Forest interior</td>
<td>Meranti semut</td>
<td>120</td>
<td>137</td>
</tr>
</tbody>
</table>

F. Abundance of the six most abundant liana species found throughout the study area.

<table>
<thead>
<tr>
<th>Liana species</th>
<th>Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fibraurea tinctoria</td>
<td>572</td>
</tr>
<tr>
<td>Rubiaceae Uncaria sp.</td>
<td>567</td>
</tr>
<tr>
<td>Rubiaceae Lucine sp.</td>
<td>498</td>
</tr>
<tr>
<td>Annonaceae Artobotrys cf. roseus</td>
<td>259</td>
</tr>
<tr>
<td>Apocynaceae Willughbeia sp.</td>
<td>139</td>
</tr>
<tr>
<td>Annonaceae Artobotrys suaveolins</td>
<td>139</td>
</tr>
</tbody>
</table>
G. Values of the Sørensen similarity index for the four forest compositions.

<table>
<thead>
<tr>
<th>Distance</th>
<th>Forest edge</th>
<th>50 m in</th>
<th>100 m in</th>
<th>Forest interior</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest edge</td>
<td>1</td>
<td>0.47</td>
<td>0.33</td>
<td>0.2</td>
</tr>
<tr>
<td>50 m in</td>
<td>0.47</td>
<td>1</td>
<td>0.68</td>
<td>0.48</td>
</tr>
<tr>
<td>100 m in</td>
<td>0.33</td>
<td>0.68</td>
<td>1</td>
<td>0.58</td>
</tr>
<tr>
<td>Forest interior</td>
<td>0.2</td>
<td>0.48</td>
<td>0.58</td>
<td>1</td>
</tr>
</tbody>
</table>
ERKLÄRUNG gemäß ASPO § 21 Abs. 10

Hiermit versichere ich, dass ich vorliegende Arbeit selbstständig verfasst, keine anderen als die angegebenen Quellen und Hilfsmittel benutzt und die Arbeit bisher oder gleichzeitig keiner anderen Prüfungsbehörde unter Erlangung eines akademischen Grades vorgelegt habe.

Ort, Datum

Unterschrift