

Disturbance effects on carbon content and tree¹
species traits in tropical peat swamp forest in
Central Kalimantan, Indonesian Borneo.

by²

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Abstract¹

Tropical peat swamp forests are unique ecosystems with a complex interplay between the forest vegetation and peat soil. The forest trees provide the material for peat formation, while the depth of the peat determines forest structure through influences on soil hydrology, chemistry, and nutrient availability. These forests are important for their provision of various ecosystem services, the vast quantities of carbon they store, and the biodiversity they contain, yet are severely threatened by degradation as a result of logging, drainage, and fire. This study aimed to investigate the effects these forms of disturbance have on forest structure and functioning. Six tree plots in mixed swamp forest of the Sabangau catchment in Central Kalimantan, Indonesian Borneo, were studied. These plots experienced differential histories of logging, drainage, and fire, and are of varying distances from the river and therefore peat depth. To determine the effects of disturbance on forest structure and carbon content, all trees in each plot were identified to species and measured to determine biomass and carbon content which depends on tree density, tree size, and species composition. Distance from the river tended to increase tree density, biomass and carbon content. Disturbance influenced species composition, with burnt edge habitat dissimilar from other secondary and primary forest, and decreased tree diameter, biomass, and carbon content. Biomass estimates of the forest, excluding peat, found total vegetation biomass to be as high as 423 Mg/ha in low disturbance interior forest. Including the peat, carbon content of low disturbance mixed swamp forest may be as high as 1977 Mg/ha, though was decreased by 30% in high disturbance areas. This was the first study to attain total carbon estimates of this forest which may be used for carbon budgeting initiatives, though comparisons of different biomass equations suggest that peat swamp-specific allometric equations are required to increase the accuracy of estimates. Changes in species composition influence not only carbon storage but also other flora and fauna in the community through changes in the traits trees possess. Twenty-three traits of the most abundant tree species in each plot were therefore measured to better understand tropical peat swamp forest ecology, develop a non-species focused habitat quality monitoring program, assess the impact tree trait changes have on primate communities, and gain descriptive information of peat swamp forest trees. River distance did not seem to affect most tree traits though disturbance affected several traits. A commonness of pneumatophores may indicate low-disturbance mixed swamp forest and could be incorporated into trait-based monitoring. This was the first study to use tree traits in this way to monitor disturbance in tropical rainforest. The changes in tree traits as a result of disturbance may have negative impacts on local communities of orangutans and gibbons, as well as other forest fauna. This knowledge can be used to improve management and conservation of tropical peat swamp forest.

List of Abbreviations¹

AGB: aboveground biomass²

AGC: aboveground carbon³

BA: basal area⁴

BD: basal diameter⁵

BGB: belowground biomass⁶

CIMTROP: Center for the International Cooperation in the Sustainable Management of Tropical Peatland⁷

CWDB: coarse woody debris biomass⁸

DBH: diameter at breast height (1.3 m above ground or aerial roots)⁹

Gt: gigatonne, equal to 10^{12} kilograms or 10^9 tonnes¹⁰

H: height¹¹

ha: hectare, equal to 10,000 m²¹²

HD: high disturbance¹³

IUCN: International Union for Conservation of Nature¹⁴

LAHG: Laboratorium Alam Hutan Gambut (*Natural Laboratory of Peat Swamp Forest*)¹⁵

LB: litter biomass¹⁶

LiDAR: Light Detection and Ranging optical imaging technology¹⁷

LD: low disturbance¹⁸

Mg: megagram, equal to 1000 kilograms or one tonne¹⁹

MRP: Mega Rice Project²⁰

TVB: total vegetation biomass (excluding peat)²¹

TVC: total vegetation carbon (excluding peat)²²

OuTrop: Orangutan Tropical Peatland Project²³

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Chapter 1: Background and Study Location¹

1.1.1 Tropical Peat Swamp Forests²

Tropical peat swamp forest is a unique ecosystem, with a complex and interdependent relationship between the forest vegetation and the soil peat (Page et al., 1999). Waterlogging creates anoxic conditions which prevent microbial decay of organic material, causing litterfall from rainforest trees to accumulate and form peat. The peat, in turn, determines the hydrological, chemical, and nutrient conditions which influence tree growth and forest structure. This dynamic interaction creates one of the most complex and diverse ecosystems on earth (Page et al., 1999).³

The accumulation of peat may continue for thousands of years (Page et al., 2004), eventually creating domes above groundwater level which can reach depths up to 20 m (Page et al., 1999). The convex surface of the dome allows no rivers to flow into them, and so the only source of water, nutrients, and solutes are atmospheric inputs such as rain, aerosols, and dust (Richards, 1996). The peat is therefore acidic and low in nutrients. These peat domes form inland, often straddling watersheds between two catchments. In pristine peat swamps the water table is close to or above the peat surface throughout the year, fluctuating with rainfall. Water levels are highest during the wet season with areas flooded over a meter, while in the dry season the water table may be just below the peat surface (Reiley et al., 1996; Wosten et al., 2006).⁴

Peat depth increases toward the center of the dome, producing a gradient¹ of nutrient availability, hydrology, chemistry and organic matter dynamics (Anderson, 1963; Page et al., 1999). The forest growing on the dome of peat is arranged in concentric circles of different forest sub-types corresponding to differences in peat depths. The outermost sub-type formed on the thinnest peat layer is mixed swamp forest. The canopy in mixed swamp forest is uneven with trees reaching up to 45 m tall and abundant undergrowth vegetation (Richards, 1996). The movement of water down slope from higher on the dome and occasional flooding during the wet season providing solutes from the river results in greater nutrient and dissolved oxygen content of mixed swamp forest compared to forest higher on the dome. There is also the potential that, on very thin layers of peat, plant roots can pass through the peat to the mineral layer below. As a result, mixed swamp forest is higher in species diversity than other forest types found in peat swamp forest, and generally supports larger trees (Richards, 1996).

The majority of the world's tropical peatlands are located in Southeast² Asia, with 62% located in the Indo-Malayan realm alone which includes Malaysia, Indonesia, Vietnam, Thailand, and the Phillipines (Yule, 2010). Southeast Asia is estimated to possess 20 to 30 million hectares of peatlands (Rieley et al., 1996). Indonesia contains the largest area of tropical peatland, with an estimated 16 to 27 million hectares (Reiley et al., 1996). More than a quarter of this is found in

Kalimantan, Borneo, with approximately three million hectares of peatland remaining in the province of Central Kalimantan (Page et al., 1999).¹

1.1.2 The Value of Tropical Peat Swamp Forests²

Tropical peat swamp forests provide numerous ecosystem services, possess important global carbon stores, and act as a reservoir for biodiversity (Aldhous, 2004; Posa, 2011).³

Ecosystem services of tropical peat swamp forest include microclimate formation and stabilization, biogeochemical cycling, and provision of a range of goods and services for both people and wildlife including resources such as fuel, timber, medicines, and hunting and fishing grounds for local communities (Reiley, 1996; Maltby and Proctor, 1996; Yule, 2010). Peatlands act as water control systems by storing water during the wet season to prevent flooding and gradually releasing water during the dry season (Wosten et al., 2006; Yule, 2010). The peat also stabilizes the landscape by preventing erosion and protects water quality for riverine, estuarine, and coastal fisheries by filtering out pollutants, sequestering heavy metals and toxins from the environment or lessening their impact (Reiley et al., 1996; Maltby and Proctor, 1996).⁴

These forests impact not only surrounding environments but also worldwide global carbon cycling and climate change (Page et al., 2002). The accumulation of peat leads to large stores of carbon. Because peat can reach depths of over 20 m (Page et al., 1999), tropical peat swamp forests are among⁵

the largest terrestrial carbon stores on earth (Page et al., 2002; Hooijer et al.,¹ 2010).

Peat swamp forests are also notable for the floral and faunal diversity they² contain, providing habitats for many highly adapted and often endemic plants and animals (Sodhi et al., 2004). Species diversity was historically assumed to be low compared to other Southeast Asian forest types due to poor growing conditions as a result of high acidity, waterlogging, and nutrient-poor soils (Yule, 2010). This belief, coupled with accessibility issues and difficult field conditions, meant very little biodiversity surveying was conducted in peat swamps until recently. Recent surveys, however, have revealed that tree diversity can be comparable and even greater than that of some forests on mineral soils (Posa et al., 2011). Over 927 flowering plants and ferns have been identified in Bornean peat swamp forest (Anderson 1963). Many rare and endangered mammalian species can be found in peat swamp forest, including elephants, tapirs, leopards, rhinoceroses, proboscis monkeys, and tigers (Yule, 2010). These forests are important for the conservation of a number of endangered primate species, including orangutans, listed by IUCN as critically endangered (Wich et al., 2008). There are also several notable rare endemic species of blackwater fish and a high diversity of birds and insects (Reiley et al., 1996). The knowledge of flora and fauna is far from complete, yet these forests are vanishing before we know what we are losing as Bornean wildlife competes with timber companies and plantations for forest space (Commitante et al., 2003).

1.1.3 Threats to Tropical Peat Swamp Forests ¹

Despite the recognized importance of peat swamp forests to ecosystem functioning, global climate change, and biodiversity, these forests experience extensive degradation and destruction. Deforestation, drainage, fire, and land conversion contribute to the rapid vanishing of tropical peat swamp forest, such that little pristine forest remains (Reiley et al., 1996). Tropical peat swamp forests are highly fragile and strongly influenced by perturbations. This fragility stems from the fact that the entire ecosystem depends on the peat substrate which in turns relies on adequate water, canopy cover, and leaf litter inputs, and even small disturbances can upset this balance (Page et al., 1999). ²

Peat swamp forests are an important source of valuable commercial timbers (Richards, 1996), and have been subject to widespread logging, both legal and illegal. Currently more than 80% of the remaining peat swamp forests in Indonesia are occupied by logging concessions, and Indonesia experiences among the greatest deforestation rates in the world, estimated at 2.2% per year in 2005 and likely increasing (Posa et al., 2011). Legal logging concessions in Indonesia employ selective logging in which trees of high value are removed using minimal mechanization with hand-held chainsaws and light weight railways to carry timber out. Selective logging results in the removal of emergent trees, and when extensive reduces canopy height and cover (Hamard et al., 2010) and alters species composition, often reducing species diversity as pioneer species colonize the gaps. More damaging than selective logging, however, is the widespread uncontrolled illegal logging. Illegal logging is believed responsible for ³

over 80% of Indonesia's timber export, with involvement by law enforcement agencies at every level (Commitante et al., 2003). A combination of events after 1998, including political chaos, widespread corruption, and unemployment as a result of economic crash, resulted in rampant illegal logging activities across Borneo, targeting unprotected forest, logging concessions, and conservation areas alike (Commitante et al., 2003). Initially only trees of highest value were removed, as in legal operations, but once these were removed trees of increasingly smaller size and value were taken. Trees as small as 15 cm diameter were cut, despite the legal limit of 30-50 cm (Commitante et al., 2003). As a result, species of high value, particularly ramin (*Gonystylus bancanus*), have been logged to near-extinction. Adding to the damage, canals are dug in the peat to allow timber to be floated out of the forest. Canals cause drainage of the surrounding peat, resulting in widespread effects on hydrology and stability, and creating susceptibility to fire as the open canopy, drier microclimate, and logging debris acting as fuel cause logged forests to be many times more likely to burn (Woods, 1989; Langner and Siegert, 2009).

Undisturbed peat swamp forest is naturally fire-resistant due to the high water table. Once drained, however, the dry peat is highly flammable and once lit the peat can burn for months both above and below the surface, with fires extremely difficult to extinguish (Woods, 1989; Wosten et al., 2006). Disturbed tropical peat swamp forests are thus more vulnerable to destruction by fire than any other forest type (Langner et al., 2007; Langner and Siegert, 2009), and because burning does not naturally occur the flora and fauna are not adapted to

cope with fire (Brown, 1998). Burned forest has a lower canopy cover, decreased species richness, and reduced tree density compared to unburned forest (Yeager et al., 2003). Subsurface fires cause the collapse of overlying material, creating additional tree mortality. Wildfires have destroyed hundreds of thousands of hectares on Borneo and are becoming more frequent as a result of the increased degradation of these forests (Woods, 1989; Page et al., 2002; Langner and Sievert 2009). Retaining the natural hydrology and blocking drainage canals in disturbed tropical peat swamp forests is the only long-term solution to control fires (Wosten et al., 2003; Harrison et al., 2009).

When peat is drained or burned it becomes oxidized and decomposes. This not only results in a permanent loss of peat, ecosystem services, and biodiversity, but also releases enormous quantities of carbon and toxins the peat has sequestered for thousands of years. Toxic materials provide damaging effects to nearby ecosystems, while carbon release has potential worldwide impacts (Maltby and Proctor, 1996; Page et al., 2002; Hooijer et al., 2010)

1.2 Study Location: Sabangau Catchment, Central Kalimantan

This study was conducted in tropical peat swamp forest in Central Kalimantan, southern Borneo, in two locations of the Sabangau catchment (Figure 1). Located west of the Sabangau River in the Sabangau Forest is the Laboratorium Alam Hutan Gambut (LAHG) (*Natural Laboratory of Peat Swamp Forest*), and to the east is Kalampangan, Block C of the failed Mega Rice Project.

Both locations historically were part of the same mixed swamp peatland ecosystem but have been differentially affected by disturbance.

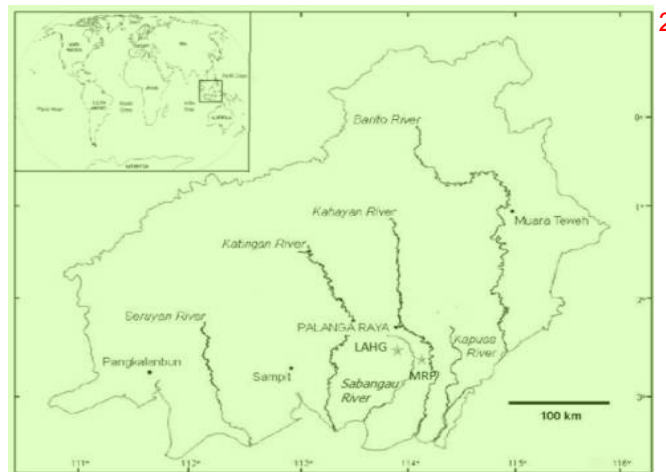


Figure 1: Map showing location of Borneo in Southeast Asia (top left) and location of the LAHG (Laboratorium Alam Hutan Gambut, Sabangau Forest) and MRP (Block C of the former Mega Rice Project, Kalampangan) study sites in Central Kalimantan, Borneo. Peat domes are formed between the Sabangau and Katingan rivers, as well as the Sabangau and Kahayan rivers. Adapted from Struebig et al. (2007) and Harrison (2009).

This region is currently managed by the Center for International Cooperation in Management of Tropical Peatland (CIMTROP), and is used by both CIMTROP and the Orangutan Tropical Peatland Project (OuTrop) for research purposes. CIMTROP is an Indonesian conservation and research institution based at the University of Palangkaraya, established to further the understanding of tropical peat swamp forest ecosystems (Harrison, 2009).

OuTrop was established in 1999 by Simon Husson and Helen Morrough-Bernard, with the goals of supporting conservation-oriented research on forest ecology and behavioural ecology of primates and other species, and to support locally-led conservation initiatives (OuTrop, n.d.). Research focuses on

behavioural ecology and population status of orangutans, gibbons, red langurs, and felids, the structure, productivity, and composition of the forest, and the effects of disturbance on this ecosystem (OuTrop, n.d.). Conservation efforts include damming of logging canals to restore hydrology and regeneration efforts of disturbed forest (OuTrop, n.d.).

1.2.2 Climate

The Sabanagau catchment is located less than 100 miles from the equator. It experiences a hot, wet, tropical climate, with high humidity and temperature consistent year-round. Rainfall is highly variable, with November to April being the wet season (Gibson, 2005). Due to climate, forests here are classified as moist tropical forest (Chave et al., 2005).

1.2.3 Site 1: Sabangau Forest

The Sabangau forest is among the best studied areas of peat swamp forest in Kalimantan. It is the largest remaining contiguous lowland rainforest in Kalimantan, covering 9,200 km² between the Sabangau and Katingan rivers. This forest is widely recognized as one of the most important conservation priorities in Borneo and as a result much of the forest (63%) is currently protected as Sabangau National Park. It is one of the deepest peat swamp forests, comprised of a mosaic of logged, regenerating, burnt, and pristine forest. Radiocarbon dating has estimated that the peat at the base was formed approximately 18,300 years ago (Page et al., 1999). Four forest sub-types are located on the peat dome: mixed swamp forest, transition forest, low pole forest,

and tall pole forest. The mixed swamp forest extends 4 km inland from the river on a layer of peat 2 to 3 m deep (Page et al., 1999). The forest is tall and stratified with an upper canopy height of 35m, a closed layer at 15-25 m, and a more open layer of smaller trees 7-12 m in height. The water table can drop to 40 cm below the peat surface at the end of the dry season, but is typically much higher and can be several meters above the peat surface during the wet season. The surface water is very acidic with an average pH of 3.6, while surface peat pH averages 3.1 (Page et al., 1999).

Sabangau is particularly important due to high abundance of flagship primate and felid species. The Sabangau catchment harbors the world's largest single remaining population of orangutans (*Pongo pygmaeus wurmbii*), listed by the IUCN as Critically Endangered, estimated to hold 37% (6,900 individuals) of the world's remaining population (Morrough-Bernard et al., 2003). It also harbors likely the world's largest population (30,000) and highest recorded density (3.92 groups/km) of endemic and Endangered Bornean agile gibbons (*Hylobates agilis albibaris*) (Cheyne et al., 2007; Cheyne et al., 2013). Sabangau also holds large densities of pig-tailed macaques (*Macaca nemestrina*; Vulnerable under the IUCN Red List) and red langurs (*Presbytis rubicunda*; Least Concern), as well as wild felids including the Sunda clouded leopard (*Neofelis nebulosa*, Vulnerable), leopard cat (*Lionailurus bengalensis*, Least Concern), flat-headed cat (*Prionailurus planiceps*, Endangered) and marbled cat (*Pardofelis marmorata*, Vulnerable) (Cheyne and MacDonald, 2011).

Located within the Sabangau forest, approximately 20 km southwest from the provincial capital of Palangkaraya, is the OuTrop research base and first site of this study, the Laboratorium Alam Hutan Gambut (LAHG) (21°31`S, 113° 90`E). The LAHG covers approximately 500 km² of the Sabangau forest and is under governmental protection as a research area in addition to the protection for Sabangau National Park (Morrough-Bernard et al., 2003; Harrison, 2009).

1.2.3.2 LAHG History²

The LAHG is a former logging concession, owned by the Setia Alam Jaya company, which was in operation 1972 to 1997. Selective logging focussed mainly on two species, ramin and meranti (*Shorea sp.*). Railways were constructed from the river into the forest to extract timber. After the last concession ended in 1997, the area experienced extensive illegal logging, peaking from 1999 to 2003. During this period, thousands of small canals, approximately 1 m deep and 1-2 m wide, were constructed by loggers to float timber out of the forest. The formation of a Community Patrol team by CIMTROP in 2003 and subsequent governmental protection of the area in 2004 has ended all logging and so the forest has since been regenerating. The CIMTROP Community Patrol Team has since constructed over 450 dams in these canals to stop drainage and allow restoration of the area (OuTrop, n.d.).

1.2.3.3 Previous Research at LAHG¹

Ongoing forestry research conducted by OuTrop focuses on composition,² structure, and dynamics of the forest. Five permanent 0.15 hectare tree plots were established in 2001 along a gradient of increasing peat depth. All trees above 7 cm diameter at breast height in each plot were tagged and identified to species. Measurements of diameter at breast and basal height are made biannually to identify changes in tree size, density, and species composition (OuTrop, n.d.). Phenology is monitored monthly, wherein approximately 2,400 trees are assessed to record whether they are flowering, fruiting, or producing new leaves. These data are used for primate behavioural research and to assess tree synchronicity, dispersal, and reproduction. Forest productivity is assessed monthly via litterfall traps, ongoing since 2005 (OuTrop, n.d.).

1.2.3.3 LAHG Tree Plots³

The five previously established tree plots at LAHG, contained within a 4⁴ km² block, were used for this study. Plots were classified as either high disturbance (HD) or low disturbance (LD) based on local knowledge of intensity and timing of disturbance (Table 1).

The three low disturbance plots (LD 1.4, LD 1.8, LD 3.0) are at increasing⁵ distance (1.4, 1.8, and 3.0 km) from the river and therefore lie on correspondingly deeper layers of peat. These plots had experienced selective logging prior to 1997 but escaped intensive illegal logging due to their distance from logging railways. One of the high disturbance plots (HD 1.8) is also located at a distance

of 1.8 km from the river. Due to its location between two of the logging railways, it¹ experienced intense illegal logging between 1998 and 2003. A second high disturbance plot is located 1 km from the river at the edge of the forest (HD 1.0). Historically the forest edge extended to the river but fires approximately 50 years ago burnt much of the riverine forest (Marchant, pers. comm.), creating a false edge. The forest has been slowly regenerating and expanding the edge back towards the river. This plot is composed of young colonizing species and is exposed to storms, wind, sun, and flooding. The third high disturbance site was located east of the river in the failed Mega Rice project (see below).

1.2.4 Site 2: Mega Rice Project, Kalampangan²

1.2.4.1 The Mega Rice Project History³

The Mega Rice Project was initiated in 1996 by the Indonesian⁴ government with the goal of converting 1.5 million hectares of pristine peat swamp forest into rice paddies to alleviate food shortages (Harrison et al., 2009). No environmental impact assessment was conducted (Commitante et al., 2003), and expert advice correctly predicting this would cause peat drying, annual fires, and destruction of the forest was ignored (Harrison et al., 2009). Satellite imaging showed that, prior to initiation of the project, the area consisted of primary, secondary and plantation forest, and some shrub land (Sabiham, 2004). One million hectares of forest were cleared, and over 4000 km of drainage channels, some up to 30 m wide, were constructed to lower the water table (Aldhous, 2004). This resulted in peat drainage, degradation, and subsidence, causing

flash flooding in wet season due loss of peat water storage potential, massive CO₂ release, and the destruction of fish stocks (Commitante et al., 2003). The peat was too acidic to grow rice, resulting in the failure of all crops and abandonment of the project in 1998 (Commitante et al., 2003). The land now lies mostly unused. 1

This project resulted in widespread destruction. In 1997, the dry peat combined with dead wood debris and dry season drought led to uncontrollable fires in the area which burned for six months (Commitante et al., 2003). The resulting haze blanketed several countries in Southeast Asia, causing failure of crops, the death of over 500 people, illness to 20 million more, and caused massive economic loss (Brown, 1998). 2

Studies quantifying the carbon release as a result of the 1997 fires found that as much as 2.57 Gt (gigaton, 10⁹ tonnes or 10¹² kg) of carbon was released into the atmosphere, the equivalence of 40% the mean annual global carbon emissions and the largest increase in atmospheric CO₂ levels in recorded history (Page et al., 2002). As a result of burning and subsidence, approximately a half meter of peat was lost (Page et al., 2002). Areas which have burnt previously become further vulnerable to fire (Woods, 1989; Langner and Siegert, 2009), and so this area now experiences annual fires during the dry season (Commitante et al., 2003). 3

The surrounding forest which was not cleared during the project is now degrading due to a loss of peat integrity, is vulnerable to fires spreading from cleared areas (Commitante et al., 2003), and experiences continued illegal logging due to increased accessibility from drainage canals and roads constructed for the project (Sabiham, 2004). Research at the MRP has attempted to quantify the destruction caused by the project. From 1991 to 1997 there was more than a 16% decrease in primary forest and an 11% decrease in secondary forest (Sabiham, 2004).

1.2.4.3 MRP Study Site²

The third high disturbance set of plots is located in Kalampangan in Block C of the former Mega Rice Project (21°35' S, 114°02' E). This area currently owned by CIMTROP and used for research purposes by OuTrop. Block C has the deepest peat of all of the MRP area with more than 16% over 3 m (Sabiham, 2004) and up to 8 m deep (Page et al., 2002). The soil has a pH below 3.5 (Sabiham, 2004).

The Mega Rice study site was not deforested by the Project or burned, but has been affected by severe drainage and indirectly by fire, and thus has experienced substantial losses of peat, vegetation, and soil moisture and stability. Due to a smaller area of forest present at the MRP site, 6 smaller plots (5 m x 100 m) were constructed in close proximity to each other, all approximately 3 km from the river (Figure 2). In concordance with previous

studies (Marchant, 2012), these plots will be considered together as a single plot¹ (HD 3.0; Table 1).

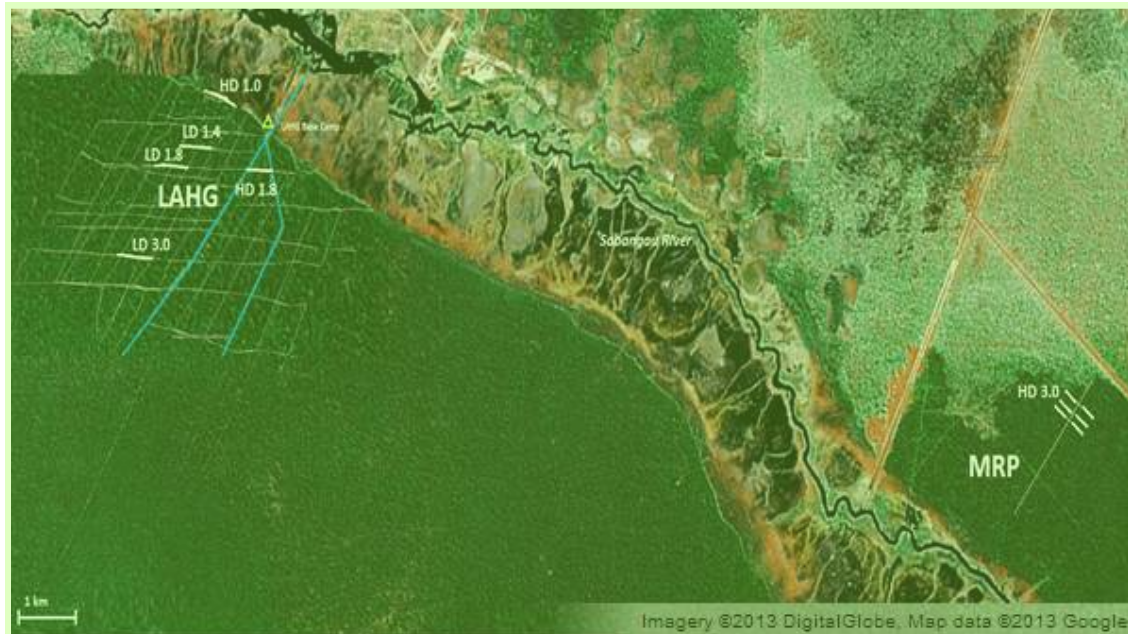


Figure 2: Location of tree plots at the Sabangau LAHG, as well as the location of logging² railways, transects used for primate behavioural studies, and LAHG base camp, with location of MRP subplots at Kalampangan. Adapted from Marchant, 2012.

Table 1: Details of six tree plots located in mixed swamp forest habitat. Peat depth⁴ estimated based on Page et al., 1999.

Plot	Disturbance Level	Disturbance Description	Distance from river	Peat depth	Size (m)
HD 1.0	High	Burning 50 years ago, edge	1.0 km	2.2 m	300m x 5m
LD 1.4	Low	Selective logging until 1997	1.4 km	2.4 m	300m x 5m
LD 1.8	Low	Selective logging until 1997	1.8 km	2.5 m	300m x 5m
HD 1.8	High	Heavy illegal logging until 2004	1.8 km	2.5 m	300m x 5m
LD 3.0	Low	Selective logging until 1997	3.0 km	3.0 m	300m x 5m
HD 3.0	High	Drainage, current	3.0 km	3.0 m	6 x 100m x 5m

1.3 Research Objectives¹

The overall goal of this study was to assess the effects that natural variations in peat depth and anthropogenic disturbance through logging, drainage, and fires, have on tropical peat swamp forest trees. The trees provide habitat and resources for nearly all other species within the forest, and so understanding the impacts of natural and anthropogenic variations on the trees will further the current understanding of this entire globally important ecosystem.²

In this study, I examined how forest traits (e.g. carbon storage) and species traits (e.g. fruiting pattern) varied with peat depth and a history of high or low levels of disturbance.³

Forest Traits Goals⁴

- Identify changes in forest traits as a result of peat depth and disturbance.⁵
- Quantify carbon content and assess the influence of disturbance on peat swamp forest carbon storage.

Species Traits Goals⁶

- Identify changes in species traits as a result of peat depth and disturbance.⁷
- Use observed variation in species traits to suggest a new method of trait-based habitat quality monitoring.
- Assess how changes in tree traits in response to disturbance may influence ape communities.

Forest traits assessed for each plot included biomass and carbon content,¹ which depend on tree density, tree size, and species composition. These measures were therefore assessed in relation to peat depth and disturbance level. Species traits included traits related to roots, size, bark, sap, growth, leaves, and phenology of trees, and the effect of peat depth and disturbance on these traits was also investigated.

This research was carried out in collaboration with the Orangutan Tropical² Peatland Project (OuTrop) and the Center for International Cooperation in Management of Tropical Peatland (CIMTROP) at the University of Palangkaraya, Indonesia.

Chapter 2: Forest Traits and Carbon Content¹

2.1.1 Tropical Peat Swamp Forest Carbon²

Tropical peat swamp forests play a major role in carbon sequestration and³ the global carbon cycle (Page et al., 2002; Aldhous, 2004). Not only is carbon stored in the vegetation, as in other forest types, but also in the peat, making these among the largest terrestrial carbon stores on earth. Even at moderate peat depths, peat swamp forest contains more than ten times the amount of carbon per unit area as other tropical forests, but with peat in Borneo reaching depths of over 20 m, the carbon storage capacity of these ecosystems is enormous (Page et al. 1999; Hooijer, 2006). Indonesian peatlands alone are estimated to hold 97 Gt of carbon (Page et al., 2011). When these forests become degraded, however, they not only lose their capacity to act as a carbon sink but begin to rapidly release carbon into the atmosphere which has been accumulating for millennia. Of the total area of peat swamp forest in Southeast Asia, it has been estimated that approximately half has been cleared and drained for agriculture, and the majority of what remains has suffered degradation and drainage from timber extraction (Verwer and van der Meer, 2010).

Human-related disturbances cause a significant loss of carbon from⁴ tropical peat swamp forest, as logging and burning lead to the removal of vegetation and drainage leads to decomposition of the peat (Hooijer et al., 2010). The high water table of pristine tropical peat swamp forest prevents

decomposition, but when drained the peat oxidizes and breaks down, releasing ¹ CO₂ (Reiley et al., 1996). Drained peat subsides rapidly such that the surface of the peat can drop by several meters over a century (Maltby and Proctor, 1996). As a result of the oxidation and decomposition of drained peat, Indonesia emits approximately 600 Mt of carbon each year (Yule, 2010).

More dramatic than the effect of peat oxidation, however, is combustion. ² Burning substantially speeds the process of peat degradation, affecting forest structure and biodiversity and releasing vast quantities of carbon dioxide. Fires, unfortunately, are common on Borneo and increasing in frequency. They are most frequent during dry periods, typically coinciding with El Niño events which occur every 5-10 years and cause severe drought (Commitante et al., 2003; Yule, 2010). Once an area has burned previously it becomes much more likely to burn again (Woods, 1989; Brown, 1998), and with up to 20 m of accumulated peat there is a substantial amount of fuel (Page et al., 1999), allowing fires to reoccur many times. These fires have enormous impacts on greenhouse gas emissions, the health of humans and wildlife, and economy. As an example, the drainage and forest clearance associated with the Mega Rice Project contributed to major fires on Borneo in 1997. More than 2.7 million ha of vegetation and peat burnt, causing the largest increase in global CO₂ levels in recorded history, releasing approximately 13-40% the amount of carbon released annually from worldwide fossil fuel emissions (Page et al., 2002).

As a result of peatland emissions from peat oxidation and burning, Indonesia is currently the third largest producer of CO₂ in the world, next to China and the United States. An initiative which attempts to reduce greenhouse gas emissions, mitigate climate change, and preserve tropical forests is Reducing Emissions through Deforestation and Degradation (REDD), wherein financial incentives are provided to countries for keeping their forests intact (Slik et al., 2010). Effective implementation of REDD initiatives requires accurate quantification of carbon content of these forests (Gibbs et al., 2007). Therefore, the first main goal of this project was to quantify carbon content of these forests and assess how it is altered by disturbance.

2.1.2 Biomass Quantification

The main carbon compartments of peat swamp forests include above- and belowground living biomass of the forest vegetation, dead biomass contained in litter and coarse woody debris, and peat (Gibbs, 2007; Verwer and van der Meer, 2010). Biomass is assumed to be 50% carbon (Basuki et al., 2009). Unlike other tropical forests where the trees are the main compartment (Gibbs et al., 2007), the carbon contained in peat swamp forest trees is dwarfed by the enormous amount in the peat. Forest vegetation, however, can still be a substantial contributor to biomass in tropical peat swamp forests, particularly in undisturbed primary forest (Verwer and van der Meer, 2010). Aboveground biomass comprises all living aboveground vegetation, including tree trunks, branches, and leaves, and is the most commonly used measurement for biomass. Belowground

biomass comprises all living coarse roots of trees, and can represent as much as 25% the total biomass in many tropical forests. Together these comprise living biomass (Verwer and van der Meer, 2010). ¹

The biomass of forest vegetation can be estimated through allometric equations derived from destructive harvesting which determines the relationship between mass and parameters such as diameter and height (Verwer and van der Meer, 2010). Allometric equations have not yet been developed specifically for tropical peat swamp forests, and so equations for other moist tropical forest types must be used (Verwer and van der Meer, 2010). Mass depends not only on wood volume, however, but also on its density (Swaine and Whitmore, 1988; Chave et al., 2005), which differs between species. Pioneer species invest in rapid growth at the expense of wood density, whereas species which are slower growing can invest more in tissue density (Swaine and Whitmore, 1988; Verwer and van der Meer, 2010). Furthermore, pioneer species with low wood density decompose more rapidly than species with higher density, contributing less to the dead organic matter pools of litter, coarse woody debris, and peat. Regenerating forest therefore typically has lower carbon storage as a result of smaller trees with lower wood density. ²

Dead organic material, including litter and coarse woody debris, can contribute to biomass. Although normally an unimportant carbon store in tropical forests due to rapid decomposition (Powers et al., 2009), dead organic matter may make larger contributions to carbon storage in peat swamp forests due to ³

the slow rates of decomposition. Published proportions of litter biomass to above-ground biomass in moist tropical forests range from 2.9% (Delaney et al., 1997) to 3.5% (Brown et al., 1995), while coarse woody debris range from 9.6% (Chambers et al., 2004) to 33.6% (Rice et al., 2004).¹

The most substantial carbon compartment in these forests is the peat, with its carbon content greatly exceeding that of the vegetation. Peat biomass varies across a peatland due to variations in peat depth, bulk density, and carbon content (Page et al., 1999; Page et al., 2002). Published data on peat depth, age, and composition in Sabangau are available from Page et al. (1999).²

2.1.3 Research Goals³

The goal of this chapter was to use data on tree density, tree size, and species composition in the study plots to quantify the carbon content of mixed swamp forest and to determine if carbon storage varies with peat depth or level of disturbance.⁴

2.1.4 Forest Trait and Biomass Predictions⁵

Disturbed plots were expected to have a high density of small trees, while low disturbance plots will have a lower density of larger trees. Species composition was predicted to show a clear pattern relating to successional stage, with differences between primary and secondary forest according to level of disturbance. These differences were expected to translate into differences in⁶

biomass between plots, with lower biomass and carbon content in high disturbance locations as a result of smaller trees with lower wood densities.

2.2 Methods

2.2.1 Data Collection

All trees within each plot equal or above 7 cm diameter at breast height (1.3 m above ground or aerial roots) had been previously tagged, identified to species by local field assistants, and diameter at breast and base height recorded most recently in 2011 by OuTrop (OuTrop, unpublished data). From these data, tree density, tree diameter at breast and base height, and species composition were assessed, along with biomass and carbon content.

2.2.2 Biomass Calculations

Estimates of total biomass, including aboveground, belowground, litter, coarse woody debris, and peat biomass were obtained as follows.

Above- and below-ground biomass for each tree in each plot was calculated using the following allometric equations:

Equation 1 $AGB = p * \exp[-1.499 + (2.148 \ln(D)) + (.207 \ln(D))^2 - (.0281 \ln(D))^3]$ (Chave et al. 2005)

Equation 2 $BGB = 0.02186 * D^{2.487}$ (Niiyama et al. 2005)

where AGB is aboveground biomass in kg, BGB is below ground biomass in kg, p is species wood density in g/cm³, and D is DBH in cm. The equation for

aboveground biomass was derived from data drawn from destructive harvesting of species from moist tropical forest of various countries (Chave et al., 2005), and belowground biomass was based on data drawn from destructive harvesting of species in lowland dipterocarp forest in Pasoh, Malaysia (Niiyama et al., 2010). All wood densities were obtained from the Wood Density Database (www.worldagroforestry.com). If more than one wood density value was available for a species, all values were averaged. For any trees which were identified only to the genus level or for which the species in that genus not available, an average of the wood densities of all species available in that genus was used. For any tree which was not identified to genus or the wood density for that genus unavailable, an average of the densities of all other trees sampled was used.

Biomass of litter and coarse woody debris was calculated using the ratio of litter and coarse woody debris biomass to aboveground biomass found in other moist tropical forests. Because the reported ratio of litter and coarse woody debris biomass varies between forests and is unknown for peat swamp forests specifically, both the lowest and highest reported values for moist tropical forest were used to calculate a low and high estimate (Verwer and van der Meer, 2010). The following equations were used:

Equation 3	$LB_{low} = 0.029 * AGB$	(low estimate)	(Delaney et al 1997)
Equation 4	$LB_{high} = 0.035 * AGB$	(high estimate)	(Brown et al 1995)
Equation 5	$CWDB_{low} = 0.0962 * AGB$	(low estimate)	(Chambers et al 2004)
Equation 6	$CWDB_{high} = 0.336 * AGB$	(high estimate)	(Rice et al 2004)

where LB is litter biomass in kg and CWD is coarse woody debris biomass in kg.¹ LB_{low} was based on data from moist tropical forest in Venezuela (Delaney et al., 1997), while LB_{high}, CWDB_{low} and CWDB_{high} were based on data from moist tropical forests in Brazil (Brown et al., 1995; Chambers et al., 2004; Rice et al., 2004).

Data published by Page et al. (1999) on depth of peat at LAHG at various distances from the river was used to estimate peat depth of each plot using simple linear regression. Based on findings by Page (2002), peat at a depth of 3 m holds approximately 1800 Mg C/ha (Verwer and van der Meer, 2010). Peat carbon content at each plot could be therefore be estimated by adjusting for peat depth.²

Total vegetative biomass (TVB), excluding peat, for each plot was attained by summing aboveground, belowground, litter, and coarse woody debris biomass. Carbon content was attained by assuming that 50% of biomass is carbon (Basuki et al., 2009). Carbon from forest biomass was added to peat carbon to attain total carbon values.³

2.2.3 Comparison of Biomass Equations⁴

Chave et al. (2005) provide two equations for calculating aboveground biomass for trees, one which includes tree height and one which does not. Equations including height are more accurate (Chave et al., 2005), but measurements of the height of each individual tree are more difficult to obtain.⁵

than only diameter at breast height and so are often not available. To determine the added accuracy obtained by including tree height for estimating biomass in peat swamp forest, the heights of 344 trees of 23 species were measured with the use of a clinometer (Section 3.2.2) and the values attained from both calculations were compared. Aboveground biomass was calculated using Equation 1, which does not include tree height, and with Equation 7 which does.

Equation 7 $AGB = \exp[-2.187 + 0.916 \cdot \ln(pD^2H)]$ (Chave et al. 2005)

where AGB is aboveground biomass in kg, p is species wood density in g/cm³, D is DBH in cm, and H is height in m.

2.2.4 Statistical Analysis

General linear models were used to assess whether there is an effect of distance from the river or disturbance level on tree density, average diameter at breast height, and total vegetative biomass of each plot. Principal components analysis was used to assess differences in species composition between plots.

Patterns were deemed statistically significant based on an alpha value of 0.5. The power of these statistical analyses was extremely low, with only 6 plots, and thus trends were discussed up to an alpha value of 0.2. All statistical analyses were performed using Minitab, SYSTAT, or Microsoft Excel with StatistXL.

2.3 Results¹

2.3.1 Tree Density and Size²

Tree density tended to increase from the edge to the interior of the forest³ (Figure 3), though results were not significant ($P=0.100$, Table 2). There was no evidence that level of disturbance was related to tree density ($P=0.442$). The number of trees in each 0.15 hectare (ha) plot ranged from a low of 226 in the edge plot (HD 1.0) to a high of 311 trees in the low disturbance interior plot (LD 3.0). Tree densities in this study thus ranged from 1506 trees/ha to 2073 trees/ha. Average density was 1734 ± 213 trees/ha.

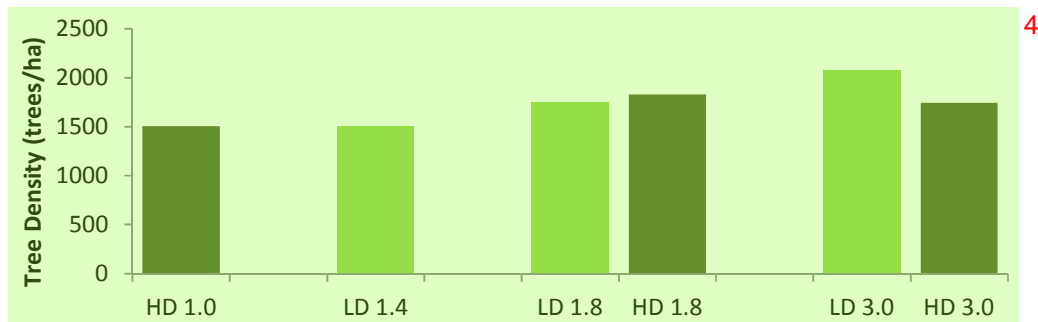


Figure 3: Density of trees (trees/ha) above 7 cm DBH for each plot. High disturbance (HD) plots are shaded dark while low disturbance (LD) plots are shaded lighter. Numbers (1.0 through 3.0) indicate distance from the river. Plots which are of equal distance from the river and therefore assumed to have been similar prior to disturbance are grouped together.⁴

Table 2: Results from a general linear model assessing the effects of distance of plot⁵ from the river and level of disturbance on tree density.

Source	Sum-of-Squares	df	F	P	Model R^2 ⁷
Distance	129168.750	1	5.523	0.100	0.691
Disturbance	128248.853	1	0.780	0.442	
Error	70156.176	3			

Tree size, as estimated by average diameter at breast height, was not significantly affected by distance ($P=0.222$), but trees did tend to be smaller in high disturbance plots ($P=0.094$) (Figure 4, Table 3). The same trends were found if basal diameter or basal area were used as a proxy for tree size (data not shown). Total basal area averaged $42.4 \pm 6.03 \text{ m}^2/\text{ha}$.

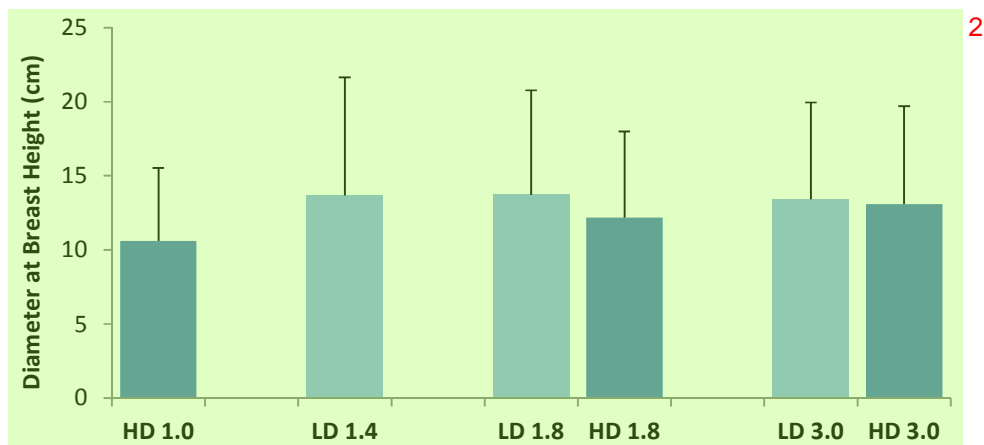


Figure 4: Average diameter at breast height (cm). High disturbance (HD) plots are shaded dark while low disturbance (LD) plots are lighter. Plots which are of equal distance from the river and therefore assumed to have been similar prior to disturbance are grouped together. Error bars are standard errors calculated across all trees in a plot.

Table 3: Results from a general linear model assessing the effects of distance of plot from the river and level of disturbance on average tree diameter at breast height.

Source	Sum-of-Squares	df	F	P	Model R^2
Distance	1.423	1	2.363	0.222	0.750
Disturbance	3.548	1	5.891	0.094	
Error	1.807	3			

2.3.2 Species Composition

A principal components analysis of species composition shows that composition of the edge plot (HD 1.0) was highly dissimilar from all other plots on both the first and second component (Figure 5). The remaining plots were very

similar along the first component, but differed according to the second component. The species whose loadings contribute most to the two components are shown in Table 4. Species with high loadings on the first component are common in the forest interior, whereas species with high loadings on the second component are abundant at the forest edge. The two interior low disturbance plots (LD 1.8 and LD 3.0) tended to cluster together, as did the two interior high disturbance plots (HD 1.8 and HD 3.0), indicating that the more disturbed interior plots tended to have more early successional species than the corresponding low disturbance plots (Figure 5).

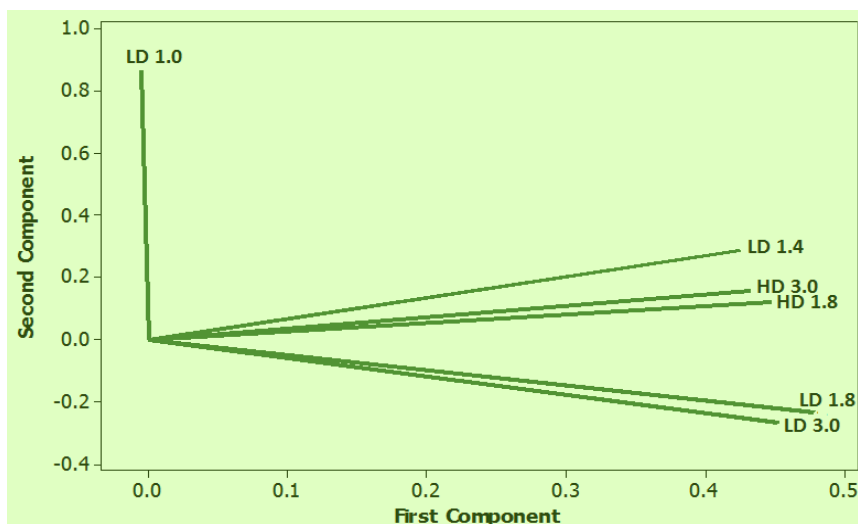


Figure 5: Principal components analysis loading plot for species composition of each plot. The first and second components accounted for 47% and 18% of the total variance, respectively.

Table 4: Local names of tree species which contributed most to the first two components of a principal components analysis and their loadings. For scientific names, refer to Appendix Table A1.

Principal Component 1		Principal Component 2	
Species Local Name	Loading	Species Local Name	Loading
Jinjit	5.775	Belawan merah	6.137
Tabaras akar tinggi	3.596	Geronggang	4.852
Pisang pisang	3.545	Tumih	3.964
Terontang	3.293	Bintan peter	2.879
Rambutan hutan	3.055	Manggis	2.462
Pampaning bitik	2.704	Alau	2.138
Jambu burung besar	2.701	Nyatoh gasas	2.072
Hangkang	2.277		
Papung	2.188		

2.3.3 Biomass and Carbon

Of the 1827 trees in the six plots, 909 trees (50%) were identified to species and had wood density available at the species level. For 771 trees (42%), a genus average for wood density was used, and for 147 trees (8%) an average wood density from all other trees was used.

Aboveground biomass values within the plots ranged from 21 Mg (megagrams, 10^3 kg or 1 tonne) at the edge (HD 1.0) to 50 Mg at the interior low disturbance plot (LD 3.0) (Table 5). Total vegetative biomass, including aboveground, belowground, litter, and coarse woody debris biomass, ranged from 26-31 Mg at the edge to 63-75 Mg in the interior. This provides estimates of 87-107 Mg of carbon per hectare at HD 1.0, while the most interior undisturbed habitat has up to 251 Mg of carbon per hectare (Table 5, Figure 6). Although results were not statistically significant (Table 6), total vegetation biomass followed the trend of increasing with distance ($P=0.055$) and decreasing with disturbance ($P=0.123$). The amount of biomass in HD 1.8 is approximately 16%

less than that of LD 1.8, while the biomass of HD 3.0 is approximately 22% less than that of LD 3.0.

Table 5: Calculated estimates for aboveground biomass (AGB) and total vegetation biomass (TVB) in tons for each plot in megagrams (Mg, 10^3 kg), as well as estimated values of biomass per hectare and carbon content per hectare, both aboveground carbon (AGC) and total vegetation carbon (TVC). *Corrected for area to be consistent with other plots.

Plot	Biomass (Mg)				Carbon (Mg)	
	AGB	TVB	AGB/ha	TVB/ha	AGC/ha	TVC/ha
HD 1.0	21	26-31	140	174-208	70	87-107
LD 1.4	49	61-73	324	404-484	162	202-242
LD 1.8	46	58-69	308	386-462	154	193-231
HD 1.8	36	45-54	240	301-360	120	150-180
LD 3.0	50	63-75	334	419-501	167	210-251
HD 3.0	42*	53-63*	283	354-423	141	177-212

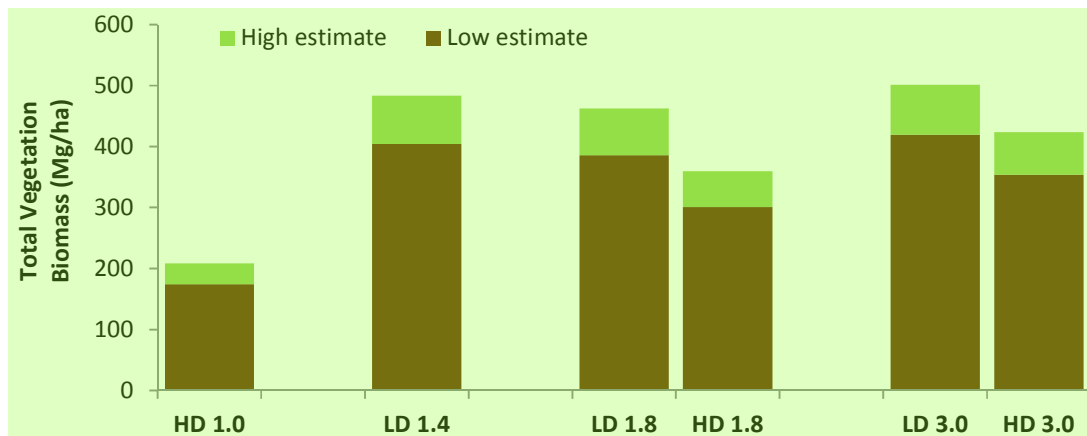


Figure 6: Calculated estimates of total biomass (Mg/ha) of total vegetative biomass including above- and belowground tree biomass, leaf litter, and coarse woody debris for six plots of mixed swamp forest. Low estimates are shaded dark while high estimates are shaded light. Plots which are of equal distance from the river and therefore assumed to have been similar prior to disturbance are grouped together.

Table 6: Results from generalized linear models assessing the effects of distance of plot from the river and level of disturbance on the high estimate of total vegetation biomass.

Source	Sum of Squares	df	F	P	R ²
Distance	699.044	1	9.335	0.055	0.834
Disturbance	338.672	1	4.522	0.123	
Error	224.661	3			

Based on the carbon content of Sabangau peat determined by Page et al. (2002) adjusted for estimated peat depth at each plot (Page et al., 1999), peat carbon ranged from 1427 Mg/ha at 1.0 km to 1800 Mg/ha at 3.0 km from the river (Table 7). The amount of carbon stored in the forest vegetation is only, on average, 12% of what is stored in the peat. Total carbon, including that of both the vegetation and peat, may be as high as 1977 Mg/ha in Sabangau low disturbance mixed swamp forest.

Table 7: Peat depth (m), peat carbon content (Mg/ha), and total carbon (Mg/ha) of both forest vegetation and peat for each plot.

Plot	Peat Depth (m)	Peat Carbon (Mg/ha)	Total Carbon (Mg/ha)
HD 1.0	2.2	1320	1427
LD 1.4	2.4	1440	1682
LD 1.8	2.5	1500	1731
HD 1.8	2.5	1500	1680
LD 3.0	3.0	1800	2051
HD 3.0	3.0	1800	1977

2.3.3.2 Comparison of Biomass Equations

The inclusion of tree height when predicting tree biomass can improve accuracy, but measurements of tree height are often difficult to obtain (Chave et al., 2005) and may not be available. Chave et al. (2005) have developed one equation which can be used when height data are available, and one which can be used when height data are not available. Estimates from these two equations had a discrepancy of 18.6% (Figure 7). Equation 1, which did not include tree height in the calculation, overestimated aboveground biomass by an average of 68.7 kg when compared to Equation 7, which included tree height. Trees above approximately 25 m tended to have Equation 1 underestimate aboveground

biomass compared to estimates from Equation 7, while those below 25 m were overestimated (Figure 8).¹

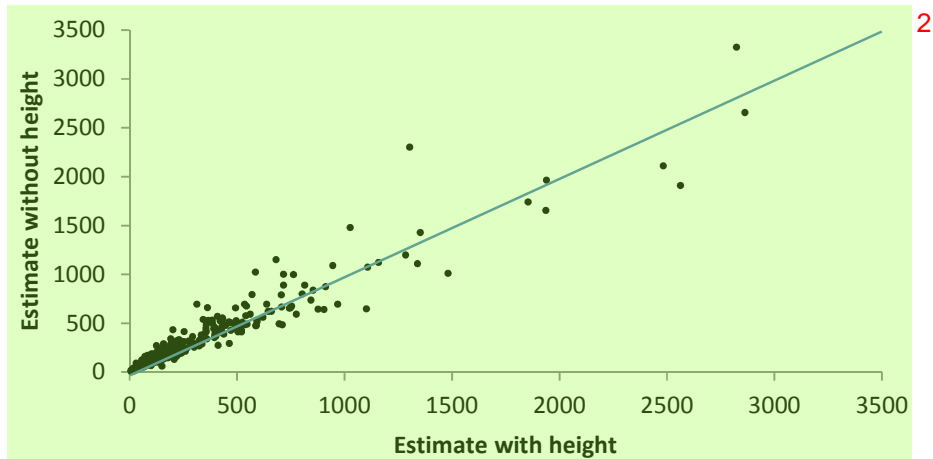


Figure 7: Estimates of aboveground biomass from an equation including height as a predictive variable and an equation not including height. The line shows where the two estimates would be equal.³

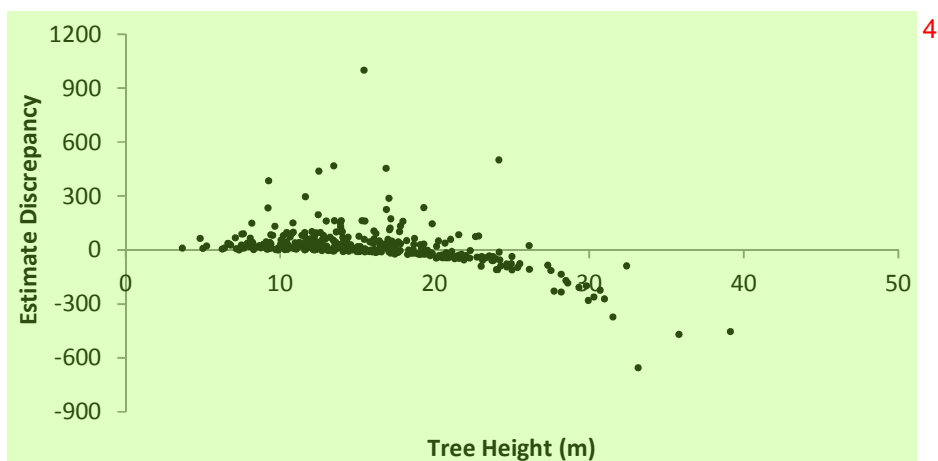


Figure 8: The discrepancy in aboveground biomass estimates between Equations 1 (not including height) and Equation 7 (including height) in relation to actual tree height.⁵

2.4 Discussion¹

Quantification of biomass in tropical peat swamp forests is critical for determining potential carbon emissions from deforestation and for implementation of carbon budgeting schemes (Gibbs et al., 2007). The biomass and carbon stored in forest vegetation depends on the number of trees, the size of trees, and the composition of species due to species-specific differences in wood density (Chave et al. 2005; Verwer and van der Meer, 2010). A change in any of these measures can result in alterations in the amount of carbon stored in the forest.

2.4.1 Tree Density³

Average tree density was 1734 trees/ha. Tree density values at LAHG attained through LiDAR analysis (Light Detection and Ranging optical remote-sensing technology) were similar to that found in this study for LD 3.0 at 1956 trees/ha (Kroseder et al., 2012), though Waldes and Page (2002) found much higher density in Sabangau mixed swamp forest at 3112 trees/ha. There is often a reciprocal relationship with tree density and tree size (Marchant, 2012). It is likely that some disturbed forest was included in measurements by Waldes and Page and so, being sampled more than ten years previous to this study, there may have been a higher density of small trees which were later replaced by a lower density of larger trees. Tree density for Sabangau is similar but higher than what has been reported in Sumatran undisturbed mixed swamp forest at 1303

trees/ha (Gunawan et al., 2012), and freshwater swamp forest in French Guiana at 1467 trees/ha (Koponen et al., 2004). ¹

Tree density of peat swamp forests is high compared to other Southeast Asian tropical forests. Lowland dipterocarp tree density has been reported as 1612 trees/ha in a forest in Central Kalimantan (Kroseder et al., 2012) and 238 trees/ha in West Kalimantan (Cannon and Leighton, 1998). Other moist tropical forest types also exhibit lower tree density. For example, primary tropical moist forest in Cameroon had a density of 221 trees/ha and Sri Lankan primary moist forest had 384 trees/ha (Brown et al., 1989). ²

Tree density tended to increase with distance from the river, contrary to predictions, with no effect from level of disturbance. Because of the trade-off between tree density and size, with either few large trees or many small trees (Marchant, 2012), it was predicted that density would be greatest at high disturbance plots and highest at the edge, since it is made of young trees colonizing outwards from the forest. However, the edge plot had the lowest density. This is likely the result of the high abundance of trees smaller than the 7 cm diameter sampling limit (Marchant, 2012). This study found no effect of disturbance on tree density. Other studies have reported changes in tree density as a result of disturbance, though the direction of change is variable. Mixed swamp forest in Sumatra found an increase in tree density ten years after selective logging, with 2,492 trees/ha (Gunawan et al., 2012), which is nearly double what was reported for unlogged forest. Similarly, logged peat swamp ³

forest at Blocks B and C of the Mega Rice Project were found to have increased density at 2429 trees/ha (Kroseder et al., 2012). The logged HD 1.8 plot did have a slightly higher density than LD 1.8 with a difference of 5%, but without additional tree plots it cannot be known whether these results would be significant. Peat swamp forest tree plots which experienced drainage, indirect fire damage, and wind damage, however, had greatly reduced tree densities, averaging 971 trees/ha (Gunawan et al., 2012). This study similarly saw a decrease in tree density as a result of drainage, with a difference in 15% between HD 3.0 and LD 3.0. Replication of plots, however, is required to uncover whether these differences would be significant. If logging tends to increase density while drainage decreases density, this could explain why no overall effect of disturbance was found in this study. The differences in the direction of effect of disturbance through logging and drainage may be explained by the persistence of trees when they are killed. In logging, trees are removed from the area leaving open spaces on the ground which can be filled by smaller trees (Finegan, 1984), resulting in an increase in density. When trees fall as a result of drainage, however, the dead trees remain and so there may not be as much exposed soil where young trees can colonize, possibly resulting in a decrease in tree density due to lower recruitment.

2.4.2 Tree Size²

Tree size, as estimated by diameter at breast and basal height, was not influenced by the distance from the river but did tend to decrease with

disturbance, as predicted. The edge plot is made of young trees colonizing outwards, and thus smaller diameters were expected (Marchant, 2012). In the logged plot, the largest trees would have been preferentially removed as these would be most valuable (Commitante et al., 2003), and in drained plots, the largest heaviest trees may be the ones most likely to fall (Yamada et al., 2001). In the logged and drained plots, the gaps would be colonized by small trees (Finegan, 1989), reducing average tree diameter. Average total basal area was 42.4 m²/ha, which is greater than values found by LiDAR in the Sabangau forest at 30.7 m²/ha (Kroseder et al., 2012).

2.4.3 Species Composition²

Species composition of the edge plot (HD 1.0) was highly dissimilar from the composition of all other plots. The two interior low disturbance plots (LD 1.8, LD 3.0) were most similar to each other in composition, and the remaining three plots (HD 3.0, HD 1.8, LD 1.8) were similar to each other.

Forest at the edge (HD 1.0) had previously burned, creating a false edge to the forest and a very harsh environment for trees attempting to reestablish. Fire can drastically alter species composition because only highly specialized species can tolerate extreme conditions. Recruitment difficulties can be experienced following fire due to the removal of mature trees and all seedlings and saplings (Wood, 1989). Recruitment may be further exacerbated by the removal of fauna after fire, resulting in a lack of seed dispersal to the area (Webb

and Peart, 2001; Nunes-Iturri and Howe, 2007). The water storing capacity of peat is altered following fire, causing previously burnt areas to flood and prevent re-establishment of vegetation (van Eijk and Lemman, 2004; Wosten et al., 2006). With a lack of canopy cover, seedlings which do germinate can be burnt by the intense sun (Graham et al., 2007) and are exposed to wind and storms. These factors create a very hostile environment at the burnt edge where only a few species can become established. This is shown by the high abundance of only a few species, with nearly a quarter of the trees represented by a single species (Section 3.3.1), and explains why regenerating forest composition at the edge is so dissimilar from secondary forest in logged or drained plots.

Species composition of the two interior low disturbance plots (LD 1.8 and LD 3.0) were similar to each other and differed most from the edge plot along both the first and second component. This was as expected, as these plots are thought to contain mainly primary forest and have similar physical conditions, and so composition would differ from secondary forest in the other plots.

The similarity in composition of the two interior high disturbance plots (HD 1.8 and HD 3.0) was also as expected as both contain high proportions of secondary forest. In both of these plots, colonizing species filled the gaps left by trees which were logged or fell due to drainage resulting in a change of composition from that of the low disturbance plots. The degree of impact on species composition by logging depends on the severity and selectiveness. Selective logging targets only a few valuable timber species, though non-targeted

species can be removed as a result of incidental damage and subsequent mortality (Cannon and Leighton, 1998). More selective logging would result in fewer species removed from the community to be replaced by colonizing species. With illegal logging operations, however, once the most valuable species are removed, less valuable species are taken (Commitante et al., 2003), potentially causing more dramatic changes in species composition.

Although the logged plot (HD 1.8) is similar to the burned plot in that much of the forest was removed, recovery has occurred at different rates because of different starting points for regeneration (van Eijk and Leeman, 2004). Burning not only removes mature trees but also alters the chemical and physical composition of peat, removes all seedlings and saplings, and often becomes flooded due to a loss of water storage capacity of the peat (van Eijk and Lemman, 2004; Wosten et al., 2006), and is exposed to intense sun (Graham et al., 2007). With logging, not all trees were removed and the peat, seedlings, and saplings were mostly spared, explaining why composition between these plots is different. The drained plot had similar species composition to the logged plot. Although the cause of the loss of trees differs, the result would be similar, with trees removed due to falling and the gaps colonized by secondary species.

Unexpectedly, LD 1.4 was most similar in composition to the logged and drained plots, suggesting there may be more secondary forest than was thought. This leads to the proposition that LD 1.4 may not be as undisturbed as was believed (Marchant, 2012; OuTrop, pers. comm.). Due to the close proximity of

this plot to the forest edge and to a logging canal (Marchant, pers. comm.), LD 1.4 may have suffered more illegal logging than was believed. If this is the case, then the classification of this plot may be more accurately described as intermediate disturbance.

2.4.3 Biomass²

Aboveground biomass ranged from 140 Mg/ha at the high disturbance edge plot, to 334 Mg/ha at the low disturbance interior plot. Total vegetation biomass, including aboveground, belowground, coarse woody debris, and litter biomass, ranged from 208 Mg/ha at the high disturbance edge to 423 Mg/ha at the low disturbance interior plot. Undisturbed mixed swamp forest may, therefore, hold as much as 251 Mg of carbon per ha contained in the forest vegetation.

This was the first study to attain complete biomass and carbon values for the Sabangau catchment, as previous studies have looked only at aboveground biomass (Boehm et al., 2011; Kroseder et al., 2012) or peat carbon (Page et al., 1999) and did not include belowground, coarse woody debris, or litter biomass estimates. Both a high and low estimate of vegetation biomass was attained based on the proportion of litter and coarse woody debris biomass found in other forests, but due to the very slow rates of decomposition of dead organic matter in tropical peat swamp forest compared to the Brazilian forests from which estimates were attained (Brown et al., 1995; Delaney et al., 1997; Chambers et al., 2004; Rice et al., 2004), true values of dead organic carbon are likely closer

to the high estimates and may even exceed those (Verwer and van der Meer,¹ 2010).

Past studies have used LiDAR to estimate aboveground biomass (Boehm² et al., 2011; Kroseder et al., 2012), rather than measuring individual trees on the ground as in this study. Aboveground biomass estimates were similar. Kroseder et al. (2012) found using LiDAR that, in unlogged areas of the Sabangau forest, aboveground biomass was 228 Mg/ha, which is similar to the average of the low disturbance plots though lower (322 Mg/ha). LiDAR allows a larger area to be covered in a shorter amount of time but is more expensive and may not be accessible to all researchers. Measuring individual trees to determine biomass is much more time-consuming and labour-intensive. Based on the pros and cons of each method, it is reassuring to confirm that similar results are attained by both methods.

The biomass values for the Sabangau catchment fit well with estimates of³ aboveground biomass for other peat swamp forests. Previous estimates for undisturbed peat swamp forests fall between 264 and 397 Mg/ha (various forests, Verwer and van der Meer, 2010; Lingga Water Catchment, Sarawak, Waldes and Page, 2002). Aboveground biomass of peat swamp forest is comparable to Amazonian rainforest estimates, averaging 289 Mg/ha (Slik et al., 2010). Compared to other Southeast Asian tropical forests, however, peat swamp forest has been reported to have lower aboveground biomass (Kroseder et al., 2012). Primary lowland dipterocarp forest has been reported to have an average aboveground biomass of 457-547 Mg/ha (Slik et al., 2010; Kroseder et

al., 2012), though other published values are similar to peat swamp forests (276¹ Mg/ha, Berry et al. 2010).

2.4.3.2 Disturbance and Peat Depth Effects on Vegetation Biomass²

Tree biomass depends on tree density, size, and species composition.³ The density of trees tended to increase with distance from the river, while the size of trees tended to decrease with disturbance. There were clear differences in species composition between the edge, high disturbance interior plots, and low disturbance interior plots. As a result, total vegetation biomass of plots, excluding peat, tended to increase with distance from the river and decrease as a result of disturbance. High disturbance plots had an average reduction in living biomass of more than 30% compared to low disturbance plots. The lack of statistically significant effects on the biomass of each plot is likely due to low statistical power.

Effects of logging on aboveground biomass have been found in other⁴ studies of peat swamp forest biomass. Kroseder et al. (2012) found that logged forest in Blocks B and C of the Mega Rice Project had biomass values 30% less than that of unlogged areas of the Sabangau catchment. These values were much lower than was seen at the logged LAHG plot in this study (160 vs. 240 Mg/ha), likely because logging in LAHG has stopped and much regeneration has occurred, while logging in the Mega Rice Project likely continues (Sabiham, 2004). Clearly the reduction in biomass as a result of logging disturbance depends on the form, selectivity, intensity, and period of regeneration. Despite

substantial illegal logging only approximately eight years ago (Marchant, pers. comm.), the biomass in the logged plot in this study (HD 1.8) was only 16% less than that of LD 1.8, suggesting the forest is capable of rapid regeneration. Berry et al. (2010) found that, following logging, regenerating forest sequestered carbon at a rate five times that of unlogged forest, and aerial sampling over the Sabangau forest found an increase of tree height up to 2 m in four years (Boehm et al., 2011). Therefore, with conservation status and prevention of further logging, it appears that heavily logged mixed swamp forest can quickly recover biomass. The rate of biomass recovery would, however, slow after the initial recolonization of forest gaps, and some estimates suggest the carbon deficit may persist for as long as 65 years (Berry et al., 2010).

The drained plot (HD 3.0) had a 20% reduction in biomass and carbon content compared to LD 3.0. Assuming the plots were similar before drainage, the loss is likely the result of tree falling due to drainage which has caused the peat to lose its integrity. Yamada et al. (2001) suggest that larger and heavier juvenile trees may be more likely to fall than smaller and lighter ones and so the same may hold for mature trees, resulting in the loss of the heaviest trees with the greatest carbon stores.

In pristine peat swamp forest, the falling of trees contributes to the formation of peat and thus carbon is not lost from the system but rather redistributed. With drainage, however, the anaerobic conditions which normally prevent decomposition are removed and thus carbon is lost from the forest. This

loss of biomass is likely to continue until drainage canals are blocked and the natural hydrology of the landscape restored (Wosten et al., 2006).¹

2.4.3.3 Peat Biomass²

Estimates of carbon content indicated that most (88%) of the forest's carbon is contained in the peat, with the remainder stored in trees, litter, and coarse woody debris. This estimate is slightly higher than that of Page et al. (2011) at 74%, possibly because this study considered only mixed swamp forest while Page et al. (2011) considered peat swamp forest in general.³

Results of this study suggest that forest biomass can regenerate fairly quickly, as was seen in the logged plot (HD 1.8). The destruction of peat, however, is virtually irreversible. The most important role of the forest, therefore, may be to protect the carbon stored in the peat. Because of the duality of this ecosystem, with reciprocal reliance of the peat and vegetation on each other (Page et al., 1999), protecting the peat carbon store means protecting the forest.⁴

2.4.3.4 Equation comparisons⁵

Estimations of tree biomass rely on allometric equations which relate tree parameters such as diameter and height to mass. The inclusion of tree height when predicting biomass can improve the accuracy of estimations, but because height is often obscured by the canopy, accurate measurements of tree height are often difficult to obtain (Chave et al., 2005). Therefore, Chave et al. (2005)⁶

developed one equation for estimating aboveground biomass of moist tropical forest which can be used when height data are available, and one which can be used when height data are not available. The equation which did not include height overestimated biomass values by 18.6%. The biomass of trees at heights greater than 25 m was underestimated, while those below 25 m were overestimated.

This equation has been used by several other studies to estimate tropical peat swamp forest biomass (e.g. Verwer and van der Meer, 2010; Kroseder et al., 2012). However, the accuracy of these equations for peat swamp forest has not been investigated. This is critical for assessing the accuracy of biomass and carbon content quantification of tropical peat swamp forest. The equation which does not include height has within it a conversion factor which estimates height based on the diameter at breast height (Chave et al., 2005). However, this conversion is based on other moist tropical forest types, rather than peat swamp forest specifically. The differences in peat swamp tree architecture may explain why such a large discrepancy between the two equations was found, and this large discrepancy suggests peat swamp-specific equations are required.

2.4.3.5 Biomass and Carbon Estimation Limitations

The largest source of error in biomass calculations likely stem from the fact that no allometric equations have yet been developed specifically for tropical peat swamp trees, and the proportion of litter and coarse woody debris biomass to living biomass in peat swamp forest have not been reported. The different

architecture of peat swamp species compared to those for which the equations used were developed reduced the accuracy of the calculations, as is exemplified by the comparison of the two biomass equations (Section 2.3.3.2). The prevalence of aerial roots is characteristic of peat swamp forest not common in other moist tropical forest types from which the allometric equations were developed (Verwer and van der Meer, 2010). This would reduce the accuracy of calculations for aboveground biomass. The highly specialized root systems of peat swamp forests have likely caused belowground biomass estimates to differ from the true value. The waterlogged and unstable conditions require an extensive and highly intertwined root system to maintain stability in the loose peat soil, and trees produce a thick superficial root mat to take advantage of the fact that the majority of the nutrients are contained in the thin top layer of peat (Richards, 1996). These root specializations likely caused discrepancies in biomass of peat swamp forest roots as a result of different rooting behavior and growth compared to the roots of Malaysian primary rainforest from which the belowground biomass equation used was developed (Niiyama et al., 2005; Verwer and van der Meer, 2010).

Although the decomposition of dead wood is generally a slow process (Palace et al., 2008), the rate of decomposition in tropical peat swamp forest is likely even slower, possibly resulting in greater proportions of coarse woody debris than even the high estimate suggests. The same may be true for litter biomass.

1 The calculations of this study assumed that the proportion of biomass in each compartment of aboveground, belowground, litter, and coarse woody debris biomass was equal between plots, which is likely not the case. Logging, burning, and drainage can influence the proportion of carbon represented by each compartment. Indirect fire damage can result in higher litterfall by trees due to smoke (Harrison et al., 2007), and so the drained plot (HD 3.0), where much of the surrounding forest has burned, may have experienced greater litterfall than plots at the LAHG. However, decomposition of litter at this site may be more rapid as a result of a lack of surface water which slows decomposition in pristine peat swamp forest. As a result of tree falling, the amount of coarse woody debris at HD 3.0 would be increased substantially, even with the higher decomposition rate. Coarse woody debris may also be larger in HD 1.8 as a result of logging debris, as has been reported in other logged forests (Palace et al. 2008).

2 Peat depth of each plot was estimated from distance from the river of each plot, based on data by Page et al. (1999) of the depth of peat at various distances from the river at LAHG. Limitations associated with this stem from the fact that this assumes that peat depth increases linearly from the river, and also assumes peat bulk density and carbon content remain constant, which may be a source of error as peat depth, density, and carbon content may be highly variable (Page et al., 1999; Page et al., 2002). Estimates also assumed that the MRP peat dome is directly comparable to that at LAHG, which is likely not the case, and as a result of subsidence of peat surface due to oxidation and degradation

as a result of drainage (Page et al., 2002), the depth of the peat at HD 3.0 is likely overestimated.

Calculations of living biomass included only that of the trees and not undergrowth vegetation, though this may not be a particularly large source of carbon due to the much lower biomass of undergrowth vegetation in comparison to that of the trees.

2.5 Conclusions

Although most results were not statistically significant, likely as a result of low sample sizes, it appeared that average tree size and species composition were influenced by disturbance. Because biomass depends on these forest parameters, disturbance can result in reduced biomass and thus carbon storage of disturbed peat swamp forest. The logged plot appears to have recovered much of its biomass, suggesting there is high regenerative capacity of secondary tropical peat swamp trees. Disturbed peat swamp forest should, therefore, receive protection to prevent further degradation which may completely destroy the area, and instead allow the forest to recover. Allowing these locations to regenerate will result in an increase in carbon storage over time, and is highly preferable to conversion of disturbed forest for other use (Berry et al., 2010). The drained plot, however, may be currently losing biomass as a result of tree falling. Until the hydrological integrity is restored, the loss of biomass will likely continue. Although tree biomass values are comparable to other tropical forests, the

carbon content of the vegetation is greatly outweighed by that of the peat. The most important role of the forest may, therefore, be to protect the peat below which, unlike tree biomass, is not renewable and cannot regenerate on a human time scale. With nearly 2000 Mg of carbon stored in a hectare of low disturbance peat swamp forest, these forests should be a priority for conservation.

The values of biomass and carbon content attained in this study are the first to provide complete carbon content estimates for Sabangau catchment mixed swamp forests, including that of both the vegetation and peat. These values can be used help to aid in improvement peatland management planning and carbon budgeting policies such as REDD and allow more precise predictions of how changes in tropical peat swamp forests may translate into emissions of greenhouse gases (Gibbs et al., 2007; Page et al., 2011).

Chapter 3: Species Traits¹

3.1.1 Functional Traits²

Species adapt to physical conditions through the traits they possess.³

Those species with traits best suited to current conditions of an area are able to out-compete others and become more abundant (Finegan, 1984). Therefore, by assessing the traits of the most successful species, knowledge of habitat can be gained. The function that a trait confers, however, is environment-specific (McIntyre et al., 1999). When physical conditions change, traits which were most common in previous conditions may no longer be advantageous. Different species with traits more suitable to new conditions may have a competitive advantage, allowing them to become the most abundant. It is in this way that disturbance causes changes in species composition through the traits a species possesses. The traits of a species determine how it interacts with other members of the community, and so changes in tree species composition affects other fauna and flora of the forest.

This chapter investigated the traits of the most successful tree species in areas of peat swamp forest to determine how natural and anthropogenic changes in forest conditions influence the prevalence of tree traits, and how, in turn, that may affect species which rely on them, as well as to collect descriptions of species to help with future species identification. This was done by collecting⁴

traits of species which will be referred to as adaptive traits, primate traits, and identification traits.¹

3.1.1 Adaptive Tree Traits²

Adaptive traits are those believed to potentially affect the ability of a species to cope with environmental conditions and thus competitive ability.³ Among the most important physical characteristics of tropical peat swamp forest is peat depth as this, in turn, influences other physical characteristics such as water dynamics, chemical composition, oxygen diffusion, and nutrient availability (Page et al., 1999). At different peat depths, different adaptive traits may therefore be selected for.

Tree flora of peat swamp forests is unique in that species must possess adaptations to the acidic, nutrient-deficient soil and high, fluctuating water levels⁴ (Posa et al., 2011). Root systems of peat swamp forest trees must be highly specialized to cope with these difficult peat conditions (Richards, 1996). Because the peat is soft and unstable, many trees develop aerial roots above ground in the form of stilts or buttresses to increase stability (Crook et al., 1997; Yule, 2010). Increasing the number, size, spread, and height of these aerial roots presumably increases tree stability. These traits are therefore expected to be more prevalent in locations which are less stable (Goldsmith and Zahawi, 2007), as has been reported in past studies (Yule, 2010).

Waterlogging is a particularly difficult characteristic of peat swamp forests⁵ to which plants must adapt. Pristine peat swamp forest may have water up to a

meter above the ground surface (Reiley et al., 1996). Pneumatophores, also known as knee roots or snorkel roots, are root structures some species project from the ground to enhance gas exchange in the waterlogged peat (Kitaya et al., 2002; Sun et al., 2004). Plants growing in more waterlogged sites, therefore, have more pneumatophores (Yule, 2010).

Forests of different successional stages favour different species traits (Finegan, 1984; Swaine and Whitmore, 1988). When trees are removed by disturbance, the species most likely to replace the lost trees are those which possess traits allowing them to establish themselves quickly and grow rapidly (Finegan, 1984; Swaine and Whitmore, 1988; Sheil and Burslem, 2003). Phenology and reproductive traits, such as dispersal method, number of seeds, and flowering and fruiting frequency, can influence a species ability to disperse and colonize new locations (Wang and Smith, 2002). Canopy shape, tree height, and leaf size and shape may influence a species ability to effectively capture resources. These traits allowing fast rates of resource acquisition would, therefore, be expected in high disturbance locations (Finegan, 1984). In later successional stages, conditions may favour traits which allow greater longevity (Finegan, 1984). Bark thickness can influence a species tolerance of fire (Marchant, pers. comm.), while growing location can influence sensitivity to abnormally wet or dry conditions (Nishimuae et al., 2007). The forest floor of peat swamps is covered with small hummocks and hollows where water pools (Nishimuae et al., 2007), and whether a tree is growing on a hummock or a hollow can affect survivorship. Trees on hollows are kept out of the water and

may have better oxygen diffusion in wet areas. During drought, however, peat swamp forest trees which are adapted to wet conditions experience higher mortality if located on a hummock due to desiccation (Nishimura et al., 2007).¹

Traits of the most successful tree species in each plot were sampled to determine how increases in peat depth, as estimated by distance from the river, alters tree traits. The traits most prevalent in high disturbance plots were compared to those of low disturbance plots to assess how the traits of species have allowed them to adapt to altered conditions. The goal was to use this knowledge to develop a method of trait-based habitat quality monitoring for tropical peat swamp forest.²

3.1.1.2 Trait-Based Habitat Quality Monitoring³

Disturbance alters the forest structure and composition (Section 2.3.2) which can negatively affect ecosystem functioning, carbon storage capacity, and the livelihood of flora and fauna which rely on the forest. However, measuring habitat quality of rainforests is difficult as there is no simple indication of disturbed conditions (Sheil and Burslem, 2003). Traditional methods of habitat quality monitoring to determine whether disturbance has occurred or to assess recovery or degradation of forest following disturbance rely on monitoring species composition (Harrison, pers. comm.). For example, van Eijk and Leeman (2004) identified key species in previously burnt peat swamp forest to indicate restoration potential. Species-focused monitoring, however, relies on accurate species identification. With over 200 species of trees so far identified in the Sabangau catchment (OuTrop, n.d.), expert botanists must be relied on to⁴

identify tree species. This causes habitat monitoring to be expensive and time-consuming. Traits of species are easier to identify than species themselves, and because a species acts on its environment through its traits, the rationale was to instead develop a monitoring technique which focuses solely on species traits, rather than the species themselves. This would allow habitat quality to be inferred through changes in tree traits. By identifying species traits indicative of disturbed or pristine conditions, a more efficient, less costly, and less time-consuming monitoring technique could be employed, requiring little expert knowledge or training to conduct.

3.1.2 Primate Tree Traits

The trees form the foundation of the forest, upon which nearly all other species rely. Changes in forest structure can therefore greatly influence all other species. Two flagship ape species present in this forest are the Bornean orangutan and the southern Bornean agile gibbon, both endangered and endemic to Borneo. The Sabangau forest contains the world's largest remaining population of orangutans (Morrough-Bernard et al., 2003) and likely the world's largest population of southern Bornean agile gibbons (Cheyne et al., 2007). These species rely on the trees for feeding, locomotion, and for orangutans, nesting, and so disruptions to forest structure can result in negative impacts on ape communities.

Both orangutans and gibbons are primarily frugivores (Galdikas, 1988; Conklin-Brittain et al., 2001). Therefore, tree traits relating to fruit production are extremely important for ape communities, including the proportion of trees which produce fruit, size of fruit trees, the regularity and frequency of fruiting, and the seasonal availability of fruit (Wich et al., 2002; Felton et al., 2003). 1

Canopy characteristics are important for both species of ape. Gibbons are entirely arboreal, performing all aspects of behavior in the canopy, while orangutans only rarely descend to the ground. Arboreal travel is much more energy efficient for orangutans, and protects them from terrestrial predators. Because fruit is distributed widely throughout the forest, apes have large ranging patterns, causing travel efficiency to greatly influence energy budget (Felton et al., 2003). Tree traits which may influence primate locomotion include tree diameter (Cheyne et al., 2013) because trees must be large enough to support the animal's weight, canopy shape which influences canopy continuity and ease of travel (Gibson, 2005), and possibly root architecture which may influence stability for travel. The height of trees is particularly important for gibbons, who preferentially nest, travel, and sing from the tallest trees (Cannon and Leighton, 1994), showing a significant preference in Sabangau for travelling in trees larger than 20 m and avoid using those below 10 m (Cheyne et al., 2013). 2

In addition to traits which also influence gibbons, orangutans are affected by tree species composition as a result of their need for trees to build nests in. All great apes build nests each night to sleep in (Sugardjito, 1986). Traits of trees 3

which may influence the decision of an orangutan of where to build a nest may¹ include tree size, root system, canopy shape, leaf size, and sap traits.

Orangutans are the largest arboreal primate, with mature females² weighing an average of 85 pounds, while adult males average nearly 200 pounds (Markham and Groves, 1990). Trees in which nests are built must therefore be strong to support their weight overnight, perhaps in wet or windy conditions. Large trees are preferred by orangutans for nesting trees (Gibson, 2005), which would be more likely to withstand their weight. The root system of a tree also influences orangutan nesting preference (Gibson, 2005) as these traits influence tree stability (Crook et al., 1997). Orangutans in Sabangau most often build nests in trees with aerial roots, with a particular preference for buttressed trees disproportionate to their abundance in the forest (Gibson, 2005), presumably because buttresses are stronger than stilted roots (Crook et al., 1997). Orangutans seem to avoid nesting in trees with pneumatophores which Gibson (2005) suggests are less stable.

Because of the branch breaking involved in nest building, orangutans³ avoid nesting in species which produce high volumes of sticky sap so as to avoid having their fur covered in sap (Gibson, 2005; Malone, 2011). Canopy shape of a tree may also influence nest building, as some branching architecture may be more easily manipulated into a platform than others (Gibson, 2005). Orangutans are known to occasionally use bundles of leaves like blankets or pillows, and use leaves as umbrellas within the nest during rain (MacKinnon, 1974; van Schaik, 2003). Orangutans may therefore prefer to nest in trees which produce large

leaves (Gibson, 2005). Some species of leaves are clearly preferable for nest building, as evidenced by the development of the habit of 'leaf carrying' in some populations of orangutans, wherein particularly good branches will be carried throughout the day until choosing a tree to build their nest in (Russon et al., 2007). Alterations in these tree traits could influence orangutan nesting behaviour. 1

Because changes in the prevalence and values of these tree traits may influence behavior and ecology of ape communities, the changes in these traits as a result of natural variations in peat depth and anthropogenic variations in disturbance regime were investigated in order to further the understanding of orangutan and gibbon ecology and aid in their conservation. 2

3.1.3 Identification traits 3

The high diversity of tropical forest trees makes identification of species difficult, often resulting in the reliance on a few experts in the field. Furthermore, many peat swamp forest species have not yet been fully scientifically described and identification guides are lacking (Graham et al., 2007). Measurements of distinguishing traits were therefore collected which would aid in future species identification and provide more complete descriptions of these species of trees. 4

Traits which can help in identification include bark texture, cambium colour, sap presence, sap flow rate, and sap colour. These traits are not believed to have strong effects on a species ability to cope with physical conditions, but are easily recognized and often distinctive. Distinct canopy shape and leaf traits 5

of some species may also help in species identification. The measurements of these traits were therefore also included in this study.

3.1.4 Species Traits Research Goals

Adaptive tree traits were measured to assess how natural changes in peat depth and anthropogenic changes in level of disturbance alter traits of the most successful tree species in order to increase the understanding of the ecology of tropical peat swamp forest trees and develop a method of trait-based habitat quality monitoring to improve and simplify monitoring of peat swamp forest. Changes in tree traits influence species which rely upon the trees, and so possible impacts of the alterations in tree traits on communities of orangutans and gibbons were explored to better understand their response to natural and man-made changes in the forest to aid in their conservation. Finally, to assist in future research conducted at LAHG, easily identifiable traits of trees were collected to assist in future tree identification and lessen the need for expert knowledge.

3.1.5 Species Traits Predictions

3.1.5.1 Adaptive Trait Predictions

At least some adaptive traits were expected to be influenced by distance from the river and disturbance. Because adaptive traits were thought to influence a species ability to cope with its environment, and changes in peat depth and disturbance alter physical conditions, these were expected to lead to changes in the prevalence of certain traits.

Traits expected to be influenced by distance from the river and thus peat depth were root traits, including proportion of trees with aerial roots and rootlets, and the number, height, spread, and circumference of aerial roots. It was predicted that the value of these traits would increase with distance from the river as the result of greater instability associated with deeper peat layers.

Traits expected to be influenced by disturbance included size traits, including diameter, basal area, and height. These were expected to be reduced as a result of disturbance due to the removal of larger trees and replacement by young trees.

3.1.5.2 Primate Trait Predictions

It was unsure how primate traits may be affected by river distance or disturbance. However, many tree traits which influence use by orangutans and gibbons are also those which influence the adaptive ability of trees, such as root, size, phenology, and reproductive traits. Therefore, any change in these traits as a result of disturbance or peat depth will influence the primates which use them.

3.1.5.3 Identification Trait Predictions

No effects of distance or disturbance were expected from most identification traits, such as bark and sap traits, as these were not thought to have a strong influence on the success of a species.

3.2 Methods¹

3.2.1 Trait Measurements²

Trait measurements were collected for the dominant species in each plot,³ defined as the five most abundant species. For each species, 15 healthy adult individuals were sampled. Due to low abundances of some trees, measured trees were not necessarily located in the plot in which they were dominant, but these were taken to be representative of the species and largely unaffected by location. Twenty-seven traits were measured for each tree. Each trait fell into 8 general types: roots (7 traits), size (3 traits), bark (3 traits), leaves (4 traits), sap (4 traits), and growth (2 traits). Additional traits relating phenology (2 traits), and reproduction (2 traits) were compiled from data collected previously by OuTrop (unpublished) and Harrison (2009). Each trait was categorized as an adaptive trait (A), meaning a trait which influences tree survival, primate use trait (P), meaning a trait which influences primate behaviour or ecology, or identification trait (I) which aid in tree species identification. The sampled traits and their purpose are summarized in Table 8.

Table 8: Traits determined for each tree, and whether purpose was as an adaptive (A),¹ primate use (P), or identification (I) trait.

Trait Category	Measurements	Purpose	Source
Roots	Type (stilted, buttressed, normal)	A, P, I	This study
	Number	A, P	
	Height (cm)	A, P	
	Spread (cm)	A, P	
	Circumference of largest (cm)	A, P	
	Pneumatophore Presence	A, P	
	Rootlet presence	A, P	
Size	Height (m)	A, P	
	Diameter at breast height (cm)	A, P	
	Basal diameter (cm)	A, P	
Bark	Thickness (mm)	A, I	
	Texture	I	
	Cambium colour	I	
Sap	Presence	P, I	
	Flow rate (cm/min)	P, I	
	Colour	I	
	Stickiness	P	
Leaves	Length	A, I	
	Width	A, I	
	Area	A, I	
	Shape (LWR)	A, I	
Growth	Whether on hummock	A	
	Canopy shape	A, P, I	
Reproduction	Number of seeds per fruit	A	Harrison, 2009 Outrop, unpublished
	Animal dispersed (Fruit production)	A, P	
Phenology	Fruiting regularity	A, P	
	Months of fruiting	A, P	

3.2.2.1 Root traits³

The type of root system of each individual tree was recorded as stilted,⁴ buttressed, or normal if no aerial roots were present. For those with aerial roots, the number of roots was recorded, defined as the number of separate bifurcations which fully penetrated the soil. Height above ground of the tallest aerial root, circumference of the largest aerial root, and spread of aerial roots were recorded to the nearest centimeter using a flexible measuring tape (Figure 9), including only those roots which fully entered the soil. The presence of

rootlets, aerial roots which had not yet entered the soil, was recorded, as was the presence of pneumatophores.

3.2.2.2 Size traits²

Tree height was determined with the use of a clinometer. Circumference at breast height at 1.3 m and basal circumference were measured to the nearest centimeter using a flexible measuring tape. For those species with aerial roots, basal circumference was recorded above the tallest root and circumference at breast height 1.3 m above that (Figure 9). Diameter at breast height and basal diameter were calculated from circumference.

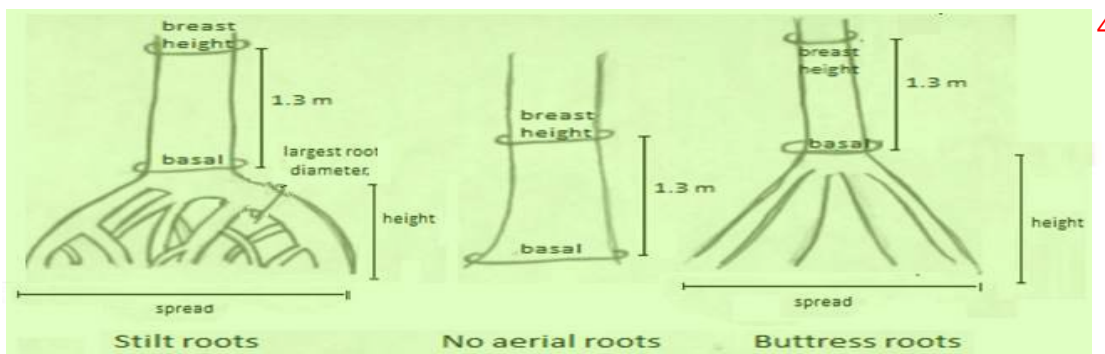


Figure 9: Diagram of root and diameter trait measurements recorded for trees with stilt, normal, and buttress roots, including circumference at breast height, basal circumference, and type, number, largest circumference, height, and spread of aerial roots.

3.2.2.3 Bark traits⁶

Bark texture was recorded subjectively as smooth, rough, ridged, flakey, or spongy. A 10 cm cut on a 45° angle was made in the bark to record cambium colour and measure bark thickness to the nearest millimeter using manual calipers.

For two species which produce burning, poisonous sap (Mertibu, Medang)¹
 2) bark thickness was not measured to avoid skin irritation during sampling.
 These species were excluded from plot averages for bark thickness.

3.2.2.4 Sap traits²

The 10 cm cut on a 45° angle was also used to determine whether sap³
 was present. For those species with sap, flow rate was determined by measuring
 the distance sap travelled from the cut in five minutes using a flexible measuring
 tape, and from this calculating a cm/minute flow rate. Sap colour and stickiness
 on a scale of 1 (not sticky) to 3 (very sticky) were recorded.

The species which produce poisonous sap were not measured and were⁴
 excluded from plot averages for sap traits.

3.2.2.5 Growth traits⁵

It was recorded whether each tree was growing on a hummock, hollow, or⁶
 flat ground, and canopy shape was recorded based on tree canopy classification
 diagrams developed by OuTrop (OuTrop, unpublished; Figure 10).

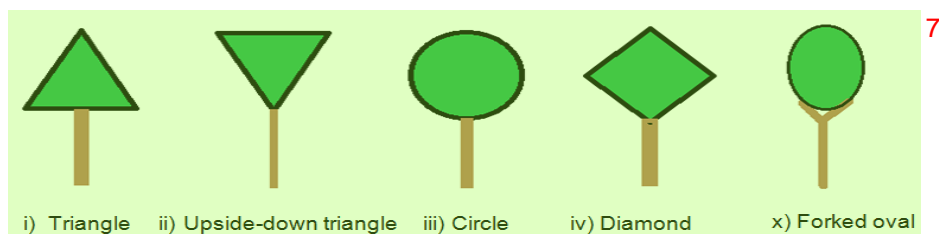


Figure 10: Diagram of canopy shape classification.⁸

3.2.2.6 Leaf traits¹

Fifteen leaves from each individual tree were collected by climbing and manually collecting, using a catapult to either shoot leaves down or to hook a rope over a branch so that leaves could be shaken off, or by using large branches from the ground to shake leaves down. Only adult leaves in good condition were collected. Each leaf was pressed overnight and a digital image taken (Fuji FinePix S200 EXR). Length, width, and area were determined using ImageJ computer software. A ratio of leaf length to width was calculated to determine approximate shape of leaves, with values closer to 1 representing rounder leaves.

3.2.2.7 Phenology and Reproductive Traits³

Data were provided for traits relating to phenology and reproduction (OuTrop, unpublished; Harrison, 2009). Long-term phenology plots have been established in the LAHG and data collected monthly since 2005 regarding regularity and timing of fruiting, as well as dispersal method (OuTrop, unpublished data). Past studies on orangutan diet have collected data regarding fruit size and number of seeds per fruit (Harrison, 2009). Because data for phenology and reproductive traits were provided from other sources rather than collected in this study, data were not available for all species. For two species (Belawan merah, Tabaras akar tinggi) it was unknown whether they bear fruit. For two species which bear fruit, data on number of seeds per fruit were not available (Mahadingan, Kemuning putih, Kenari). For three species (Kemuning

putih, Bintan peter, Mahadingan) phenology data were not available. These species were excluded from plot averages for those traits. Long-term phenology data were used to categorize each species as fruiting regularly with a set schedule, frequently but not on a regular schedule, or irregularly and infrequently (OuTrop, unpublished).

3.2.3 Plot Averages²

Data from all sources were compiled along with data collected in the field to form a comprehensive collection of 27 traits for each species. For each measured trait, a species average was found by taking the average of the 15 sampled trees. Plot averages for each trait were determined using a weighted average according to the proportion each species made of the dominant species. For any trees for which a measurement was not attained, that value was excluded from calculation of the species average.

3.2.4 Statistical Analysis⁴

A principal components analysis was used to compare each plot in terms of adaptive traits and primate traits (Table 8). A general linear model was used to assess whether there was an effect of distance from the river or level of disturbance on the plot averages of each trait. Patterns were deemed statistically significant based on an alpha value of 0.5. The power of these statistical analyses was extremely low, with only 6 plots, and thus trends were discussed

up to an alpha value of 0.2. All statistical analyses were performed using Minitab¹ or SYSTAT software.

3.3 Results²

3.3.1 Dominant Species³

Because of equal abundances of some of the most abundant species, up⁴ to eight species were sampled in some plots (Table 9). Twenty-three species in total were sampled between the six plots. The scientific and local names of these can be found in the Appendix (Table A1). Ten species were dominant in more than one plot, and two species were dominant in more than two plots. In all plots except the edge plot (HD 1.0) there was overlap in the dominant species.

Table 9: Dominant tree species and density in each plot. *Species is dominant in two plots **Species is dominant in more than two plots

Plot	Dominance Rank	Species Code	Density (per m ²)
HD 1.0	1	BM	0.044
	2	Gg	0.024
	3	T	0.017
	4	BP	0.013
	5	Mh	0.012
LD 1.4	1	MS**	0.014
	2	NG*	0.009
	3	Mk	0.008
	4	RH*	0.006
	5	BRM	0.005
	5	Jj**	0.005
	5	Mb*	0.005
	5	Tb*	0.005
LD 1.8	1	Tb*	0.012
	2	MDB*	0.009
	3	PP*	0.009
	4	JK	0.007
	5	K*	0.007
	5	M2*	0.007
HD 1.8	1	PB	0.017
	2	MS**	0.016
	3	RH*	0.013
	4	M2*	0.011
	5	JBB	0.010
LD 3.0	1	Hk	0.017
	2	Jj**	0.015
	3	MS**	0.011
	4	MDB*	0.011
	5	KP	0.009
	5	K*	0.009
HD 3.0	1	NG*	0.113
	2	Jj**	0.073
	3	Mb*	0.063
	4	PP*	0.055
	5	Tbt	0.040

Because of differences in species richness, evenness, and abundance of the dominant trees, the dominant species represented a different proportion of each plot. The edge plot (HD 1.0) had the lowest species evenness and so the

dominant species represented a larger portion (73%) of the plot, while the dominant species represented 29-40% of the other plots (Figure 11).

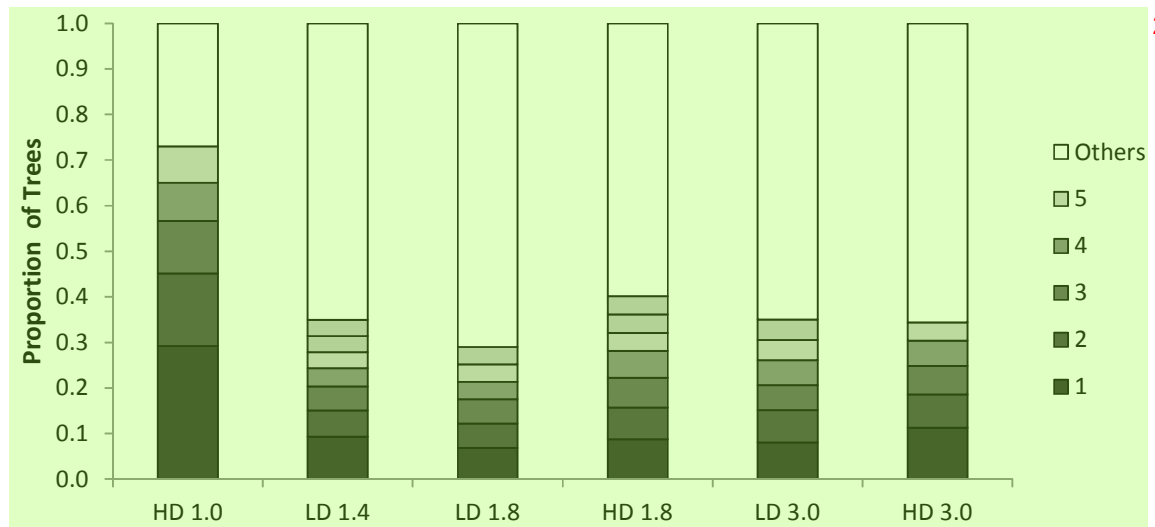


Figure 11: Proportion of total trees that the 'dominant' trees which were sampled make up. 'Others' did not have functional traits measured. Note that because of equivalent abundances, there may have been several species which were the fifth most abundant in the plot.

3.3.2 Adaptive Traits

A principal components analysis of adaptive traits showed that the two interior low disturbance plots (LD 1.8 and LD 3.0) were very similar along both the first and second components, and differed from all other plots along the second component. The other plots tended to cluster together (Figure 12). The traits which contribute most to the first component were root traits, leaf traits, and fruit traits. Trees in low disturbance interior plots (LD 1.9 and LD 3.0) tended to have more and larger aerial roots, more pneumatophores, more elongated leaves, and more trees which produce fruit. The traits which contribute most to

the second component include traits relating to tree size, fruiting regularity, growth location, and bark thickness, with trees in the low disturbance interior plots tending to have larger trees, thinner bark, and more growing on hummocks (Table 10). The first component explains 49.1% of the variance, while the second component explains 27.5% of the variance.

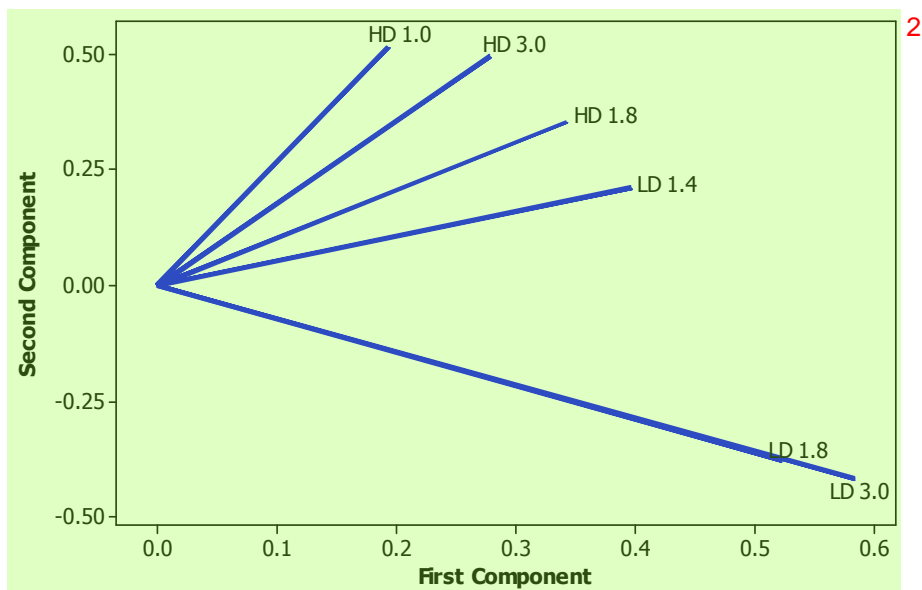


Figure 12: Principal components analysis for adaptive tree traits for the six study plots.

Table 10: Adaptive traits which contribute most to the first two components of principal components analysis and their loadings.

Principal Component 1		Principal Component 2	
Trait	Loading	Trait	Loading
Aerial root height	0.999	Tree diameter at base	0.857
Aerial root spread	0.984	Regular fruiting	0.855
Rootlets	0.957	Hummock growth	0.852
Diameter of largest root	0.957	Tree diameter at breast height	0.843
Number of aerial roots	0.948	Bark thickness	0.760
Pneumatophores	0.923		
Leaf shape	0.870		
Fruit production	0.814		
Leaf width	0.869		
Frequent fruiting	0.769		
Aerial roots	0.752		

3.3.3 Primate Traits

A principal components analysis showed that the interior low disturbance plots (LD 1.8, LD 3.0) were also very similar to each other with regards to primate traits along both the first and second component. All high disturbance plots (HD 1.0, HD 1.8, HD 3.0) were very similar along the second component, and very different from the interior low disturbance plots along the second component (Figure 13). Traits which contributed most to the first component related to aerial roots and fruit production, whereas traits relating to tree size and sap production contributed most to the second component (Table 11). In addition to having a greater prevalence and size of aerial roots, low disturbance interior plots had greater sap production, sap flow, and tree height. The first component accounted for 49.5% of the total variance in the data, while the second component accounted for 28.5% of the total variance.

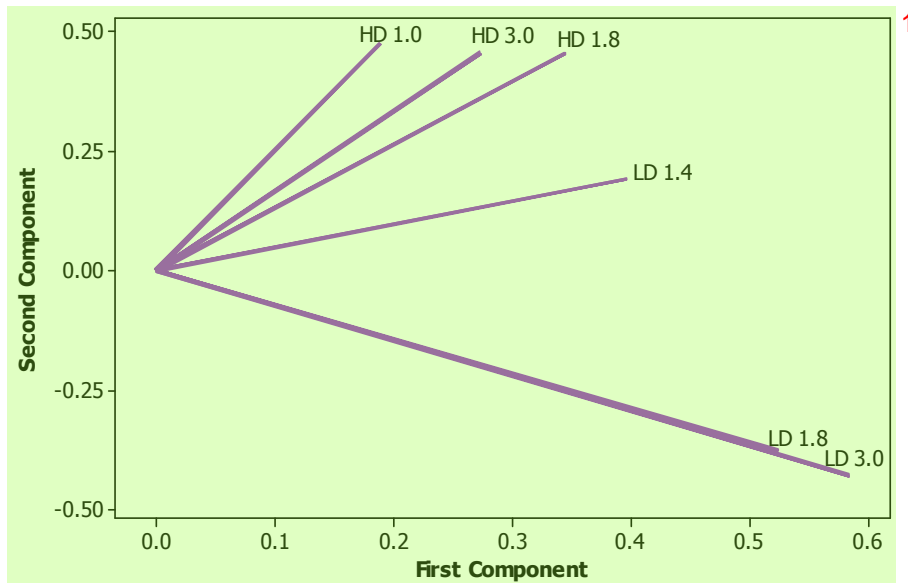


Figure 13: Principal components analysis loading plot for primate tree traits for each plot.

Table 11: Primate traits which contribute most to the first two components of principal components analysis and their loadings.

Principal Component 1		Principal Component 2	
Trait	Loading	Trait	Loading
Aerial root height	0.960	Regular fruiting	-0.978
Aerial root spread	0.948	Sap stickiness	-0.942
Diameter of largest root	0.958	Sap production	-0.751
Pneumatophores	0.914	Tree diameter at breast height	-0.784
Number of aerial roots	0.910	Tree height	-0.635
Sap flow	0.910		
Frequent fruiting	0.814		
Fruit production	0.728		

3.3.4 Individual Traits Analysis

3.3.4.1 Root traits

The effect of disturbance on root traits was also seen in analyses of individual traits (Table 12). Aerial roots in low disturbance plots tended to be more prevalent, numerous, and of greater height, spread, and circumference, and with a greater prevalence of rootlets, compared to high disturbance plots (Figure 14). On average, 78% of dominant trees in low disturbance plots had

aerial roots while in high disturbance plot an average of 39% of dominant trees¹ had aerial roots. Distance from the river had no effect on root traits.

Table 12: Results from general linear models assessing the effects of distance of plot² from the river and level of disturbance on root traits.

Variable	Source	SS	df	F	P	Model R ²
Presence	Distance	0.026	1	0.727	0.456	0.837
	Disturbance	0.213	1	5.877	0.094	
	Error	0.109	3			
Number	Distance	22.344	1	0.828	0.430	0.664
	Disturbance	127.242	1	4.718	0.118	
	Error	80.913	3			
Height	Distance	217.636	1	1.710	0.282	0.808
	Disturbance	1278.975	1	10.048	0.050*	
	Error	381.864	3			
Spread	Distance	430.706	1	430.706	0.221	0.873
	Disturbance	3083.798	1	3083.789	0.026*	
	Error	543.916	3	181.305		
Circumference	Distance	135.686	1	3.039	0.180	0.740
	Disturbance	212.048	1	4.749	0.117	
	Error	133.948	3			
Rootlets	Distance	0.017	1	1.364	0.327	0.816
	Disturbance	0.053	1	4.130	0.135	
	Error	0.038	3			

*P > 0.05⁴

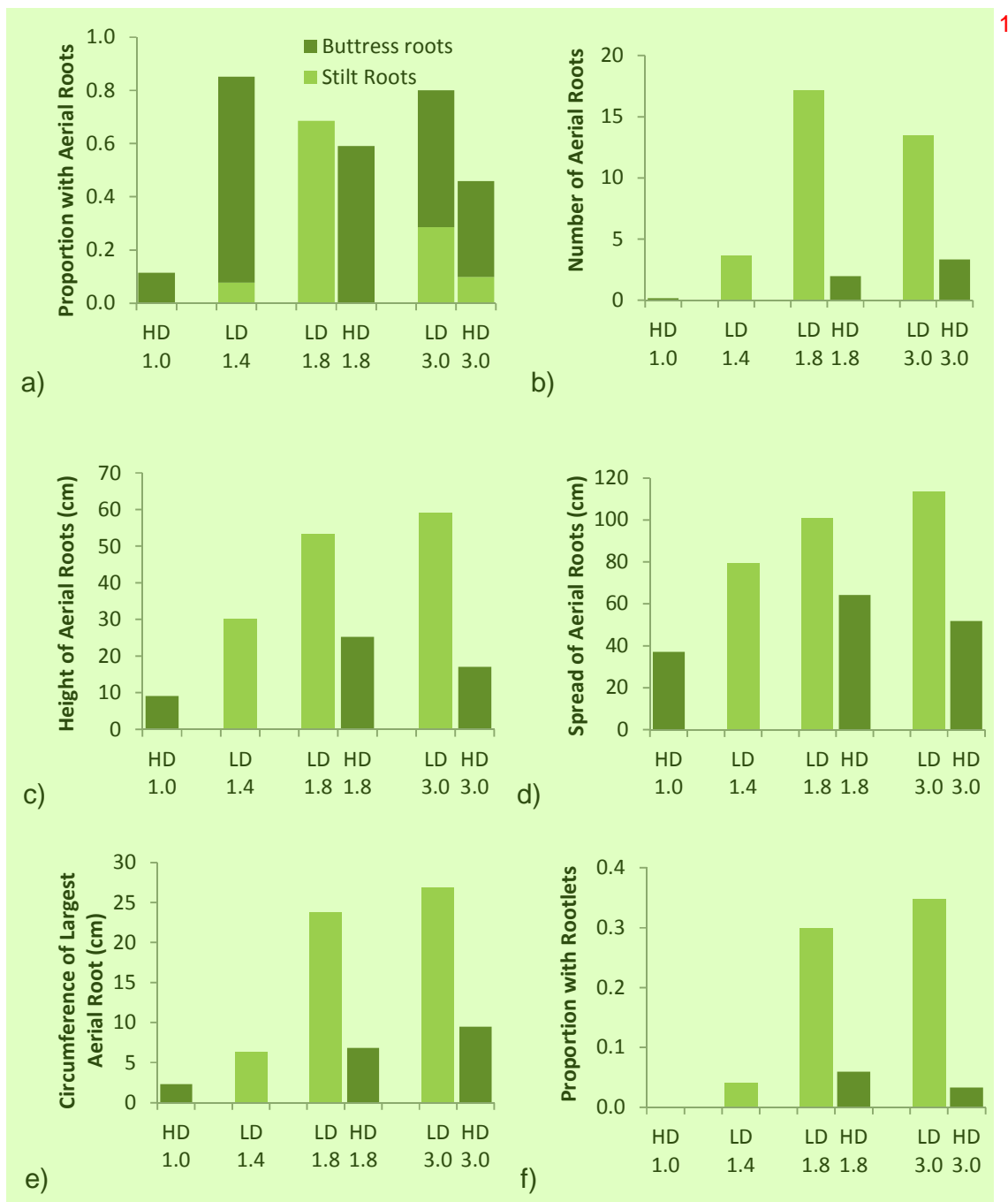


Figure 14: Average root trait values for each plot, including (a) proportion of dominant trees with aerial roots, (b) number of aerial roots, (c) height (cm) of aerial roots, (d) spread (cm) of aerial roots, (e) circumference (cm) of largest aerial roots, (f) proportion of trees with rootlets. All plots were are equal distance from the river and thus assumed to have been similar prior to disturbance are grouped together. For b-f, high disturbance plots are shaded darker than low disturbance plots.

Pneumatophores were common in both interior LD plots, present for approximately one-third of all dominant trees, but absent from all other plots (Figure 15). Statistical support for an effect of disturbance was weak ($P=0.168$), however, and there was no effect of distance ($P=0.502$) (Table 13).

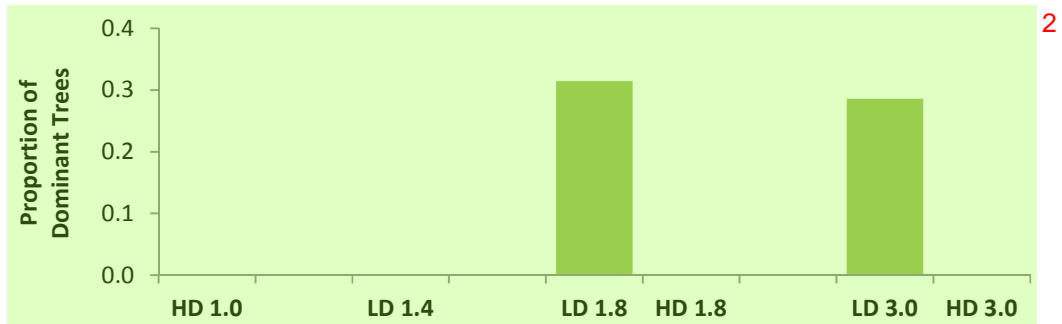


Figure 15: Proportion of dominant trees in each plot which possessed pneumatophores.

Table 13: Results from a general linear model assessing the effects of distance of plot from the river and level of disturbance on the presence of pneumatophores.

Source	SS	df	F	P	Model R^2
Distance	0.010	1	0.578	0.502	0.579
Disturbance	0.055	1	3.278	0.168	
Error	0.051	3			

3.3.4.2 Phenology and Reproductive Traits

Phenology and reproductive traits had large contributions to both the first and second components of principal components analysis for adaptive and primate traits. The proportion of dominant trees which produce fruit (animal dispersed) was significantly affected by disturbance ($P=0.012$) (Table 14). Low disturbance plots had, on average, 65% of dominant trees producing fruit while high disturbance plots had 37% of dominant trees that produce fruit (Figure 16). Fruit availability, the number of months in a year where at least one of the

dominant species in the plot was predictably fruiting, ranged from a low of 3 months (HD 3.0) to a high of 10 months (HD 1.8), but was not related to disturbance ($P=0.439$), and either was the proportion of trees fruiting predictably or frequently (Figure 17, Table 14). Distance from the river had no effect on any fruit traits (Table 14).

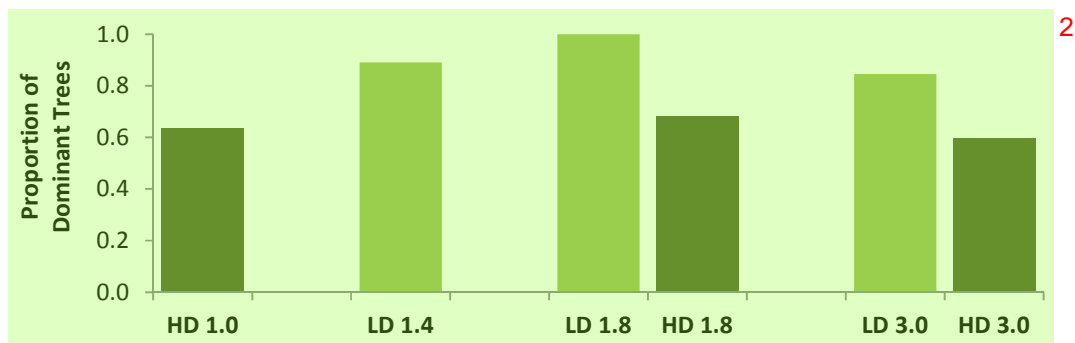


Figure 16: Proportion of the dominant trees which produce fruit in each plot. High disturbance (HD) plots are shaded dark while low disturbance (LD) plots are lighter. Plots which are of equal distance from the river and therefore assumed to have been similar prior to disturbance are grouped together.

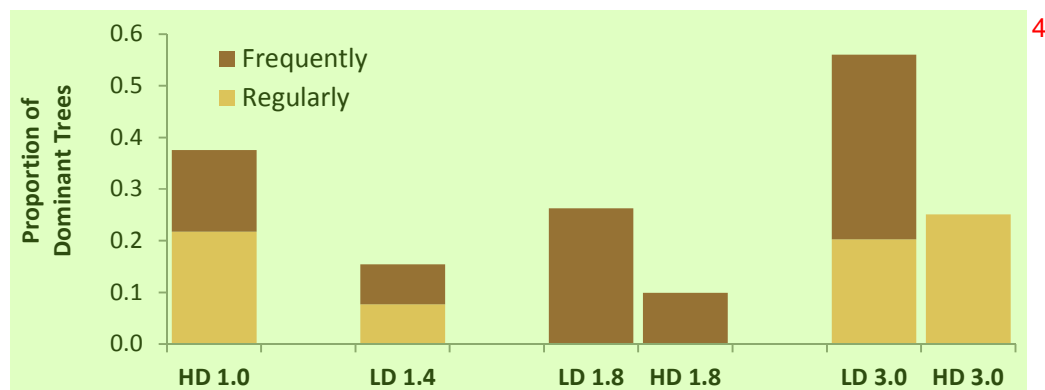


Figure 17: Proportion of dominant trees in each plot that fruit regularly (light shading) or not regularly but frequently (dark shading). All other fruiting trees produced fruit infrequently and unpredictably. Plots which are of equal distance from the river and therefore assumed to have been similar prior to disturbance are grouped together.

Table 14: Results from general linear models testing the effect of distance from the river and level of disturbance on the proportion of trees that produce fruit and the number of months in a year when fruit is regularly available.

Variable	Source	SS	df	F	P	Model R^2
Fruit production	Distance	0.004	1	1.083	0.374	0.908
	Disturbance	0.116	1	29.311	0.012	
	Error	0.012	3			
Fruit availability	Distance	2.297	1	0.275	0.636	0.249
	Disturbance	6.622	1	0.794	0.439	
	Error	25.036	3			

3.3.4.3 Leaf measurements

Leaf traits had a large contribution to the first component for principal components analysis of adaptive traits. Leaf area was not significantly affected by level of disturbance ($P=0.889$) (Table 15). Leaf length and width were similarly not affected (data not shown). However, leaves in high disturbance plots were significantly rounder (the ratio of length to width closer to a value of 1) than leaves in low disturbance plots ($P=0.003$) (Figure 18). Distance from the river had no effect on leaf traits (Table 15).

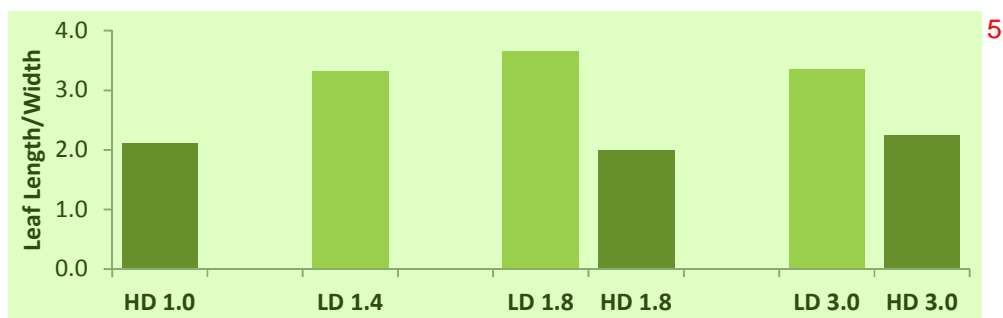


Figure 18: Average shape of leaves (leaf length/width) for each plot. High disturbance (HD) plots are shaded dark while low disturbance (LD) plots are lighter. Plots which are of equal distance from the river and therefore assumed to have been similar prior to disturbance are grouped together.

Table 15: Results from a general linear model assessing the effects of distance of plot from the river and level of disturbance on sap traits.

Variable	Source	SS	df	F	P	Model R^2
Leaf area	Distance	64.772	1	0.796	0.438	0.221
	Disturbance	1.888	1	0.023	0.889	
	Error	244.061	3			
Leaf shape	Distance	.0004	1	0.129	0.744	0.966
	Disturbance	2.598	1	83.641	0.003**	
	Error	0.093	3			

3.3.4.4 Sap measurements

Sap traits had a high contribution to the second component of the principal components analysis for primate traits. Trees in interior plots were more likely to produce sap ($P=0.068$), but there was no effect of disturbance ($P=0.918$). Sap colour and stickiness were not affected by disturbance or distance from the river (Figure 19, Table 16). For those species which did produce sap, the rate of sap flow significantly increased with distance ($P=0.035$) and tended to decrease with disturbance ($P=0.064$) (Figure 20). All species in HD 1.0 and HD 1.8 which produced sap had very viscous sap which had flow rates of 0 cm/min, with sap often not apparent until cuts were inspected the following day.

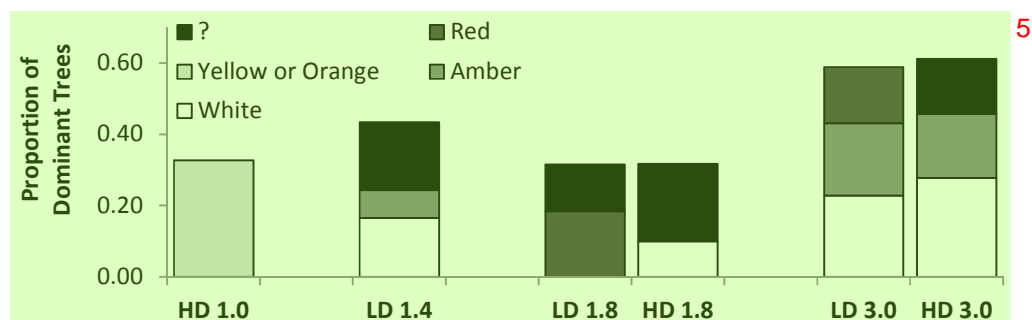


Figure 19: Proportion of trees in each plot that produce sap, and the colour of sap produced. Plots which are of equal distance from the river and therefore assumed to have been similar prior to disturbance are grouped together. A question mark indicates poisonous sap for which the colour could not be determined.

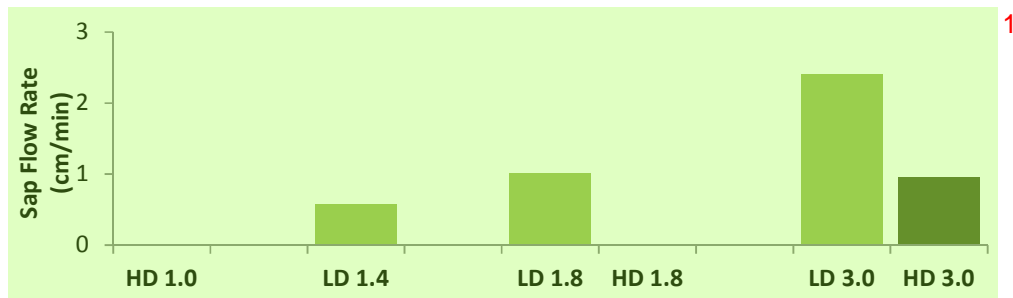


Figure 20: Average rate of sap flow (cm) from sap-producing trees from a 10 cm cut into the bark on a 45° angle. High disturbance (HD) plots are shaded dark while low disturbance (LD) plots are lighter. Plots which are of equal distance from the river and therefore assumed to have been similar prior to disturbance are grouped together.

Table 16: Results from a general linear model assessing the effects of distance of plot from the river and level of disturbance on sap traits.

Variable	Source	SS	df	F	P	Model R ²
Sap presence	Distance	0.068	1	7.807	0.068	0.726
	Disturbance	0.000	1	0.012	0.918	
	Error	0.026	3			
Sap flow rate	Distance	2.004	1	13.548	0.035	0.888
	Disturbance	1.226	1	8.287	0.064	
	Error	0.444	3			
Sap stickiness	Distance	0.323	1	2.273	0.271	0.592
	Disturbance	0.103	1	0.724	0.484	
	Error	0.284	3			

3.4 Discussion

3.4.1 Dominant Species

Some species were found only in one plot, and so may be specialists to that type of habitat. In particular, the dominant species in the edge plot (HD 1.0) were dominant in only this plot and so may specialize to edge conditions (Marchant, 2012), supporting the proposition that hostile edge habitat requires species specially adapted to those conditions (Section 2.4.3). Other species were

more common, dominant in several plots and so may be generalists to interior conditions (e.g. Jinjit, Meranti semut, Tabaras akar tinggi; Marchant, 2012).¹

3.4.2 Adaptive Traits²

Traits believed to influence a species ability to cope with current conditions and competitive ability included those relating to roots, size, growth, leaves, bark, and phenology. Tree traits influenced by changes in peat depth as distance from the river increases were investigated to better understand tropical peat swamp forest ecology, and changes as a result of disturbance were investigated to better understand how the forest adapts in response and to develop a trait-based monitoring system.³

No adaptive traits were significantly affected by distance. It was expected that root traits would increase with distance from the river and peat depth but this was not observed, possibly due to low statistical power. As distance from the river increases, the peat depth and thus instability increases, putting greater selection pressure for traits such as aerial roots which would enhance stability (Goldsmith and Zahawi, 2007; Yule 2010). The only traits significantly influenced by distance from the river were sap traits, with the proportion of trees which produced sap and the flow rate of sap increasing with distance. These results were not expected, as sap traits are not thought to contribute substantially to a species ability to colonize new locations, face competitors, or cope with physical conditions.⁴

The principal components analysis showed clear divisions between plots¹ according to disturbance, with both components showing a clear progression from plots with the lowest severity of disturbance (LD 3.0 and LD 1.8) to the greatest (HD 1.0). Analyses of individual traits showed similar patterns, with effects of disturbance on root traits, fruit production, and leaf shape. Disturbance therefore alters physical conditions, causing different species traits to dominate.

3.4.2.2 Traits Influenced by Disturbance: Trait-Based Habitat Quality² monitoring

The development of a trait-based monitoring system requires identification³ of species traits indicative of disturbed or pristine conditions which are easily recognized and easily sampled, with clear distinction in this trait between high and low disturbance areas. Traits which appeared to be affected by disturbance included root traits, size traits, sap production and flow rate, leaf shape, and the proportion of trees which produce fruit. However, not all of these traits are suitable for trait-based monitoring.

Size measurements (diameter at breast height, basal diameter, height) for⁴ the dominant species in each plot followed the trend of decreasing with disturbance, similar to the whole plots (Section 2.3.1). This was as expected as high disturbance plots would have a greater proportion of younger, smaller trees (Marchant, 2012). However, the monitoring of size traits to assess disturbance would require measurement of all trees. This would be time-consuming, particularly for tree height, and the distinction between high and low disturbance

plots is not clear. Size measurements are therefore not optimal traits for trait-based monitoring. ¹

High disturbance plots had significantly rounder leaves than low disturbance plots. Size and shape influence leaf function through energy balance, gas exchange, and supply and support of leaf tissue, and therefore optimum leaf shape likely varies according to environment (Winn, 1999). Leaf shape, however, is difficult to assess from the ground, and removing leaves from the canopy is extremely difficult (pers. obs.). The distinction between a leaf that is round and one which is not would be subjective and arbitrary unless measuring. Leaf shape monitoring is therefore not a suitable method for assessing disturbance. ²

The proportion of trees which produce fruit was significantly decreased in disturbed plots. Species rely on various dispersal vectors for spreading seeds. Animal ingestion of fruit bearing seeds is a common method of seed dispersal (Richards, 1996; Webb and Peart, 2001). Species which do not produce fruit must rely on other dispersal methods such as wind (Webb and Peart, 2001). Primates, gibbons in particular, are among the most important seed dispersers in the forests they are found (McConkey and Chivers, 2006). If animals are driven from a location as a result of disturbance (MacKinnon, 1974; Felton et al., 2003), there may be reduced establishment of fruit-bearing trees as a result of the lack of dispersal vectors, leading to a higher proportion of trees which disperse by other methods and thus do not produce fleshy fruit (Webb and Peart, 2001). This ³

may explain why disturbed plots had a lower proportion of animal dispersed fruit-bearing trees. For example, the removal of large seed-dispersing primates due to bushmeat hunting in the Amazon resulted in reduced recruitment of particular tree species, even in the lack of any other form of disturbance (Nunes-Iturri and Howe, 2007). Monitoring the proportion of trees which produce fruit, however, would not be a suitable method of trait-based monitoring because fruit is only produced at certain times of the year (OuTrop, unpublished), and only once a tree has reached maturity (Dawson et al., 2001). ¹

Sap traits were not expected to be influenced by peat depth or disturbance ² as these were collected as primate and identification traits. However, the proportion of trees that produce sap and the rate of sap flow were significantly decreased with disturbance. Incorporating sap monitoring into trait-based surveying would require cutting each tree and recording sap presence and flow rate. This would be time-consuming and, therefore, sap traits are not suitable for trait-based monitoring. In addition, because some species produce an irritating sap, some degree of species identification would be required to avoid discomfort during sampling.

Disturbance significantly reduced the spread and height of aerial roots, ³ and may have resulted in a decrease in the proportion of trees with aerial roots and the number of aerial roots per tree. Aerial roots are an adaptation to the unstable soil (Richards, 1996), an issue which may be particularly salient for climax species which may persist for a long time (Swaine and Whitmore, 1988).

Colonizing species are expected to invest more in rapid establishment and growth than traits which would allow long-term persistence (Swaine and Whitmore, 1988), possibly explaining why secondary forest in high disturbance plots had a lower prevalence and size of aerial roots compared to low disturbance plots. Aerial root sampling could be incorporated into monitoring programs as they are easy to identify, though because aerial roots were present in disturbed locations and may require measurements of size and number, this could be time-consuming.

Pneumatophores were common in both interior low disturbance plots (LD 1.8 and LD 3.0), exhibited by approximately a third of the dominant trees, and absent from all other plots. A high prevalence and commonness of pneumatophores may, therefore, be indicative of interior mixed swamp forest which has experienced low levels of disturbance. There was not a statistically significant effect of disturbance on pneumatophores since pneumatophores were not present in LD 1.4. This may support the proposition that LD 1.4 may be better characterized as having experienced an intermediate level of disturbance (Section 2.4.3).

Pneumatophores are adaptations to the swampy conditions characteristic of pristine peat swamp forests (Wosten et al., 2006). Hydrological conditions easily become disrupted by disturbance (Wosten et al., 2006), such that this trait may no longer be selected for in highly disturbed areas. Species which colonize gaps left after logging, burning, or tree falling from drainage are those which grow

rapidly (Finegan, 1986), investing energy primarily into vertical growth until established in the canopy (Yamada et al., 2001). Like aerial roots, pneumatophores may be costly structures which species that put all resources into rapid growth would likely lack. Pneumatophores appear to only be a trait of climax community in this forest. The lack of pneumatophores at the drained plot (HD 3.0) may be the result of a bias toward the felling of species with this trait. Gibson (2005) suggested that trees with pneumatophores may be less stable than trees without, though it is unclear why this may be.

Pneumatophores are easily recognized so little training would be required to monitor this trait, and trees would not need to be manipulated or anything removed for sampling. A single tree can produce numerous pneumatophores and can be present at considerable distances from the trunk (pers. obs.) and so, when present, pneumatophores may be fairly abundant. These characteristics make pneumatophores a good trait to incorporate into monitoring programs. If this trait is only found only in climax communities in low disturbance conditions, surveying of species composition to determine whether disturbance has occurred would be unnecessary as the simple survey of whether pneumatophores are common may yield similar results. An area of mixed swamp forest which does not have abundant pneumatophores may indicate the area has experienced disturbance and is comprised of secondary forest. An increase in the prevalence of this trait over time may suggest the area is recovering.

Further research is required to determine whether pneumatophores are indicative of pristine mixed swamp forest conditions and applicable to other forests.

To the authors knowledge, this is the first time that traits have been used in this way to indicate disturbance in rainforests. Trait-based monitoring will allow fast and inexpensive determination of whether an area has likely experienced disturbance and monitor the recovery or degradation of an area over time, allowing inferences to be made as to effects on flora and fauna in the forest, carbon release, and impacts on surrounding ecosystems without requiring taxonomic expertise.

3.4.3 Primate Traits

Orangutans and gibbons in the Sabangau catchment rely on the trees for nearly all aspects of life, including feeding, travel, and sleeping. Several studies have found decreased densities and altered behavior of orangutans (MacKinnon, 1974; Rao and van Shaik, 1997; Felton et al., 2003; Morrough-Bernard et al., 2003) and gibbons (Nijman, 2001; Cheyne et al., 2013) as a result of disturbance. This study aimed to identify the precise mechanisms of this by investigating changes in tree traits which influence primate use. A principal components analysis of primate traits showed a clear distinction between the high disturbance plots and the interior low disturbance interior plots, with LD 1.4 intermediary. The first component, contributed to most by root traits, fruit

production, and sap flow, showed a clear progression with severity of disturbance. The second component, which included fruiting regularity, sap production and stickiness, and tree diameter and height, showed a distinction between the high disturbance and low disturbance plots. Any change in the prevalence or value of traits used by these primates will result in changes in their behavior which may have negative consequences.

3.4.3.1 Feeding Traits²

Fruiting traits are of critical importance to both orangutans and gibbons, as fruit comprises the majority of their diets (Galdikas, 1988; Conklin-Brittain et al., 2001). Food availability is correlated with gibbon (Hamard et al., 2010) and orangutan (Felton et al., 2003) densities. In a principal components analysis, fruiting traits showed a progression relating to disturbance severity, showing that the proportion of trees which produce fruit and the regularity and frequency of fruiting is influenced by anthropogenic disturbance. General linear models showed that the proportion of dominant trees which produce fruit was decreased in high disturbance plots. This is similar to findings by Felton et al. (2003). Furthermore, the average size of trees in high disturbance plots was decreased, and so, because crop yield of a tree is correlated with diameter with larger trees producing more fruit (Chapman et al., 1992), trees in high disturbance plots which do produce fruit may produce a smaller amount. Orangutans maximize foraging efficiency by showing a preference of foraging in the largest fruit trees (Felton et al., 2003), with a strong preference for trees above 50 cm diameter at breast height found in one study (Wich et al., 2002). Gibbons show a similar

preference for large fruit trees (Cheyne et al., 2013), yet this is the category of trees decreased by logging and drainage and absent from the edge (Section 2.3.2; Marchant, 2012). Furthermore, trees may take many years to mature and be able to produce fruit (Dawson et al., 2001), and so the change in age structure resulting in the removal of mature trees and replacement by immature trees may also decrease fruit availability. Decreases in food availability may result in increases in home range size and subsequent decreases in density (Singleton and van Schaik, 2001).

The regularity and frequency of fruiting may also be altered as a result of disturbance. Tree species were categorized as fruiting regularly on a predictable schedule, frequently but not predictably, or irregularly and infrequently (OuTrop, unpublished). Fruiting frequency is important as trees which produce fruit frequently will have fruit available more often throughout the year, while regularity is important because it allows apes to predict when fruit will be available (Vasey, 1991), thus maximizing foraging efficiency. Because trees which are currently fruiting can be widely distributed, searching the forest for fruit without prior knowledge of where fruit may be is an inefficient strategy, especially because this constantly changes throughout the year. Orangutans and other great apes are known to produce mental maps of the forest, capable of not only remembering where specific fruit trees are, but also when they fruit and the most efficient route to them (Vasey, 1991). This, however, is only possible if the tree fruits regularly or frequently. Disturbed plots had an increased proportion of trees which fruited irregularly. For these trees, it would not be known when they fruit without

checking, which is highly inefficient. It is conceivable that gibbons produce mental maps in a similar fashion. Without this capability, the apes would be in danger of expending too much energy while searching for food (Vasey, 1991). Together these trait changes suggest that apes may be negatively affected by disturbance as a result of the reduction in fruit availability and predictability. ¹

3.4.3.2 Size traits ²

Plot averages for tree height and diameter of dominant trees tended to decrease with disturbance. Similar trends were observed for average diameter of all trees in the plot (Section 2.3.1). Gibbons are particularly influenced by reductions in height of trees due to their preference of singing (Whitten, 1982; Reichard, 1998), sleeping (Reichard, 1998), and travelling (Cannon and Leighton, 1994; Cheyne et al., 2013) in the tallest trees. ³

Gibbons are monogamous territorial apes, living in small family groups which sing at dawn to delineate and defend their territory (Whitten, 1982), often involving counter-singing between groups. Home range sizes are large (Singleton & van Schaik, 2001), and so gibbon songs must be loud to be heard by other groups, and may be heard from more than a kilometer away (Whitten, 1982). Height above the ground increases long-distance sound transmission in forest, and so the tallest trees, typically emergents, are selected for singing (Whitten, 1982; Reichard, 1998). A reduction in the height of trees may reduce ⁴

sound transmission and result in increased inter-group conflict due to a lack of effective communication between groups. ¹

Gibbons, particularly females with infants and juveniles, sleep in the largest available trees, presumably as an anti-predator adaptation (Reichard, 1998). Reichard (1998) found gibbons mostly slept in trees above 25 m, averaging 32 m, with individuals in the tree mostly above 20 m. The reduction in tree height observed in this study as a result of disturbance may therefore increase detection of gibbons by predators while sleeping. ²

Gibbons prefer to travel through trees greater than 21 m in height at Sabangau, possibly because larger trees are more likely to have a continuous canopy (Cheyne et al., 2013). Canopy continuity affects orangutans as well (Felton et al., 2003). Travel requires a considerable amount of energy, and so gibbons and orangutans have evolved to travel in the most energetically-efficient way through the canopy (Cannon and Leighton, 1994; Felton et al., 2003; Cheyne et al., 2013). Canopy discontinuity from decreased tree size or fallen trees can disrupt travel efficiency. When confronted with a gap in the canopy, orangutans and gibbons must either travel a longer distance to go around the gap (Cheyne et al., 2013), or orangutans may descend to travel on ground (Felton et al., 2003). More energy must be spent to traverse a forest with more canopy gaps than if it were continuous, and there may also be an increased risk of falling (Felton et al., 2003). Greater energy demands of locomotion have been found in orangutans in disturbed Sumatran forests (Rao and van Shaik, 1997), ³

and selective logging has been shown to have altered gibbon locomotion in Sabangau (Cheyne et al., 2013). The reduction in tree size as a result of disturbance may, therefore, result in greater energy expenditure during travel.

3.4.3.3 Orangutan Nesting Traits

Orangutans build nests for sleeping, building a new nest each night (Sugardjito, 1986). Orangutans prefer to nest in buttressed trees, though also often nest in stilted trees (Gibson, 2005). The decrease in the proportion of trees with aerial roots and size of aerial roots in high disturbance plots may result in there being fewer suitable nesting trees at disturbed sites. This, coupled with the reduced average size of trees, may make trees less stable and able to support orangutan weight. If strong trees are not available, orangutans may tie together several trees when building nests (Gibson, 2005). This change in behaviour may require more energy and time than building a platform from a single tree, increasing energy demands and decreasing time available for foraging. If the availability of nesting trees is reduced, they may also be more likely to reuse nesting trees, which could increase parasite loads (Reichard, 1998). This was observed in the Mega Rice Project where multiple orangutan nests were observed in a single tree (pers. obs.).

Unlike gibbons which prefer to sleep in the tallest trees, orangutans of different sex and age classes in Sabangau use different heights for sleeping, presumably as a result of differential vulnerability to predators and conspecifics (Sugardito, 1986; Gibson, 2005). Orangutans also prefer different diameters and

canopy shape for nesting trees according to sex and age (Gibson, 2005).¹
Subordinate individuals in the population, females and adolescents, prefer larger and taller trees (Gibson, 2005). This suggests that perhaps a high degree of diversity in tree species may be preferable so that orangutans of all age and sex can exhibit their preferences.

Orangutans avoid nesting in trees which produce sap to avoid getting it on their fur, almost never nesting in trees that produce sap (Gibson, 2005; Malone, 2012). This study found that the proportion of trees producing sap and the flow rate of sap was significantly decreased by disturbance, so this may mitigate the changes in tree size and stability.²

Aside from the changes in sap traits, all changes in primate traits as a result of disturbance would have negative consequences, possibly providing the mechanism by which disturbance in tropical peat swamp forests leads to reductions in densities of orangutans and gibbons.³

3.4.4 Identification Traits⁴

Complete descriptions of the traits of the 23 most abundant tree species in the Sabangau catchment mixed swamp forest were collected, including traits which can be easily recognized and used to distinguish species. There were no trends in most traits measured for the purpose of helping in future identification, as was expected as these are not thought to influence a species adaptability or competitive ability, aside from sap traits as discussed previously. It is hoped that⁵

in future traits can be collected for more species so that understanding of this forest at the species level can be increased.

3.4.5 Limitations

Only the most abundant species could be sampled due to time and logistical constraints. These species were taken to be representative of the entire plot, though this may not necessarily be the case. This is not believed to be problematic for adaptive traits since the most successful species should be those best suited to conditions of that location, but may be a source of error for primate traits, as rare species may have disproportionately large impacts on primate use. The sampled fruit traits may not be representative of the plot as a rare species may comprise a large portion of orangutan and gibbon diet, and the dominant species may not be a preferred food. Species which were dispersed by animals were assumed to have comprised part of the ape's diet, though this may not be the case as these species may be dispersed by methods other than ingesting seeds in fruit and may be dispersed by animals other than orangutans or gibbons. Future work could focus on those tree species known to be favored food items for orangutans and gibbons and assess how the distribution and abundance of these changes in different areas of the forest and according to disturbance.

The sampled trees were not necessarily in the plot for which they were taken to be representative of. The sampled traits were assumed to be representative of the species and therefore not greatly influenced by location,

though this may not be the case for all traits. Most categorical traits, such as sap presence or root type, should be consistent regardless of location. Quantitative traits, however, such as height or number of roots, may be more sensitive to location, and so the trees measured for that trait may not perfectly reflect the true value for that plot. However, a species which produces, for example, many aerial roots is expected to do so in different locations, though the exact number may differ. In future it would be ideal to collect tree traits from the plot in which they are meant to represent, which would allow comparisons of traits of the same species in different locations to be compared.

3.4.6 Conclusion²

The traits of the most abundant species of trees in different areas of the forest were influenced by disturbance, though most were not significantly affected by distance from the river. Changes in traits included both adaptive traits and traits which influence primate use. The best trait to incorporate into trait-based monitoring appears to be a high prevalence of pneumatophores to indicate pristine conditions. This trait is easy to recognize, often abundant when present, and would be fast and simple to survey. Further research in other peat swamp forests is required to confirm whether pneumatophores are indicative of pristine conditions. Locations that were highly disturbed had alterations in tree traits which influence primate use, including fruiting patterns, tree size, and root and sap traits, which would likely cause changes in feeding, locomotion, and sleeping behavior of orangutans and gibbons in disturbed forest. This could have negative

impacts such as decreased energy intake, increased energy expenditure, increased vulnerability to predators, increased inter-group conflict, and increased parasite loads. The apes in this forest can act as indicators (Harrison et al., 2005), and so these results may apply to other canopy-dwelling animals in the community which may similarly be influenced by disturbance as a result of changes in tree traits.

Chapter 4: Conclusions¹

Disturbance in peat swamp forest by logging, drainage, and burning may² reduce average tree size and alter species composition, resulting in a reduction in forest vegetation biomass and carbon content. With as nearly 2000 Mg of carbon per hectare stored in low disturbance mixed swamp forest, the degradation of these forests could be catastrophic. Furthermore, forest degradation can have negative impacts on orangutans and gibbons, two endangered and endemic flagship ape species, through the alteration of tree traits they rely on, and would likely have similar effects on other faunal species as well. The protection of these forests should therefore be a priority to preserve the carbon store and biodiversity they contain. Monitoring programs of peat swamp forest habitat quality may incorporate surveying of pneumatophore prevalence to indicate areas of low disturbance, which would greatly decrease the money, time, and expertise required for peat swamp monitoring.

4.2 Limitations³

The greatest limitation of this study was that only six tree plots were used.⁴ Plots at an equal distance from the river were assumed to have been similar prior to disturbance, but due to small-scale variations in nutrient levels, peat chemistry, depth, and hydrology (Page et al., 1999) this may not be the case. Studies which used replicate plots in Bornean dipterocarp forest found that species composition varied between plots before disturbance (Verburg and van Eijk-Bos, 2003), and

so it is likely that pre-disturbance variations existed in plots in Sabangau as well. ¹

Pre-existing differences may have been incorrectly inferred to be a result of different peat depth or disturbance. For example, the lack of pneumatophores at HD 3.0 was assumed to be a result of a loss of species with this structure as a result of disturbance, though it is possible pneumatophores were absent from this location before disturbance.

Different forms of disturbance are likely to have different effects. Therefore ² it would have been optimal to have looked at logging, drainage, and burning separately to uncover the unique effects of each.

4.3 Significance ³

This was the first study to attain total biomass and carbon estimates for ⁴ the Sabangau catchment mixed swamp forest, including carbon from aboveground, belowground, coarse woody debris, litter, and peat biomass. The estimates for low and high disturbance areas will allow more precise predictions of how the degradation of these forests translates into greenhouse gas emissions and aid in improvement of peatland management and carbon budgeting initiatives such as REDD (Page et al., 2011).

To my knowledge, this was the first study to explore the use of tree traits ⁵ as a proxy of habitat quality in tropical rainforests. Trait-based monitoring will increase the efficiency and ease and decrease the cost of habitat quality monitoring in peat swamp forest, in comparison to species-focused monitoring

programs, improving tropical peatland management. Understanding precisely ¹ how forest alterations as a result of disturbance influence primate behavior and density will aid in their conservation.

Appendix¹

Table A1: List of sampled tree species scientific and local names, and the plots in which they were dominant and their dominance rank in that plot. Provided by OuTrop (unpublished).²

Scientific Name	Local Name	Species Code	Plots dominant in (dominance rank)
<i>Blumeodendron elateriospermum</i>	Kenari	K	LD 0.8 (5), LD 2.0 (5)
<i>Calophyllum cf. lanigerum</i>	Mahadingan	Mh	HD Edge (5)
<i>Calophyllum hosei</i>	Jinjit	Jj	LD 0.4 (5), LD 2.0 (2), HD 2.0 (2)
<i>Combretocarpus rotundatus</i>	Tumih	T	HD Edge (3)
<i>Cratoxylon arborescens</i>	Geronggang	Gg	HD Edge (2)
<i>Ctenolophon parvifolius</i>	Bintan rambut merah	BRM	LD 0.4 (5)
<i>Dactylocladus stenostachys</i>	Mertibu	Mb	LD 0.4 (5), HD 2.0 (3)
<i>Elaeocarpus mastersii</i>	Mankinang	Mk	LD 0.4 (3)
<i>Horsfieldia crassifolia</i>	Mendarahan daun besar	MDB	LD 0.8 (2), LD 2.0 (2)
<i>Licania splendens</i>	Bintan peter	BP	HD Edge (4)
<i>Lithocarpus cf. dasystachys</i>	Pampaning bitik	PB	HD 0.8 (1)
<i>Litsea cf. Elliptica</i>	Medang 2	M2	LD 0.8 (5), HD 0.8 (4)
<i>Mesua sp.</i>	Tabaras akar tinggi	Tb	LD 0.4 (5), LD 0.8 (5)
<i>Neoscortechinia kingii</i>	Pupu polanduk	Pp	LD 0.8 (3) HD 2.0 (4)
<i>Nephelium lappaceum</i>	Rambutan hutan	RH	LD 0.4 (4), HD 0.8 (3)
<i>Palaquium cochlearifolium</i>	Nyatoh gagas	NG	LD 0,4 (2), HD 2.0 (1)
<i>Palaquium leiocarpum</i>	Hangkang	Hk	LD 2.0 (1)
<i>Shorea teysmanniana</i>	Meranti semut	MS	LD 0.4 (1), HD).8 (2), LD 2.0 (3),
<i>Stemonurus cf. scorpiodes</i>	Tabaras tidak punya akar	Ttdk	HD 2.0 (5)
<i>Syzygium garcinifolia</i>	Jambu burung besar	JBB	HD 0.8 (5)
<i>Syzygium sp.</i>	Kemuning putih	KP	LD 2,0 (4)
<i>Tristaniopsis sp.</i>	Belawan merah	BM	HD Edge (1)
<i>Xylopi fusca</i>	Jangkang kunging	JK	LD 0.8 (4)

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