

How Degradation Type Impacts Natural Regeneration in a Tropical Peat-Swamp Forest



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Abstract

Within the last few decades Southeast Asian tropical peat-swamp forests have been increasingly better studied with greater understanding of their importance to global conservation. This rise in attention began towards the end of the 20th century as the scientific community started to recognise the vital role they play in global carbon storage and other ecosystem services. Now, this forest ecosystem is known to harbour diverse fauna and flora populations, some of which are the last remaining strongholds of highly threatened species. Despite this, tropical peat-swamp forests are being severely degraded due to widespread logging, yearly forest fires, and unregulated land conversion. This has led to a significant reduction in the remaining area of pristine forest, as well as globally significant carbon emissions, and many peatlands are now covered only by patchy, degraded forest or pioneer vegetation communities. With degradation set to continue, it is vital to improve our understanding of how these degraded peatlands will change over time and determine how to restore tropical peat-swamp forest communities.

Chapter one investigates whether tropical peat-swamp forest vegetation is capable of regenerating naturally in a protected but previously degraded forest. The vegetation communities in the logged and burned areas, within the recovering Sebangau forest, were surveyed and compared to the undisturbed forest to identify the severity to which they have been altered. The results suggest that regeneration potential is highly dependent on the type of degradation faced, with selectively logged forest showing many signs of positive regeneration after just 15 years. Conversely, vegetation surveys in two burned forest areas, 4 years and 14 years post-fire, show that regeneration is greatly inhibited and without assistance these sites will remain low in diversity and plant cover.

Chapter two builds on the findings of the previous chapter by examining how faunal biodiversity responds to the aforementioned degradation. This study surveyed the fruit-feeding butterfly population in the selectively logged, relatively undisturbed, and 4 years post-fire forest area, over a full year, as this taxonomic group is a useful indicator of a habitat's wider biodiversity. The results were congruent with those in chapter one, as the selectively logged forest contained a population with highly similar abundance, species richness, and composition as recorded in the relatively undisturbed forest. Whereas surveys in the burned forest show an almost complete loss of butterflies, indicating a significant loss of fauna diversity.

Overall, this thesis draws two main conclusions which both have large implications for the conservation of the tropical peat-swamp forest ecosystem. Firstly, selectively logged forests are capable of regenerating naturally, and if further degradation can be prevented these areas can have significant conservation value, especially when considering the lack of pristine forest. Secondly, burned tropical peatlands show little capability of natural regeneration and are likely to be inhospitable for the region's fauna. Therefore, significant assistance will be required to restore forest cover, prevent further carbon emissions, and help conserve many threatened species.

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General Introduction

The formation, distribution, and importance of tropical peatlands

In decades gone by tropical peat-swamp forests were considerably less well understood than other tropical forests and were assumed to have lower species abundance and diversity (Posa *et al.*, 2011). Aside from a few early studies they received less scientific attention until the 1990s, as efforts were focused on the region's dipterocarp forests (Page *et al.*, 1999; Husson *et al.*, 2018). This played some part in the situation of today, where broadscale destruction of this vital, but unprotected, habitat contributes to global species extinctions (Giam *et al.*, 2012), greenhouse gas emissions (Page *et al.*, 2002), and a human health crisis (Forsyth, 2014).

The formation of tropical peatlands significantly predates those in boreal and temperate regions, with inland Bornean peatlands initially forming 20,000 to 40,000 years ago (Anshari *et al.*, 2001; Anshari *et al.*, 2004; Rieley *et al.*, 2008). The majority of tropical peatlands, however, are much younger and formed within the last 7,000 years with accumulation rates peaking 4,000-5,000 years ago (Yu *et al.*, 2010; Dommain *et al.*, 2011). This expansion occurred in the coastal regions of Southeast Asia as the sea-level fell and regional rainfall increased towards the end of the Holocene (Dommain *et al.*, 2011). In addition to Southeast Asia, expansive peatlands have been identified across the tropical regions of South America and Africa and it is likely that the extent of tropical peatland is still underestimated (Gumbricht *et al.*, 2017; Dargie *et al.*, 2017, Xu *et al.*, 2018).

Expansive peatlands in the tropics seem almost counterintuitive, as the formation of peat requires decomposition to be slower than primary production in order to allow undecomposed organic matter to accumulate (Chimner and Ewel, 2005). Yet the consistently warm and humid conditions, characteristic of the tropics, typically allow for the fastest decomposition rates globally (Hall and Silver, 2013). Tropical peat formation is typically reported to be a result of consistent waterlogging, alongside acidic and anoxic conditions, which inhibits microorganisms from breaking down the organic matter (Qualls and Haines, 1990; Hergoualc'h and Verchot, 2011). However, it may be more complex, as whilst the leaves of tree species restricted to tropical peat-swamp forests show very limited decomposition, leaves of a non-peat-swamp forest species readily decompose in the same conditions (Yule and Gomez, 2009). Therefore, it may actually be due to the physical and chemical adaptations of the leaves, initially as a response to costly herbivory in the nutrient-poor ecosystem, that is preventing decomposition and leading to the accumulation of peat (Yule and Gomez, 2009).

As knowledge has grown, perhaps the most well recognised feature of tropical peat-swamp forests is their role in carbon sequestration and storage. Global peatlands cover only 3% of the Earth's surface yet contain 1/3 of all carbon held in soil (Rydin and Jeglum, 2013; Page *et al.*, 2011). Temperate and boreal peatlands are well documented (Jauhiainen *et al.*, 2005), yet the importance of the role of the tropics in global carbon storage is still to be fully understood. Discovery of previously unknown tropical peatlands continues to occur which in turn leads to increases in the estimation for the tropical peatland carbon pool (Dargie *et al.*, 2017). Previous reports placed the tropical peatland carbon pool at 88.5 Gt, 17-19% of the world's total (Page *et al.*, 2011). However recent discoveries in the Afrotropics have increased this 104.7 Gt (Dargie *et al.*, 2017). Furthermore, new mapping estimations in South America potentially triple the size of the tropical peatland carbon pool suggesting the total could be as much as 350 Gt (Gumbricht *et al.*, 2017). Southeast Asia is hugely important to the tropical peatland total as it is known to hold 68.5 Gt of carbon (Page *et al.*, 2011). Indonesia's importance, in particular, cannot be overstated as the nation contains 80% of Southeast Asia's peatland by area and 57.4 Gt of carbon (Page *et al.*, 2006; Page *et al.*, 2011).

The biodiversity of tropical peat-swamp forests

Despite improved recognition of their role in the global carbon cycle, even today few extensive studies of the biodiversity supported by tropical peat-swamp forests have been published (Harrison and Rieley, 2018). The most well studied species in tropical peat-swamp forests are the flagship primates such as the Bornean orangutan (*Pongo pygmaeus*) (Harrison and Rieley, 2018). Tropical peat-swamp forests are now known to be a highly important refuge for this iconic species, due to the deforestation of other forest types, with the Sebangau forest, Central Kalimantan, supporting the largest protected population (Posa *et al.*, 2011; Utami-Atmoko *et al.*, 2017). Many other primates are also dependent on tropical peat-swamp forest including species of gibbon (*Hylobates spp.*: Hamard *et al.*, 2010; Quinten *et al.*, 2010), langur (*Presbytis spp.* and *Simias concolor*: Smith *et al.*, 2013; Quinten *et al.*, 2010), macaque (*Macaca spp.*: Nowak, 2012), tarsier (*Tarsius bancanus borneanus*: Blackham, 2005) and slow loris (*Nycticebus coucang menagensis*: Blackham, 2005).

The true number of animal species found in tropical peat-swamp forests is unknown and likely much higher than currently recorded, yet, the most extensive list to date has identified 123 mammals, 268 birds, 75 reptiles, 27 amphibians, and 219 fish (Posa *et al.*, 2011). Many of these species are additionally found in other forest types, but the populations in tropical peat-swamp forests are crucial as 45% of the mammal species and 33% of the birds are recognised as near threatened or worse (Posa *et al.*, 2011). The freshwater fish of tropical peat-swamp forests are of particular importance given the high species richness and endemism. Of the 219 species recorded 80 are restricted solely to this forest type, with 31 found only in a single location (Posa *et al.* 2011). Again, the true numbers are likely to even greater as surveys across Bornean tropical peat-swamp forest are significantly lacking and it has been suggested that separate areas of tropical peat-swamp forest may contain endemic populations (Kottelat *et al.*, 2006).

In addition to the fauna, tropical peat-swamp forests harbour a greater number of plant species than any other global peatland ecosystem (Posa *et al.*, 2011). 1,411 plant species have been identified in Southeast Asian peat-swamp forests (Giesen *et al.*, 2018), with up to 122 tree species per hectare (Mirmanto, 2010). Early research identified that the vegetation across an entire peat dome occurs in a sequence of distinct phasic communities which are arranged in concentric zones radiating out from the centre of the dome (Anderson, 1963). The plant species diversity of these communities has been found to decrease as habitat type changes from the outer shallow areas to central deep areas of the peat dome (Anderson, 1983; Brady, 1997). In addition to diversity, above ground biomass is significantly reduced in the central forest habitats (Waldes and Page, 2002). However, in the Sebangau forest, an anomalous tall and diverse forest was identified on deep peat at the centre of the peat dome (Page *et al.*, 1999). This is explained by the presence of an old decaying peat surface which over the last 2500 has increased the nutrient availability allowing for a more diverse and productive forest. Additionally, whilst this concentric pattern is found in all tropical peat-swamp forests the characteristic species and phasic communities' species compositions differ (Rieley *et al.*, 1996). As a result, each tropical peat-swamp forest is different, varying due to the local hydrology, peat depth, nutrient availability, and local species availability (Page *et al.*, 1999; Posa *et al.*, 2011).

The threats to tropical peat-swamp forests and associated problems

Until the early 1980s, tropical peat-swamp forests in Southeast Asia remained relatively untouched by anthropogenic pressures and existed in a natural fire-proof state (Miettinen *et al.*, 2016). This soon changed as the forests were identified as a new untouched resource for widespread logging (Miettinen and Liew, 2010; Page *et al.*, 2009). This initial logging however created a much greater problem as the degradation disrupted the forest's natural fire resistance (Siegert *et al.*, 2001). Now fires are an annual phenomenon in degraded tropical peat-swamp forests and almost 30% of peatlands in Kalimantan have burned in the last 20 years (Hoscilo *et al.*, 2009; Vetrta and Cochrane, 2020).

Within Southeast Asian tropical peat-swamp forests the consequences of logging are now virtually ubiquitous (Miettinen *et al.*, 2016; Dohong *et al.*, 2017). This is, in part, the result of a significant reliance upon the timber industry during the 1970's and 1980's, which saw the number of logging concessions in Indonesia rise from 71 to 580, covering 60 million hectares of forest (Poffenberger, 1997; Brockhaus *et al.*, 2012). During this time overexploitation of the region's dryland forests, due to increasing demand and poor management practices, led to the initial extraction of timber from previously undesirable peatlands (Poffenberger, 1997; Barber, 1998; Silvius and Diemont, 2007). Since the turn of the millennium many more peat-swamp forests across the Indo-Malayan region have been classified as production forests from which timber harvesting is legally allowed (Yule, 2010). The scale and intensity of logging varies markedly from one forest to another and often tend to be categorised as selective logging, a catch-all term with no clear definition (Hughes, 2017). Additionally, despite the existence of protected forest areas, as well as a permanent moratorium on new peatland concessions (Harrison *et al.*, 2020; Astuti, 2021), illegal logging still occurs within these forests due to a lack of enforcement (Barr *et al.*, 2006).

Evidently logging directly results in a reduction of pristine forest cover via the harvesting of trees and as of 2015 only 7.4% peat-swamp forests in Kalimantan remained untouched (Miettinen *et al.*, 2016). Yet it is not only this direct harvesting that reduces forest cover but the associated infrastructure that the industry requires (Dohong *et al.*, 2017). The total length of roads and railways used to extract timber increased 34% and 25%, respectively, in just the 6 years from 1991 to 1997 (Böhm and Siegert, 2001). These networks of roads and railways significantly increase forest fragmentation and planned Indonesian infrastructure development is predicted to decrease habitat connectivity in Kalimantan from 89% to 55%, impacting 42 protected areas (Alamgir *et al.*, 2019).

More significantly than roads and railways, illegal logging in tropical peat-swamp forest has left behind networks of extraction canals which continue to degrade the forest decades after the cessation of logging (Wösten *et al.*, 2008). These canals are often hand-dug or cut into the peat using chainsaws and serve the purpose of floating logs out of the forest (Wösten *et al.*, 2008). A combination of logging and, more importantly the extraction canals, has resulted in significant changes to the hydrology and understory microclimate in degraded tropical peat-swamp forests (Hardwick *et al.*, 2015). Whilst they were once waterlogged year-round, the peat soil in degraded areas now dries out during the dry season as canals drain the forest and the water table falls to depths of 40cm or more below the soil surface (Wösten *et al.*, 2008). This allows fires to not only burn the forest vegetation but also up to 100 cm below ground in the dried peat soil (Usup *et al.*, 2004). These subterranean fires are incredibly hard to extinguish and can smoulder below ground for weeks on end (Siegert *et al.*, 2004). Degraded tropical peat-swamp forests are now 5 times more likely to burn, and experience fire densities of 15 to 30 times greater, than non-degraded peatlands or other forest types (Miettinen *et al.*, 2012; Vetrta and Cochrane, 2020).

The most destructive fires occur in years when the El Niño-Southern Oscillation causes severe droughts in Southeast Asia (Hoscilo, 2009; Wooster *et al.*, 2012). Over the last 50 years, El Niño events have been associated with significant increases in the area burnt by fire during 1972/73, 1982/83, 1994, 1997/98, 2002, 2006, 2009, and 2015 (Page *et al.*, 2013; Vetruta and Cochrane, 2020). The fires of 1997/98 and 2015 are the most significant on record, burning 4.5 million ha and 4.6 million ha, respectively (Liew *et al.*, 1998; Lohberger *et al.*, 2018). Whilst the estimated area is greater for the 2015 fire the 1997/98 fire is widely considered to have been considerably larger and estimates suffer due to reduced resolution of satellite imagery (Field *et al.*, 2016; Lohberger *et al.*, 2018). As both fire events combusted millions of hectares of peatland, they produced a transboundary haze that blanketed much of Southeast Asia in toxic smog and will lead to tens of thousands of excess and premature deaths (Kunii *et al.*, 2002; Tacconi, 2016; Vetruta and Cochrane, 2020). The 1997/98 fire burnt from August 1997 to March 1998 and released somewhere between 0.81 Gt and 2.57 Gt of CO₂, equivalent to 13%-40% of the annual global carbon emissions from fossil fuels (Page *et al.*, 2002). Estimations for the 2015 fire, which burnt from July – October, fall within the same range at 0.89 Gt – 1.29 Gt (Lohberger *et al.*, 2018). Given that El Niño events are set to increase in frequency and intensity forest fires pose a significant threat to the future of tropical peat swamp forests (Cai *et al.*, 2014; Cole *et al.*, 2015)

These catastrophic fires are initially started by small-holders, larger corporations, and government agencies all using fire as a cheap and effective tool to clear land for agriculture and plantations (Page *et al.*, 2002). These managed fires rapidly grow out of control and are further exacerbated by the exceptionally dry conditions (Page *et al.*, 2002). This association between tropical peat-swamp forest land-use change and fire is well recognised with the Mega Rice Project being the most obvious case (Konecny *et al.*, 2016; Hoscilo, 2009). The failed project aimed to convert 1 million hectares of tropical forest, 61% of which was peat-swamp forest, into cultivated rice fields (Hoscilo, 2009). The project started in 1995 and over 4000km of drainage canals were dug into the peat-swamp to reduce the water table, however, it became clear that the peatland was unsuitable for agriculture due to the acidic and nutrient-poor soils (Sulistiyanto, 2005; Hoscilo, 2009). Then in 1997 51.3% of the Mega Rice Project was devastated by fire leading to the project being abandoned in 1999 (Page *et al.*, 2002). Since 1999, areas of the Mega Rice Project have burnt almost every single year (Putra *et al.*, 2008).

The failed Mega Rice Project highlights why tropical peatlands were initially not desirable for agriculture or plantations as it is very difficult to reclaim the naturally swampy land (Posa *et al.*, 2011). However, conversion did start to occur slowly during the 1980s and then significantly increased after the turn of the millennium when the availability of more accessible lands on mineral-soil decreased (Miettinen *et al.*, 2016). With agricultural and plantation land now covering 50% and 46% of peatlands in Kalimantan and Sarawak, respectively, managed land conversion is responsible for the greatest loss of tropical peat-swamp forest within Southeast Asia (Miettinen *et al.*, 2016; Barthel *et al.*, 2018). Oil palm and *Acacia* are the primary crops grown due to the high economic potential and the vast global demand for palm oil, pulp, and paper (Lo and Parish, 2013). However, despite the undeniable economic benefits for countries like Indonesia and Malaysia (Pacheco *et al.*, 2017), this land conversion has resulted in globally significant carbon emissions with tropical peatlands in Southeast Asia changing from a carbon sink to a carbon source (Miettinen *et al.*, 2017).

Clearing the tropical peat-swamp forest is one of the first steps required for conversion and not only does this remove entire swathes of essential habitat but it ceases the carbon sequestration and storage provided by tropical peatlands. As the plant biomass of a plantation is considerably smaller than that of a tropical peat-swamp forest the carbon sequestration capability is significantly reduced (Tonks *et al.*, 2017). Furthermore, the volume of leaf litter is greatly reduced and, therefore, so is the potential production of peat (Anshari *et al.* 2010). Alongside clearance, the peatlands are drained to

reduce the water table and improve the suitability for crops (Posa *et al.*, 2011; Tonks *et al.*, 2017). However, this drainage increases the depth of the oxygenated zone of decay within the peat profile and allows for the aerobic decomposition of the organic matter which forms the peat (Tonks *et al.*, 2017). The decomposition of peat emits vast quantities of carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O) from the soil surface back into the atmosphere all year-round (Furukawa *et al.*, 2005). Additionally, not only are these greenhouse gases being emitted from the peat surface, but considerable quantities of dissolved organic carbon are leached into the drainage canals and lost via runoff in the waterways (Rixen *et al.*, 2016). This mechanism of carbon loss has been found to release much older carbon that may have been stored for hundreds or thousands of years (Evans *et al.*, 2014).

Furthermore, the drainage and conversion of tropical peat-swamp forests can lead to irreversible subsidence (Rieley and Page, 2008; Hooijer *et al.*, 2012). In the first year after conversion, the peat surface has been recorded to have subsided 75cm (Hooijer *et al.*, 2012), with additional decreases from 2cm – 8.5cm a year after that (Rieley and Page, 2008). This is the result of decomposition, compaction by heavy machinery, contraction of organic fibres through drying, and compression of deeper peat due to the loss of buoyancy of surface peat when the area is drained (Hooijer *et al.*, 2012). Over time this irreversibly changes the porosity and bulk density of the peat and prevents the percolation of water which can have significant consequences for regional water management and flooding (Tonks *et al.*, 2017).

The degradation of tropical peat-swamp forests by logging, fire, and land-use change are heavily intertwined (Harrison *et al.*, 2020). Whilst fires are used to clear land for agriculture and plantations, agricultural and plantations are themselves highly vulnerable to fire (Marlier *et al.*, 2015; Cattau *et al.*, 2016). Ultimately there is a positive feedback cycle between the initial logging degradation, forest fires, and land conversion which has resulted in the transition of huge swathes of pristine tropical peat-swamp forest into degraded forest, secondary forest, or open wastelands (Miettinen *et al.*, 2016).

The extent of forest loss in Southeast Asia is unquestionably leading to significant population declines in the region's fauna (Sodhi *et al.*, 2010). Faunal biodiversity inhabiting tropical peat-swamp forests are under ever increasing pressure from both forest loss and direct health consequences, similar to those experienced by people, as a result of the intense nature of fires in the ecosystem (Harrison *et al.*, 2016). Additionally, the toxic smoke haze produced by peat fires, which blankets much of Southeast Asia (Koplitz *et al.*, 2016), significantly alters the behaviour of fauna, shown by decreases in the frequency and duration of gibbon singing as well as a prolonged reduction in complexity of the dawn chorus (Harrison *et al.*, 2007; Lee *et al.*, 2017).

The impact of selective logging on fauna is likely less destructive than forest fires, with the conservation value of logged tropical forest ecosystems previously recognised. For example, Bornean dipterocarp forests retained 90% of faunal biodiversity despite a loss of 53% of above ground biomass (Berry *et al.*, 2010). Additionally, meta-analysis of more than 100 publications from logged forests across the tropics shows a retention of 85% of species in mammals, birds, invertebrates, and plants (Putz *et al.*, 2012). Though, comparatively, less is known about the biodiversity in logged tropical peat-swamp forests. Logged Malaysian peat-swamp forest has shown high avifauna species richness especially when compared to oil palm plantation (Hawa *et al.*, 2016). Yet, orangutan density decreased by roughly 20% in logged areas potentially due to fewer fruiting trees and an increased abundance of canopy gaps (Felton *et al.*, 2003). Furthermore, mammalian species richness decreased with increased logging intensity in the North Selangor Peat Swamp Forest, Peninsular Malaysia (Adila *et al.*, 2017).

Whilst the responses of invertebrate populations are widely understudied (Outhwaite *et al.*, 2020), Lepidoptera are often surveyed to gain an understanding of how the wider faunal biodiversity is responding to habitat degradation. This is because aspects of their life history, specifically short generation time, high mobility, and high habitat sensitivity, allow them to be highly responsive to changes in their environment (Bonebrake *et al.*, 2010). This technique has been used widely in temperate regions, as well as tropical forest ecosystems, and has identified that short-ranging, forest-specialists are most negatively affected by habitat degradation (Charrette *et al.*, 2006; Koh *et al.*, 2007; Bonebrake *et al.*, 2010). Currently few results have been published from tropical peat-swamp forest, however, one previous study found declines in species richness and diversity in areas with greater canopy loss (Houlihan *et al.*, 2013).

The regeneration of tropical peat-swamp forests

Regeneration can broadly be split into two categories, natural regeneration or active restoration. The definitions of these categories can be unclear but principally they refer to the level of human intervention in the process of ecological recovery (Reid *et al.*, 2018). Natural regeneration is typically the process by which a degraded site returns to its pre-disturbance state by regaining its native species composition, original structure, and ecological function without human assistance (Chazdon and Guariguata, 2016). Whereas active restoration covers a range of human intervention strategies that aim to alter or accelerate this regeneration (Holl and Aide, 2011). The strategies used depend on the requirements of each site but regularly involve direct seeding or planting nursery-grown seedlings (Crouzeilles *et al.*, 2017).

One key difference between the two regeneration methods is the associated cost. Natural regeneration is substantially less expensive which allows for its use over much larger areas and has been reported to provide a greater return on investment for restoration success (Chazdon and Guariguata, 2016). On the other hand, whilst the cost of active restoration of degraded tropical peat-swamp forest does differ depending on the severity of degradation, it can cost up to US\$25,000 per hectare (Hansson and Dargusch, 2017). In 2016, the Indonesian government established the Badan Restorasi Gambut, the Peatland Restoration Agency, with an initial aim to restore 2 million hectares of degraded peatland by 2020. However, the estimated cost is likely to be greater than US\$4.6 billion which is considerably more than the US\$200 million budget (Hansson and Dargusch, 2017). Despite the costs, policymakers tend to prefer active restoration due to the greater predictability in time and space targets, as well as the possibility for planting economically valuable species (Chazdon and Guariguata, 2016).

The combination of limited financial resources and mixed success of both regeneration methods has led to much debate as to whether one method should be preferred over the other. A recent meta-analysis concluded that natural regeneration is more successful at restoring multiple measures of biodiversity and vegetation structure in tropical forests when controlling for the large variation in biotic and abiotic factors between individual sites (Crouzeilles *et al.*, 2017). However, this finding has been questioned with the suggestion that natural regeneration sites have a positive selection bias, meaning natural regeneration is only measured in areas where the forest has at least partially returned (Reid *et al.*, 2018). Further questions were raised regarding a lack of consistency in the categorisation of sites as natural regeneration or active restoration, as well as the appropriateness of meta-analysis when individual sites vary so dramatically (Reid *et al.*, 2018). Additionally, much of the literature suggests active restoration will be required in tropical peat-swamp forests due to the severity of degradation, regeneration barriers, and apparent ubiquity of low biodiversity or retrogressive succession (Blackham *et al.*, 2014; Page *et al.*, 2009; Gunawan *et al.*, 2012).

Given that only 6% of tropical peat-swamp forests remain in their natural state, the regeneration of degraded peatlands is essential for the conservation of this ecosystem and the species it supports (Miettinen *et al.*, 2016). Furthermore, regeneration is essential to stop the emission of greenhouse gases and prevent future peatland fires (Wijedasa *et al.*, 2020). Previous research has suggested that tropical rainforests regenerate best when left to naturally regenerate (Crouzeilles *et al.*, 2017). However, the potential success of natural regeneration is not so clear in tropical peat-swamp forests where regeneration is highly dependent on the type, frequency, and intensity of degradation (Van Eijk *et al.*, 2009; Gunawan *et al.*, 2012; Blackham *et al.*, 2014). Additionally, effective conservation will require site by site assessment and generic universal approaches are unlikely to be successful in the long term (Graham *et al.*, 2017).

Thesis purpose and research aims

Therefore, this thesis aims to improve the understanding of natural regeneration in tropical peat-swamp forests, with the hope to aid in their conservation. The thesis focuses on degradation caused by selective logging and fire due to the vast extent of these degraded forests and peatlands which now are now left unmanaged (Miettinen *et al.*, 2016; Harrison *et al.*, 2020). If conversion to plantation can be prevented, this presents the opportunity for forest regeneration within these sites to vastly increase the area of much needed secondary forest (Graham *et al.*, 2017; Harrison *et al.*, 2020).

Chapter one will seek to understand how both fire and selective logging have impacted the vegetation of the forest, with particular focus on the tree species community and understory vegetation. By comparing the regenerating vegetation with a relatively undisturbed forest condition this thesis hopes to draw insights into the likelihood of degraded forests returning to their original condition without human intervention. Following on from chapter one, chapter two will assess the faunal biodiversity of these degraded forests to gain a better understanding of how biodiversity regeneration depends on the forest vegetation. This is highly important as it will assess the value of these degraded forests in conserving the regions threatened faunal biodiversity. This will be done by surveying the populations of fruit-feeding butterflies in relatively undisturbed, selectively logged and burnt forest areas. By surveying for a full year any influence of season will be accounted for, allowing for a more detailed understanding of differences in species richness, diversity, and composition among forest conditions.

Study site

All field research was conducted in the Natural Laboratory of Peat-Swamp Forest (NLPSF, 500 km², 2° 19' S, 113° 50' E), which is located within the wider 9200 km² Sebangau Forest, Central Kalimantan, Indonesia. The Sebangau Forest is a domed ombrogenous peat-swamp forest composed of four main habitat types: mixed-swamp forest, low-pole forest, tall-pole forest, and low-canopy forest (Page *et al.*, 1999). The climate is tropical with a typical wet season, October/November – May/June, followed by a dry season, June – September. Average temperatures and annual rainfall are high (mean maximum: 28.9°C, mean minimum: 22.0°C, rainfall: 2,912mm yr⁻¹) (Harrison, 2009). The NLPSF has been the focus of extensive research and has a pre-established 4km² transect grid within the mixed-swamp forest habitat. It is managed by the Centre for International Cooperation in Sustainable Management of Tropical Peatland, at the University of Palangka Raya, in collaboration with the Borneo Nature Foundation. The NLPSF was selectively logged for roughly 40 years, with legal logging stopping in 1997 and illegal logging continuing until 2004 (Schreven *et al.*, 2018). Old logging canals remain, and the NLPSF's history has left it susceptible to yearly dry season forest fires, with destructive fire events occurring during El Niño years (Cattau *et al.*, 2016). As a result, the NLPSF is now made up of a mosaic of forest conditions in varying stages of degradation and natural regeneration, making it ideal for understanding forest regeneration. This study will focus on four of the forest conditions within the NLPSF: A 8.7km² area which burnt on a single occasion during October of 2015, the 'Old Burn Site' (OBS). A 0.03km² forest area which burnt on a single occasion in 2006, the 'New Burn Site' (NBS). An unquantified expanse of forest located to the east of the logging railway which experienced both legal and illegal logging for roughly 40 years, the 'Selectively Logged Forest' (SLF). Forest to the west of the logging railways which, whilst the exact extent of logging is unclear, is largely believed to have experienced minimal degradation so is representative of 'Relatively Undisturbed Forest' (RUF). See Figure 1 below for a satellite imagery map of the study site.

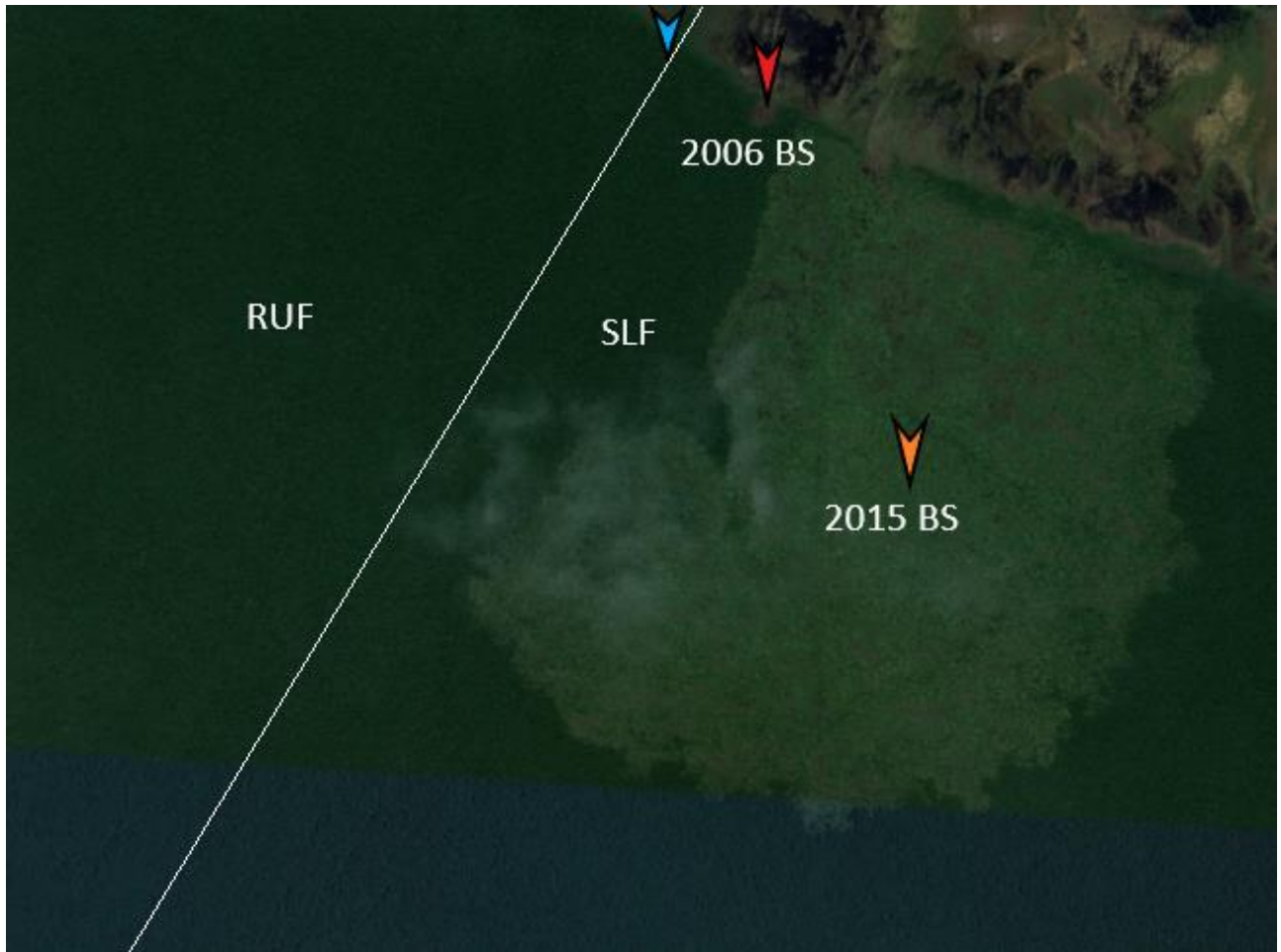


Figure 1: A satellite imagery map of the forest area surveyed within the 600,000 ha Sebangau Forest. The blue marker shows the location of the Natural Laboratory of Peat-Swamp Forest camp. From the Sebangau river, through camp, runs a 6km disused light railway which is represented by the white line. To the west of the railway is the Relatively Undisturbed Forest (RUF) whereas Selectively Logged Forest (SLF) is located to the east. The small patch of forest loss shown by the red arrow is the 2006 Burn Site (OBS) and measures 0.03km². The greater area of forest loss shown by the orange arrow is the 2015 Burn Site (NBS) and measures 8.7km². The top right corner shows riverine habitat along the boundary of the forest. Satellite imagery was obtained from Google Earth.

Chapter One: The Vegetation Communities of a Tropical Peat-Swamp Forest Degraded by Selective Logging and Forest Fires

Abstract

Tropical peat-swamp forests are integral for global carbon storage and conserving vital populations of endangered species. Yet this forest ecosystem is experiencing extensive degradation resulting in a near total loss of pristine forest in Southeast Asia. This study investigated the consequences of two common degradation types, selective logging and forest fires, by surveying the flora present in the multiply degraded Sebangau Forest, Central Kalimantan. The tree population and understory vegetation community were recorded in 15 habitat plots in each of four forest conditions: relatively undisturbed, historically selectively logged, 14 years post-fire, and 4 years post-fire. Historically selectively logged forest shows high natural regeneration potential evidenced by the high similarity with relatively undisturbed forest, including comparable tree density, tree species richness and an indistinguishable understory vegetation community. Yet significant differences were still identified in tree species composition and an absence of the tallest trees in logged forest. Conversely, both fire degraded sites displayed an almost entire absence of trees in addition to a dominance of early coloniser species in the 4 years post-fire site and a high abundance of *Nepenthes* spp. in the 14 years post-fire site. This shows that even a single fire event in can result in an altered ecological state with low diversity and little chance of natural regeneration. The results presented here highlight the importance of considering degradation type in the conservation of tropical peat-swamp forest. Logged forests can hold significant conservation value if further degradation is prevented whereas burnt forest will require significant investment and human intervention.

Introduction

Indonesian tropical peat-swamp forests remained almost entirely untouched until the 1980s as more valuable timber resources were primarily harvested from dryland forests (Silvius and Diemont, 2007; Graham *et al.*, 2017). However, as the dryland forests became depleted and demand for resources increased (Barber, 1998), extensive degradation began starting with widespread logging and leading to transmigration programmes, land conversion, and forest fires (Silvius and Suryadiputra, 2005; Wösten *et al.*, 2006; Silvius and Diemont, 2007). This has since resulted in a continual threat to the diverse forests, despite improved understanding of their global significance, and as of 2015 only 6% of tropical peat-swamp forests remained in a pristine natural condition (Miettinen *et al.*, 2016).

One of the most widely occurring types of degradation in tropical peat-swamp forests is selective logging (Miettinen *et al.*, 2016). The term selective logging broadly describes a host of timber extraction methods whereby trees are harvested depending on the species and size, typically *Shorea albida* and *Gonystylus bancanus* (Verwer and van der Meer, 2010). It is sometimes highly regulated, restricting the harvesting of trees to maintain the sustainability and ecological integrity of the forest system (Zimmerman and Kormos, 2012). These restrictions can involve minimum time left to regenerate, minimum and maximum felling diameter, and limited harvest per unit area (Zimmerman and Kormos, 2012). Alternatively, selective logging can be a much looser term and encompass small scale illegal logging activities that can cause twice the amount of avoidable damage through a lack of management and training (Putz and Redford, 2010; Sasaki and Putz, 2009; Franke *et al.*, 2012).

Due to the inaccessible swampy terrain, tropical peat-swamp forests are logged using handheld chainsaws (Cannon *et al.*, 1994). This is typically less intensive, requiring little infrastructure (Franke *et al.*, 2012), and therefore should be less destructive (Felton *et al.*, 2003). However, there are mixed views on selective logging and its sustainability within a tropical peat-swamp forest ecosystem. Mammal species richness is high in a logged Malaysian tropical peat-swamp forest, 25 years post logging, in areas in which vegetation has recovered (Adila *et al.*, 2017). Whilst others have shown poor peat quality with reduced microbial biomass and enzyme activity (Könönen *et al.*, 2018), continued decrease in biomass beyond cessation of logging (Englhart *et al.*, 2013) and reduced primate density (Felton *et al.*, 2003).

However, it is clear that selective logging can break down the natural fire resistance of a tropical peat-swamp forest and open the door to the greater threat of forest fire (Siegert *et al.*, 2001; Page *et al.*, 2002). Logging creates canopy gaps that allow more light to reach the understory (Numata *et al.*, 2006; Wedeux and Coomes, 2015). This light decreases the humidity of the understory and dries the peat surface, creating a hotter and less stable understory microclimate (Hardwick *et al.*, 2015). To make matters worse illegal logging often leaves behind unwanted dead wood debris, quite literally adding fuel to the potential fire (Siegert *et al.*, 2001; Osone *et al.*, 2016).

Yet it is not the felling of trees that is the primary cause of devastating peatland fires, but the drainage that results from the use of timber extraction canals (Jaenicke *et al.*, 2010). These hand-dug canals continue to drain the wider forest area years after the cessation of logging, which causes a significant reduction in the water table and greatly increases the fire risk (Dommain *et al.*, 2010; Franke *et al.*, 2012). In the Sebangau National Park 273 canals, totalling 673km, were dug by illegal loggers between 1997 and 2006 as a cheaper replacement to the previously used railways (Kasih *et al.*, 2016). Subsequent conservation projects have focused on damming these canals (Dohong *et al.*, 2017), but the scale of damming needed across Kalimantan requires significant financial investment as canals

have additionally been used to drain millions of hectares of peat-swamp in an attempt to create ultimately unproductive agricultural land (Hansson and Dargusch, 2017).

The severity of degradation caused by fire, and subsequent regeneration potential, depends on the intensity and regularity of fire events (Page *et al.*, 2009; Hoscilo *et al.*, 2011; van Eijk *et al.*, 2009). Forests that burn just once with low-intensity fires can reach diversity and biomass levels comparable to a relatively undisturbed forest (Page *et al.*, 2009). However, as intensity and regularity increase regeneration slows and the once diverse forests become dominated by just a few pioneer species (Hoscilo *et al.*, 2008). At the most severe end of the scale, retrogressive succession occurs (Page *et al.*, 2009). Yearly fires result in vast areas becoming dominated by pioneer species, ferns, and sedges, never progressing from the first successional stage. Prolonged deep wet season flooding, resulting from reduced peat permeability, peat subsidence, and a lack of transpiration, additionally prevents the establishment of tree species (Wösten *et al.*, 2006). Then as the dry season returns the flooding evaporates, the water table falls and pioneer species become kindling for the next fire (Page *et al.*, 2009).

Given the vast scale of degraded peatlands, and the significant shortfall in the allocated restoration budget, active restoration is simply not financially viable for all sites (Hansson and Dargusch, 2017). In total, across Southeast Asia logged tropical peat-swamp forests cover 4.3 million ha and an additional 3.2 million ha are classified as open undeveloped, typically fire degraded, wastelands (Miettinen *et al.*, 2016). Therefore, understanding of the process of natural regeneration, and identifying any areas in which forest vegetation may regenerate, could allow for more effective use of limited conservation funds.

This study aims to address the issues presented above by surveying the natural regeneration of vegetation within the Sebangau National Park, Central Kalimantan, Indonesia. To better understand how regeneration potential is affected by degradation type this study will survey three degraded forest conditions: historically selectively logged (SLF), 14 years post-fire (Old burn site: OBS), and 4 years post-fire (New burn site: NBS). Additionally, the vegetation of the relatively undisturbed forest (RUF) will be surveyed to gain an understanding of how these degraded areas have been altered from their original condition. As well as comparing degradation types, the different ages of the fire degraded sites will provide this study with the opportunity to understand post-fire succession within the Sebangau National Park.

More specifically, the study will record the following components of each forest condition: (1) The vegetation community present in the understory. (2) Species identification of mature trees. (3) The structure of the tree stand, with regards to density, diameter at breast height, and height. (4) The abundance of tree seedlings and saplings.

It is hypothesised that the new burn site will be widely dominated by coloniser plant types, predominantly ferns and sedges, due to the recent degradation removing much of the typical tropical peat-swamp forest vegetation and dramatically altering abiotic conditions (Page *et al.*, 2009). Mature trees, of fire-resistant species (van Eijk *et al.*, 2009), may still be present but abundance and species diversity will be significantly reduced compared to all other forest conditions. Additionally, tree seedling and sapling regrowth will likely be limited due to inhospitable abiotic conditions and reduced seed abundance (Graham and Page, 2012).

The old burn site will show greater signs of regeneration, due to the additional time, containing both degraded land colonisers and tropical peat-swamp forest species in both the understory and tree community (van Eijk *et al.*, 2009), resulting in a vegetation community sharing similarities with both the new burn site and the relatively undisturbed forest. Disturbance-specialist tree species will be

present (Blackham *et al.*, 2014), possibly alongside forest species that survived the initial degradation, yet the area will lack the species composition, density, and larger trees typically seen in undisturbed forest (van Eijk *et al.*, 2009). However, this partial canopy may ameliorate harsh light intensity allowing a return of typical tropical peat-swamp forest understory plant types as well as increased tree seedling and sapling recruitment (Graham and Page, 2018), when compared to the new burn site.

Finally, it is hypothesised that the selectively logged forest will show high levels of regeneration and be largely comparable to the relatively undisturbed forest in the understory, tree community, and seedling and sapling abundance. This is because of the comparative reduced intensity of logging and a significantly longer regeneration time. However, the tree community may lack species which were targeted due to their commercial value and will likely possess a higher density of smaller trees due to the previous harvesting of tall trees with a large diameter at breast height (Park *et al.*, 2005; Verwer and van der Meer, 2010).

Methods

Transect and Plot Layout

Within the mixed-swamp forest habitat of the NLPSF four forest conditions were surveyed: relatively undisturbed forest, selectively logged forest, the old burn site, and the new burn site. In each forest condition, three parallel transects were established and separated by a minimum of 100m. Along each transect five habitat plots were surveyed, a total of 15 plots per condition. Plots were spaced 50m along each transect and 5m perpendicular to the transect, alternating either side of the transect.

Habitat Plot Surveys

The habitat plots had a nested design with a 2m x 2m plot inside a 5m x 5m plot inside a 10m x 10m plot. The plot design was implemented to increase the efficiency of sampling. The size of plot used to survey each vegetation type was decided based on the smallest plot which could adequately represent the distribution of that plant type. To get a full understanding of the flora community, and structure of each forest condition, the following components were recorded within each plot:

- 10m x 10m plot
 - Tree composition: In the field trees were identified by local botanists using the local species name, these were later converted to scientific names. Height and circumference at breast height (CBH, 1.3m above ground) were recorded for all trees in each plot. Trees were defined as height $\geq 1\text{m}$ and $\text{CBH} \geq 31\text{cm}$. Height was recorded categorically: $1\text{m} \leq H < 6\text{m}$, $6\text{m} \leq H < 11\text{m}$, $11\text{m} \leq H < 16\text{m}$, $16\text{m} \leq H < 21\text{m}$, $21\text{m} \leq H < 26\text{m}$, $26\text{m} \leq H < 31\text{m}$.
- 5m x 5m plot
 - Understory vegetation: The abundance of pitcher plants (*Nepenthes spp.*), lianas (long-stemmed, woody vines which depend on trees for support), vines (shorter with non-woody stems but also climb up trees), woody-stemmed shrubs, Pandanaceae, rattan (*Calamus spp.*), and rasau (riverine *Pandanus spp.*). Understory plants were recorded in these groups, rather than by species, due to the lack of clarity in species identification of many plants in the Sebangau forest (Husson *et al.*, 2018).
 - Total combined percentage cover of all fern species.
 - Saplings: The total abundance of tree saplings, defined as height $\geq 1\text{m}$ and $\text{CBH} < 31\text{cm}$.
- 2m x 2m plot
 - Seedlings: The abundance of all tree seedlings, defined as height $< 1\text{m}$ and $\text{CBH} < 31\text{cm}$.

Statistical Analysis

To assess the effectiveness of tree species sampling, in each forest condition, species accumulation curves were produced. The Chao 1 species richness estimator, an abundance-based estimator, was additionally used to estimate the true total number of species in each forest condition.

To visually assess differences in the understory vegetation, and tree species composition, among the forest conditions non-metric multidimensional scaling (nMDS) was used to produce ordination plots using the Bray-Curtis dissimilarity index. This approach was chosen as the data contained a high number of zero values, and because of the stricter assumptions required by other ordination techniques such as principal component analysis (Kenkel, 2006). Bray-Curtis was the chosen index as both the understory vegetation dataset and the tree species dataset are abundance counts. Vector-fitting analysis was used to overlay, on the ordination plot, the understory vegetation plant types and tree species which correlated with the ordination.

Prior to nMDS, the understory vegetation data was square-root transformed to level the importance of dominant and rare species. Due to the high presence of denuded and empty samples, a dummy variable was added to the understory vegetation and tree species datasets. This dummy variable improves the erratic behaviour of the Bray-Curtis coefficient by increasing the similarity of the denuded samples when they are known to be denuded for the same ecological reason (Clarke *et al.*, 2006). In turn, the increased similarity allows a more meaningful placement of these samples in the ordination, whereas without it the nMDS may not reach convergence or may not accurately represent the true differences in beta diversity. For well-populated samples, with many observations, the additional dummy variable does not dampen any true dissimilarity as it was given the lowest possible value, 1.

Following this, permutational multivariate analysis of variance (PERMANOVA) was performed to test for significant differences in the composition of understory vegetation, and tree species, among the forest conditions. Again, the Bray-Curtis dissimilarity index was used. Homogeneity of multivariate dispersion was then checked to assess the reliability of the PERMANOVA and identify significant differences in within condition variation.

To identify any differences in tree abundance and species richness, between the forest conditions, linear mixed-effects models were constructed with forest condition as a fixed effect and transect included as a random effect. Tree DBH was compared using Levene's test and Mann-Whitney U test. A Chi-Square test of independence was used to compare the number of trees each tree height category. Heights categories were consolidated into larger groups. Additionally, to better maintain the original height categories, midpoints were calculated from the categorical height data and a T-test was performed to compare the height of trees in each forest condition.

Finally, differences in the abundance of seedlings and saplings across all four forest conditions were determined using one-way analysis of variance (ANOVA), with Tukey's HSD post-hoc tests. As sapling abundance was not normally distributed a Kruskal-Wallis test was used to test among conditions, followed by a post hoc Dunn's test with Bonferroni correction.

Analysis was performed in R studio 3.6.3 (R Core Team, 2019). The package '*Vegan*' was used to perform multivariate analysis (v2.5-6; Oksanen *et al.*, 2019). All figures were produced using '*ggplot2*' (v3.1.1; Wickham, 2016).

Results

Understory Vegetation

The ordination plot produced by nMDS of the Bray-Curtis dissimilarity matrix for the composition of understory vegetation shows three clusters of habitat plots, suggesting three distinct types of understory (Figure 1, $k = 2$, stress = 0.167). The old burn site contains the most distinct understory as shown by the highest degree of separation from the other forest conditions. It also shows a tight clustering of plots around the ellipse, indicating the old burn site has a largely homogenous understory composition. The new burn site plots create the second clustering which is the most highly separated from old burn site clustering, thus showing a substantial difference in the understory vegetation of the two burned sites. The new burn site clustering is additionally separated from the selectively logged forest and relatively undisturbed forest, although, due to the large variation within the new burn site understory, as seen by the greater spread of plots, the new burn site shows slight overlap with the relatively undisturbed forest and selectively logged forest. This indicated that the new burn site, relatively undisturbed forest, and selectively logged forest have shared plant types within their respective understories. Finally, the relatively undisturbed forest and selectively logged forest conditions heavily overlap in the centre of the ordination and are responsible for the third distinct cluster. Therefore, the ordination suggests the selectively logged forest and relatively undisturbed forest conditions contain understory vegetation compositions which are indistinguishable from one another.

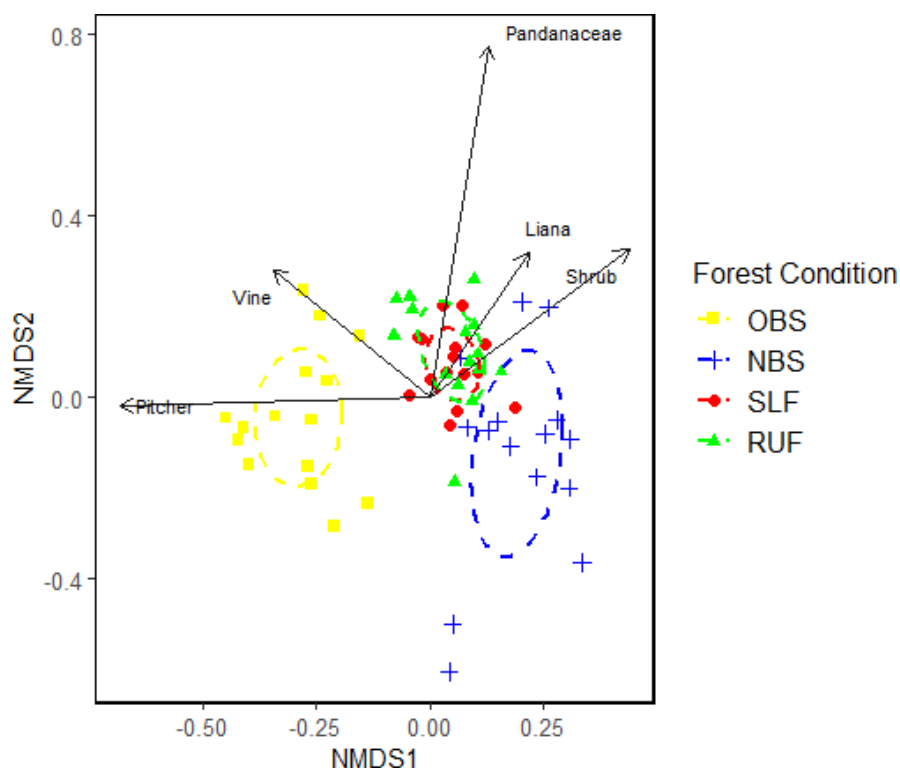


Figure 2: Non-metric multidimensional scaling of the Bray-Curtis dissimilarity matrix of understory vegetation variables by forest condition. Each point represents a habitat plot in each forest condition, $n=15$ for each condition. NMDS1 and NMDS2 display the two dimensions of the nMDS ($k = 2$, stress = 0.167, random starts = 50, iterations = 999). Arrows represent vector-fitting of significant variables ($p < 0.01$) with the vector length representing differences in r^2 values and vector direction pointing towards the area of maximum correlation.

Both burn sites show generally low abundances of typical peat-swamp forest understory vegetation such as liana, rattan and rasau. However, they differ starkly in those plant types which they do contain, pitcher, vine, and shrub plants, which causes the large separation of the burn sites in the ordination (Figure 1). Pitcher plants are characteristic of the old burn site, present in 13/15 plots, with 7 plots containing more than 10 plants and 1 plot as many as 54. Yet, pitcher plants are entirely absent in the new burn site. Likewise, vines are found in 14/15 plots in the old burn site but only 6/15 plots in the new burn site. Alternatively, shrub plants are found in 13/15 new burn site plots, reaching 23 plants in a single plot, yet are completely absent in the OBS.

In contrast, the relatively undisturbed forest and selectively logged forest completely overlap due to both forest conditions containing all the understory vegetation plant types recorded in this study, across their respective plots. This additionally explains the central placement of the selectively logged forest and relatively undisturbed forest between the two burned sites. Vines, which are highly abundant in the OBS, are the most ubiquitous understory vegetation plant type in the relatively undisturbed forest and selectively logged forest as they are present in every plot. Whereas the overlap of the relatively undisturbed forest and selectively logged forest with the new burn site is due to the three conditions sharing a high abundance of both shrub plants and Pandanaceae.

The vector-fitting analysis, overlaid on the ordination, shows 5 of the understory vegetation plant types (Pitcher ($r^2=0.486$, $p=0.001$), Liana ($r^2=0.189$, $p=0.004$), Vine ($r^2=0.254$, $p=0.003$), Shrub ($r^2=0.283$, $p=0.002$) and Pandanaceae ($r^2=0.659$, $p=0.001$)) are significantly correlated with the ordination. The vector directions support the above patterns observed in the ordination as they highlight the strong correlations between forest conditions and plant types, and where plant types are shared between forest conditions.

PERMANOVA analysis of the understory vegetation showed significant differences in the understory composition among the four forest conditions ($F_{3,56}= 16.2$, $p = 0.001$, $R^2 = 0.464$). However, as seen in the ordination plot (Figure 1), the two burned sites show a greater dispersion of plots than the relatively undisturbed forest and selectively logged forest. As a result, a subsequent ANOVA of homogeneity of multivariate dispersion identified significant differences in within group dispersion across the four conditions ($F_{3, 56}= 3.48$, $p = 0.022$). Therefore, the significant differences in understory composition may not be due, or not only due, to the forest condition but also the dispersion of points.

In addition to the understory vegetation included in the ordination, percentage cover of ferns shows very large differences between the four forest conditions. In the new burn site ferns are highly dominant, present in every plot, with a mean percentage cover of 74%. In contrast, fern species show very low abundance in all other forest conditions, recorded in only a single old burn site plot with a 5% cover, two selectively logged forest plots both 2%, and four relatively undisturbed forest plots with a 1% or 2% cover.

Tree Species Composition

Across the study a total of 364 trees were recorded from 57 different species, when identified using local names. After conversion to binomial scientific names this equated to 51 separate species, as some local names were only convertible to genus level. The relatively undisturbed forest contained the greatest number of both individual trees and species, 189 and 47, respectively. The selectively logged forest contained marginally fewer with 157 individual trees and 43 species. However, the two burned sites showed an almost entire loss of tree cover, with only 17 trees in the old burn site and just 1 in the new burn site. Additionally, all trees in the burned sites were all a single species, *Combretocarpus rotundatus*. Oppositely, in the relatively undisturbed forest and selectively logged forest there is a more even composition of tree species and the most abundant species do not

dominate. The selectively logged forest most abundant species was *Shorea teysmanniana*, yet only accounted 11.5% of total trees. In relatively undisturbed forest *Elaeocarpus mastersii* and *Tetractomia tetrandra* were joint most abundant and only 6.35% each. As the burned sites contained so few trees, of only one species, they were excluded from all further statistical tree analysis. This is to allow for a clearer understanding of any differences between the selectively logged forest and relatively undisturbed forest and to prevent any potential influence of the burned sites.

Species accumulation curves were produced for the relatively undisturbed forest and selectively logged forest to assess the completeness of tree sampling. The species accumulation curves of the relatively undisturbed forest and selectively logged forest do not reach asymptote and therefore increased sampling effort is likely to increase the number of species identified in both forest conditions (Figure 2). The Chao 1 richness estimator estimated the true species richness of the relatively undisturbed forest to be 55.3 species (SE \pm 5.86) and 71.1 species (SE \pm 18.0) for the selectively logged forest.

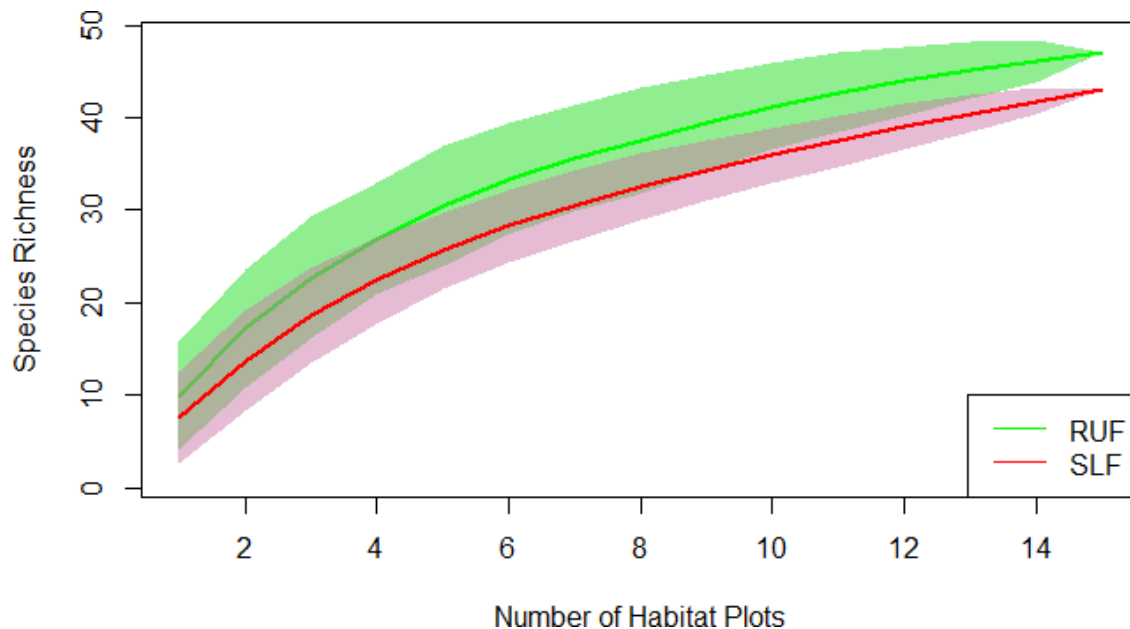


Figure 3: Mean species accumulation curves for the tree species richness of the relatively undisturbed forest (RELATIVELY UNDISTURBED FOREST: green) and selectively logged forest (SELECTIVELY LOGGED FOREST: red) within the NLPF. 15 habitat plots were surveyed in each forest condition. Random permutations = 100 and the shaded areas represent a 95% confidence interval.

To visually compare the tree species composition of the selectively logged forest and relatively undisturbed forest an ordination plot was, again, produced by nMDS of the Bray-Curtis dissimilarity matrix (Figure 3, $k = 3$, stress = 0.180). The plot shows a slight degree of separation, with relatively undisturbed forest habitat plots largely in the top of the ordination and selectively logged forest plots in the bottom. However, there is considerable overlap and large within group variation indicating substantial similarity between the two forest conditions.

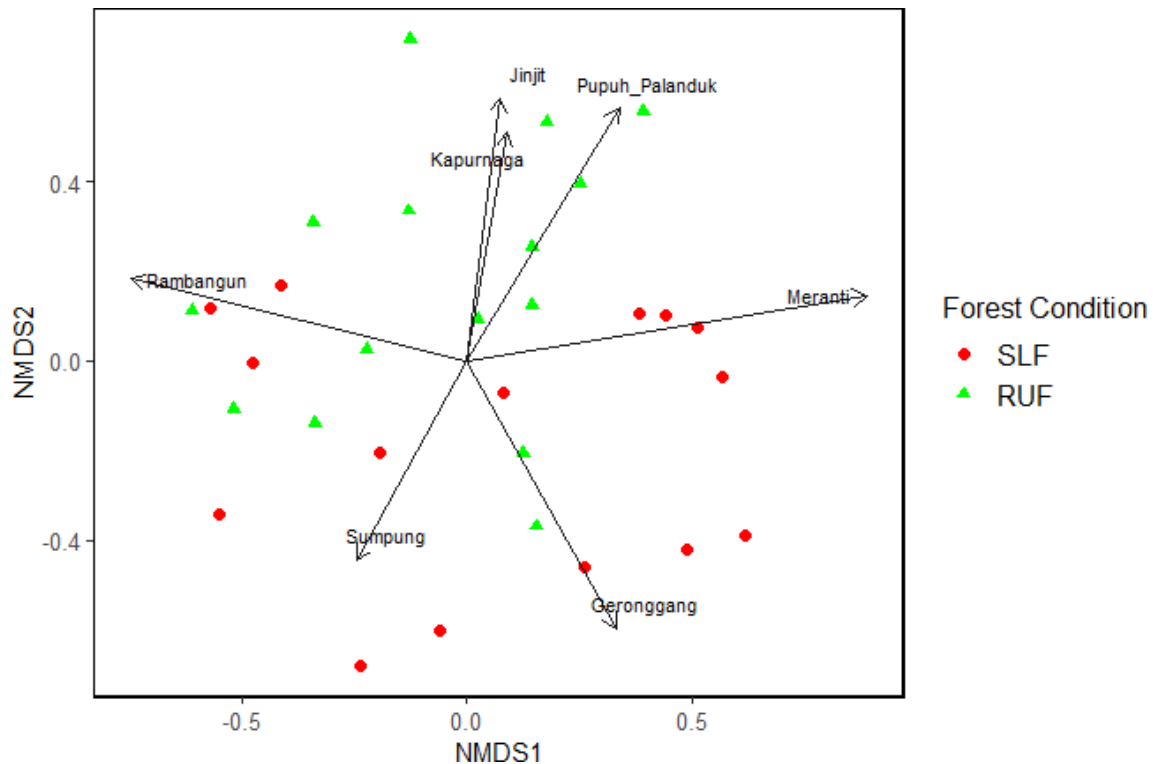


Figure 4: Non-metric multidimensional scaling of the Bray-Curtis dissimilarity matrix of tree species composition by forest condition. Each point represents a habitat plot in each forest condition, $n=15$ for each condition. Forest conditions included are the relatively undisturbed forest (RUF: green) and the selectively logged forest (SLF: red). NMDS1 and NMDS2 display the first two dimensions of the nMDS ($k = 3$, stress = 0.180, random starts = 50, iterations = 999). Arrows represent vector-fitting of significant variables ($p < 0.01$) with the vector length representing differences in r^2 values and vector direction pointing towards the area of maximum correlation. Vectors are labelled using local tree species names (converted in text below).

Vector-fitting analysis was used to identify the tree species which best explain the pattern of the ordination. Of the 57 local name species, 7 were significantly correlated ($p < 0.01$) with the ordination: Geronggang (*Cratoxylum glaucum*), Jinjit (*Calophyllum hosei*), Kapurnaga (*Calophyllum sclerophyllum*), Meranti (*Shorea teysmanniana*), Pupuh Palanduk (*Neoscortechinia kingii*), Rambangun (*Tetractomia tetrandra*) and Sumpung (*Ilex hypoglauca*). Overall, the direction of the vectors into areas where the forest conditions do overlap shows that there is not an association of specific tree species in each condition, rather those species were found in high density in habitat plots in both the selectively logged forest and relatively undisturbed forest. Although three species, Jinjit, Kapurnaga, and Pupuh Palanduk, do appear to show high density in plot only in the relatively undisturbed forest, however, improved sampling may change this.

However, a PERMANOVA test found that the separation in clustering, seen in the ordination, of the relatively undisturbed forest and selectively logged forest is significant and therefore the two forest conditions do significantly differ in their respective tree species composition ($F_{1,28} = 1.90$, $p = 0.027$, $R^2 = 0.064$). Additionally, despite both conditions displaying a visually large spread of plots, an ANOVA of homogeneity of multivariate dispersion shows there is not a significant difference in the within group dispersion of the relatively undisturbed forest and selectively logged forest ($F_{1,28} = 0.001$, $p = 0.974$). Additionally, habitat plots in the two forest conditions do not contain a different number of tree species despite slight differences in mean tree species richness (Mean richness: RUF = 10, SLF = 8.01; $t_{30} = 1.57$, $p = 0.191$).

Forest Structure

Tree density in the selectively logged forest varied from 5 to 15 trees per plot (0.01 ha) with a mean density of 10.9 trees. The mean density was slightly higher in the relatively undisturbed forest, 12.6, and the forest condition showed greater density variation, 6 to 25 trees. However, no significant difference was identified between the density of trees between the relatively undisturbed forest and selectively logged forest ($t_{30} = 1.57$, $p = 0.191$).

Tree size varied considerably within both forest conditions, as seen by the large variation in DBH with both conditions recording a smallest possible size of 9.87cm (31cm circumference) and maximum values of 60.2cm and 77.4cm in the relatively undisturbed forest and selectively logged forest, respectively (Figure 4). However, median DBH was almost identical, 15.9cm in the relatively undisturbed forest compared to 15.3cm in the selectively logged forest. Furthermore, it was found that the trees do not differ in size between the two forest conditions as no significant difference was found in either variance or median of tree DBH (Levene's Test: $F_{1,344} = 1.70$, $p = 0.194$; Mann-Whitney U: $W_{157,189} = 13864$, $p = 0.294$).

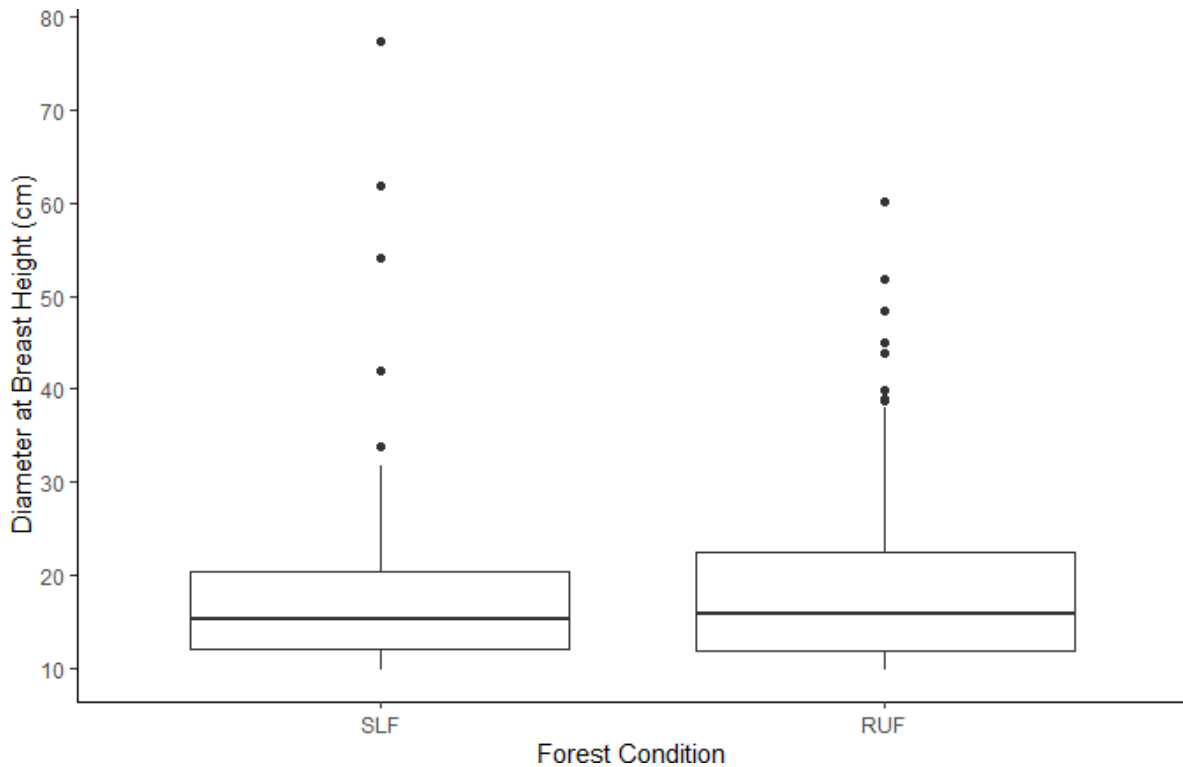


Figure 5: The Diameter at Breast Height (DBH) of trees recorded in the selectively logged (SLF) and relatively undisturbed (RUF) forest conditions. Median DBH SLF = 15.3cm and RUF = 15.9cm. DBH values calculated by conversion of recorded circumference measurement.

A chi-squared test of independence was used to assess differences in tree height between the relatively undisturbed forest and selectively logged forest. The height categories had to be consolidated into $1m \leq h < 16m$ and $16m \leq h < 31m$ for the counts to be sufficiently large enough for the test. A significant relationship between forest condition and tree height was identified ($\chi^2 = 5.16$, $df = 1$, $p = 0.0232$), with residuals analysis showing that the result was due to comparatively more tall trees in the relatively undisturbed forest. To better maintain the initial profile tree heights the midpoint of each height category was used as a proxy for individual tree heights in order to perform additional analysis. Using the midpoints, no significant difference was identified in the heights of trees between the relatively undisturbed forest and selectively logged forest (Welch's T-test: $t_{343.64} = -1.61$, $p = 0.109$). Additionally, despite the relatively undisturbed forest containing more tall trees in the categorical analysis, both forest conditions shared the same modal height category, $11m \leq h < 16m$, and the mean height of the selectively logged forest, calculated using midpoints, was actually marginally taller, 13.45m compared to 12.74m.

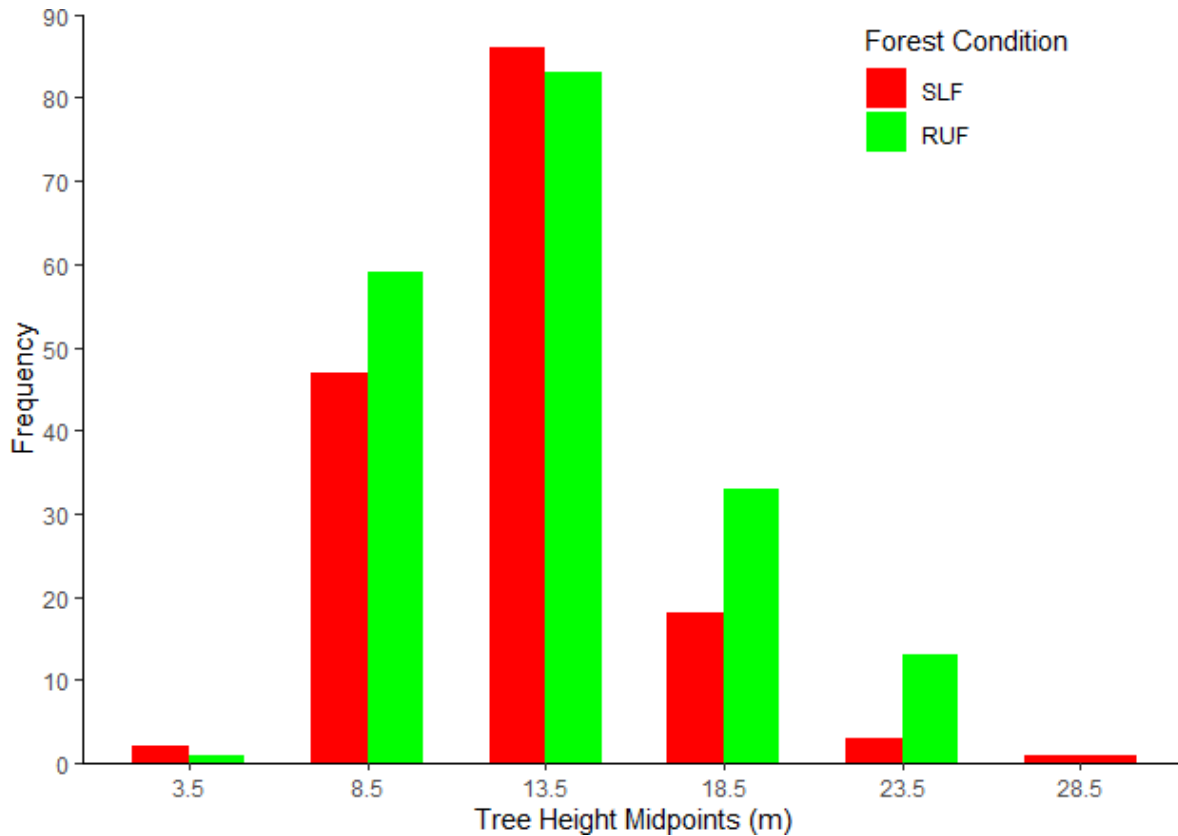


Figure 6: The frequency of trees recorded in each height class in both the selectively logged (SLF: red) and relatively undisturbed (RUF: green) forest conditions in the NLPSPF. Midpoint values calculated from the categorical classes used for estimating tree height. 3.5m represents $1m \leq h < 6m$, 8.5m represents $6m \leq h < 11m$, 13.5m represents $11m \leq h < 16m$, 18.5 represents $16m \leq h < 21m$, 23.5 represents $21m \leq h < 26m$, 28.5 represents $26m \leq h < 31m$.

Seedling and Sapling Abundance

Mean seedling abundance was highest in the relatively undisturbed forest and selectively logged forest, both 20.2, and decreased in the old burn site and new burn site, 12.1 and 4.13, respectively. Mean sapling count displayed the same trend with the most abundant condition being relatively undisturbed forest, 25.1, followed by selectively logged forest, 22.0, then old burn site, 19.5, with new burn site being the least abundant, 9.93. As expected, the abundance of seedlings was found to differ significantly between forest conditions (Square root transformation, ANOVA: $F_{3,56} = 14.47$, $p < 0.001$), and so too did the abundance of saplings (Kruskal-Wallis: $H_3 = 26.4$, $p < 0.001$). Post hoc analysis showed that new burn site plots contained significantly fewer seedlings and saplings than all other forest condition (Seedlings: Tukey'sHSD: 2006: $p = 0.008$; Logged: $p < 0.001$; Undisturbed: $p < 0.001$. Saplings: Dunn's Test with Bonferroni adjustment: 2006: $Z = 2.84$, $p = 0.027$; Logged: $Z = -3.63$, $p = 0.0017$; Undisturbed: $Z = -4.96$, $p = 0$). However, seedling and sapling abundance did not differ among old burn site, selectively logged forest and relatively undisturbed forest despite variation in means.

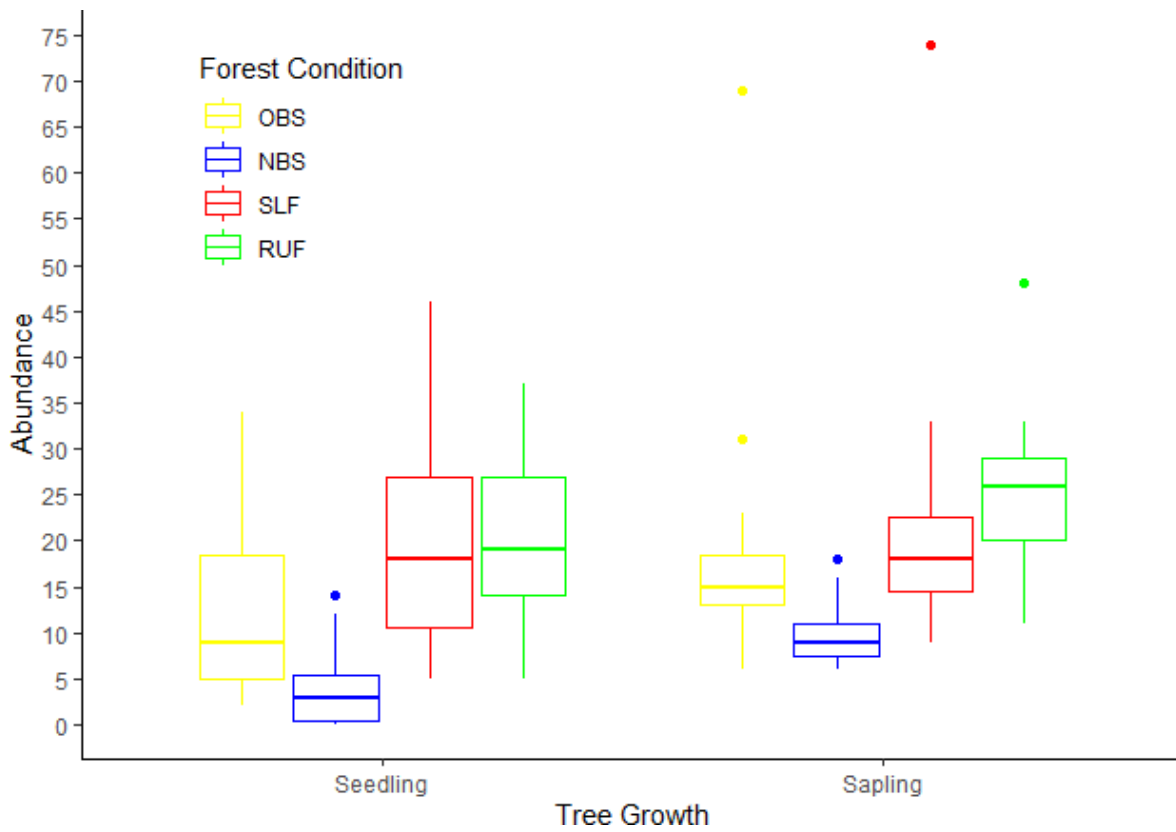


Figure 7: The abundance of seedlings and saplings in the old burn site (yellow), new burn site (blue), selectively logged (red) and relatively undisturbed (green) forest conditions of the NLPSPF. Seedling abundance was counted in 2m x 2m quadrants, whereas sapling abundance was counted in 5m x 5m quadrants.

Discussion

The results presented in this study show clearly that the success of natural vegetation regeneration within the Natural Laboratory of Peat Swamp Forest is greatly dependent on the type of degradation the forest area experienced. The two forest areas degraded by fire are no longer covered by diverse forest and appear highly unlikely to return to their original state. Whereas the historically selectively logged area of the NLPSF is displaying positive signs of successful natural regeneration and, in roughly 15 years, is largely indistinguishable from the relatively undisturbed forest. It is, however, important to note that the surveys conducted in this study were all within a single tropical peat-swamp forest. Additionally, all plots representing each forest condition were located within a single area of that condition, due to the nature of degradation within the site. Therefore, it is important to acknowledge the possibility for pseudo-replication. As spatial autocorrelation of habitat plots limits the independence of each plot, and the subsequent data, it therefore reduces the confidence of significant results identified in this study. However, that does not invalidate the results present here and important insights can still be drawn.

Natural Regeneration Post-Fire

Despite previous studies reporting the possibility for natural regeneration after a single forest fire (van Eijk *et al.*, 2009), the results from this study do not support this and highlight the severity of even a single fire event. The high diversity of trees found in the relatively undisturbed forest is entirely absent in both the new, and old, burn sites, where only *C. rotundatus* is recorded, contrary to the study's hypotheses which predicted an increase in tree diversity with years of regeneration. Although reduced tree diversity has been observed before (van Eijk and Leenman, 2004; Blackham *et al.*, 2014), this finding of only a single species is considerably more extreme. A study of regeneration 13 years post-fire in Block A of the former Mega Rice Project identified 72 tree species and contained both pioneer and mature forest species (Blackham *et al.*, 2014). Despite this study surveying a smaller area, a much greater diversity of trees would be expected if successful regeneration were to be occurring, especially given that the old burn site is now 14 years post-fire. Additionally, the significant reduction in seedling and sapling abundance further highlights the suppression of natural regeneration in the new burn site. More positively, tree regeneration in the old burn site may increase with time as the abundance of seedlings and saplings is significantly greater than in the new burn site and more comparable to the relatively undisturbed forest. However, as this study did not identify the species of seedlings and saplings it is unknown if this new tree growth includes the greater diversity of species required to truly be comparable to the tree community of the relatively undisturbed forest.

As well as a total lack of diversity, tree growth is incredibly sparse in both the old burn site and new burn site and there is a total loss of the closed canopy typical of a tropical peat-swamp forest. This was unexpected in the old burn site and is more consistent with observations from degraded peatlands burnt multiple times (van Eijk and Leenman, 2004). In these sites, regular dry season fires lead to retrogressive succession and eventually the degraded peatland is entirely devoid of trees (van Eijk and Leenman, 2004). If the increased seedling and sapling growth continue to occur in the OBS, the regeneration of a closed canopy composed mostly of pioneer species may be possible, however, even in sites with greater regeneration, it will take multiple tree generations (Blackham *et al.*, 2014).

Tropical peat-swamp forest species have previously been identified as fire-tolerant and capable of surviving even multiple fires, with 26 species of tree, palm, and climber identified (van Eijk *et al.*, 2009). Whilst this does not appear to be the case in this study, as the new burn site contained only a single tree, it is unknown if more trees initially survived the 2015 fire and have died in the years since. Furthermore, resprouting from roots and stumps has been observed as another important mechanism

of tree regeneration in a burnt tropical peat-swamp forest as it increases the diversity of species present and accelerates regeneration after fires (van Eijk *et al.*, 2009; Blackham *et al.*, 2014). Resprouting may play some role in regenerating the new burn site, although it would likely be to a very limited degree as it was only observed a couple of times and not officially recorded.

Whilst the old burn site and new burn site contain roughly equally depauperate tree communities, a greater difference was identified in their respective understories. A difference was expected due to the additional years of regeneration in the OBS; however, it was unexpected that the two fire degraded sites would show greater difference with each other than either do with the selectively logged forest and relatively undisturbed forest. Though, ultimately, both the old burn site and new burn site lacked the diversity of understory plant types present in the relatively undisturbed forest, with both fire degraded sites showing high abundances of only one or two understory plant types. In the old burn site, the highly abundant understory plant type was *Nepenthes* species. Whereas woody shrub species were found in high abundance in the new burn site and, as previously observed in degraded peatland (Blackham *et al.*, 2014), were recorded in high densities on areas of raised debris.

The greatest difference, however, is the vast colonisation of long-range wind-dispersed fern species which are present in all new burn site plots, with an average cover of 74%. Ferns are not a common feature of a mature peat-swamp forest understory in the NLPSF, only present in 4/15 relatively undisturbed forest habitat plots with just a 1% or 2% cover. Additionally, ferns were almost entirely absent in the old burn site, contrary to the study's initial hypothesis. This fern colonisation, and domination, is a common observation in fire degraded tropical peat-swamp forest and previous research within Central Kalimantan has identified *Stenochlaena palustris* and *Blechnum indicum* as dominant species (Cleary and Priadjati, 2005; van Eijk *et al.*, 2009; Page *et al.*, 2009; Blackham *et al.*, 2014).

These differences between the old burn site and new burn site are likely due to differing regeneration barriers within the two sites but it may additionally provide an insight into the successional processes within a fire degraded tropical peat-swamp forest. Which could in turn allow for predictions of the future flora composition of degraded peatland, especially the new burn site. Whilst the flora community of the old burn site was not surveyed in the years following the fire, it is reasonable to assume it was similar to the current new burn site. This is because prior to 2006 they were part of one continuous forest, both experienced a single fire event, and the current degraded sites are separated by only a few hundred metres. Furthermore, this study shows that the additional years of regeneration in the old burn site has not resulted in the site containing vegetation with a greater similarity to undisturbed forest. If this trend continues the successional stages occurring are likely to create an entirely alternative ecologically state with significantly reduced diversity.

Regeneration Barriers

Abiotic conditions

Firstly, after a forest fire has occurred the abiotic conditions of the degraded peatland are vastly different to those of a mature undisturbed forest (Graham *et al.*, 2017). One well recognised change is the loss of forest vegetation and a closed canopy which dramatically decreases the humidity and increases the peat surface temperature and light intensity (Graham *et al.*, 2017). Additionally, the hydrology of degraded peatland changes from a stable near-surface water table to season dependent extremes, characterised by wet season flooding and dry season desiccation (Dommain *et al.*, 2010). These changes are likely both playing a role in the burnt areas of the NLPSF meaning the degraded

peatland is inhospitable for mature forest species and that the immediate regrowth of forest species is prevented (Page *et al.*, 2008).

As vegetation surveys took place towards the end of the wet season, when the water table is at a yearly high point (Lampela *et al.*, 2016), one of the most notable abiotic differences observed in this study was the widespread and deep flooding present in the new burn site. Despite not being formally recorded, water covered the vast majority of the new burn site, and the depth of flooding exceeded 1m in places. The deepest flooding was centred around an old logging canal cut into the peat which bisects the new burn site and connects to Sebangau river. Comparatively, even though surface water covered much of the old burn site it was considerably less deep. To the contrary, this level of flooding is not seen in an undisturbed tropical peat-swamp forest, as was observed in both the relatively undisturbed forest and selectively logged forest. Whilst year-round waterlogging is typical, the forest floor is rarely entirely submerged due to the hummock/hollow microtopography and convex peat dome which keeps water continually moving whilst creating areas of ground above and below the water table (Page *et al.*, 1999; Wösten *et al.*, 2006; Lampela *et al.*, 2014). Previous studies have additionally observed that fire degraded peatland is generally flatter and lacks the water regulation provided by forest vegetation (Lampela *et al.*, 2016).

Whilst these harsh conditions observed in burnt peatlands are not favourable for forest species, pioneer fern and sedge species can tolerate them (van Eijk and Leenman, 2004). As ferns produce large quantities of spores, which are dispersed over long distances by the wind, they can quickly cover large areas of degraded peatland (Cleary and Priadjati, 2005; Blackham *et al.*, 2014). The fern domination then further prevents the reestablishment of tree species as they outcompete slow-growing seedlings for light and space (van Eijk and Leenman, 2004; Shono *et al.*, 2006). Surveys of the new burn site presented in this study clearly support these observations, as ferns dominated the site. In more extreme cases dense fern growth can lead to a negative cycle of recurrent fires and retrogressive selection, as the highly flammable plants act as kindling during the dry season drought preventing the secondary successional stages from ever occurring (Page *et al.*, 2009). Alternatively, one study suggests that this dominant fern colonisation is an essential first stage of natural regeneration (van Eijk and Leenman, 2004). Over many years the rapid growth and death of ferns lead to the accumulation of organic matter which elevates the ground surface above the flooding level and provides other plant types with a chance of establishing (van Eijk and Leenman, 2004).

In addition to explaining the observed differences between the two burnt sites and the forested areas of the NLPSF, the intensity of light and flooding may partly be responsible for the distinctly different vegetation communities recorded within the old burn site and new burn site. Given the landscape surrounding both sites, as well as the considerably smaller size of the old burn site, the old burn site may be experiencing less intense conditions due to the greater presence of surrounding forest (Figure 1). Whilst further research would be required to investigate this, mature forest does affect the microclimate within nearby degraded forest patches (Baker *et al.*, 2014). Additionally, the stark differences observed in flooding height indicate that this may be occurring. When combined with the possible amelioration of sunlight, due to shade provided by the surrounding forest and slightly greater number of trees, these potential differences in abiotic conditions may be allowing for the greater abundance of tree seedlings and saplings in the old burn site, which are only partially tolerant to flooding and light (Graham *et al.*, 2017).

Nutrient cycling

The second regeneration barrier likely to be occurring in the burnt areas of the NLPSF is the reduced efficacy of nutrient cycling, in the already nutrient-poor system (Rieley *et al.*, 2005; Graham, 2013). Nutrient availability in a tropical peat-swamp forest depends on the constant cycling between new plant growth and the production leaf litter and therefore available nutrients are concentrated at the surface of the peat not deeper in the soil (Lampela *et al.*, 2014). Immediately after a fire event nutrient availability is high, however changes in hydrology mean these nutrients are quickly leached from the peat surface and lost into waterways (Lampela *et al.*, 2014). Additionally, with the absence of new leaf litter production to continue the nutrient cycling, regeneration in degraded peatlands is limited by a lack of nutrient availability (Wösten *et al.*, 2008; Graham *et al.*, 2017). 10 tropical peat-swamp forest tree species have shown decreased growth in lower nutrient conditions and therefore may have limited survival in degraded peatlands (Yuwati *et al.*, 2015).

These extremes of nutrient availability post-fire may be playing a role in the NLPSF, with increased availability in the new burn site and deficiency in the old burn site. Additionally, nutrient deficiency may be evidenced by the increased abundance of *Nepenthes* species in the old burn site. *Nepenthes* species can be highly abundant in degraded forest as they feed on insects or animal faeces and do not require soil with high nutrient content (Latiff *et al.*, 2014). Three species have been identified within the NLPSF and their typical high abundance in low pole forest or at the centre of the peat dome further supports this explanation as these areas also experience low nutrient availability (Husson *et al.*, 2018; Page *et al.*, 1999; van Eijk and Leenman, 2004). Furthermore, the near total absence of *Nepenthes* from all other forest conditions surveyed in this study suggests that in the years since the initial fire the old burn site has experienced a significant loss in nutrient availability which is limiting the regeneration of other tropical peat-swamp forest species.

Seed deficiency

Not only do tropical peat-swamp forest species suffer from reduced chances of survival in fire degraded peatlands, but the peatlands themselves also have a reduced source of seeds required to regrow the forest (Blackham *et al.*, 2013; Graham and Page, 2018). Temperate forests hold a large bank of dormant seeds in the soil which then germinate and recolonise after disturbance (Bakker *et al.*, 1996). However, the warm and wet conditions of tropical forests favour immediate germination and therefore have a significantly reduced seedbank (Corlett 2009). Furthermore, the seedbanks present in tropical peat-swamp forests were found to be an order of magnitude smaller than other tropical forests (Graham and Page, 2018). There is also the possibility that as peat-swamp forest fires burn below ground they will destroy the already small seedbank (Ballhorn *et al.*, 2009; Giesen, 2004; Blackham *et al.*, 2014). As the number of seeds still present in a degraded peatland, from before the fire, is likely to be very small there is an even greater importance on the seeds being dispersed into the degraded peatland, the seed rain (Blackham *et al.*, 2013). However, the seed rain in degraded peatland is dominated by a small number of wind-dispersed species and small-seeded species dispersed by passerines such as the yellow vented bulbul (Blackham *et al.*, 2013). The dispersal of larger seeded species is considerably reduced as they rely on mammals and larger birds which are less likely to cross into degraded peatland (Blackham *et al.*, 2013; Corlett, 2017). Therefore, initial tree regeneration will be species poor, compared to undisturbed forest. Remnant trees and artificial perches do increase the species diversity of the seed rain by attracting frugivores, however, subsequent seedling recruitment is no more diverse than open areas (Graham and Page, 2011).

This seed deficiency is likely to be playing a more significant role in the new burn site due to the scale of the burnt site, 8.7km². Despite the new burn site being contained within the wider Sebangau forest, which could function as a seed source, seed dispersal may be limited as previous studies has found significantly reduced dispersal at distances greater than 300m from the forest edge or even less than 100m for some canopy dominant species (Corlett, 2009; Wijedasa *et al.*, 2020). In addition to the reduced size of the old burn site, the area may benefit from the small presence of wind dispersed *Combretocarpus rotundatus* trees which could attract avifauna and increase seed dispersal (Graham and Page, 2017).

Natural Regeneration Post-Logging

The most abundant understory plant type in both the selectively logged forest and relatively undisturbed forest is Pandanaceae, of which there are five known species in the NLPSF (Husson *et al.*, 2018). Pandanaceae has previously been suggested to be an indication of forest disturbance found growing in areas with canopy gaps or preferring the forest edge (Lampela *et al.*, 2016; Frank, 2013). However, the results of this study do not support this, especially as Pandanaceae abundance was greatest in the undisturbed forest. Lianas, too, have been reported as thriving in disturbed forests, growing rapidly in canopy gaps created by logging (Schnitzer and Bongors, 2002). Whilst liana abundance was greater in the selectively logged forest, they were also commonly found in the undisturbed forest, present in 10/15 habitat plots. Given that at least 35 species are found in the NLPSF (Husson *et al.*, 2018), it is more likely that lianas are important to all successional stages in the peat-swamp forest community (Letcher and Chazdon, 2012).

Differences do still remain between the selectively logged forest and relatively undisturbed forest despite 15 years of regeneration since logging stopped. As hypothesised, the selectively logged forest contains a significantly different tree species composition, however, species richness is not significantly reduced. It is important that these findings are treated with caution as increasing sampling effort may have increased the number of species identified in both forest conditions. Therefore, the results of this study may not be truly reflective of the two forest conditions. Interestingly, however, the Chao 1 estimator estimated the species richness to be considerably higher in the selectively logged forest, 71, than the relatively undisturbed forest, 55, although with a large standard error. Whilst this is unexpected, increased species richness post logging has been observed in Ghanaian tropical forest due to the presence of both pioneer and climax species simultaneously (Asase *et al.*, 2014)

Species composition differences have previously been explained by the presence of newly grown pioneer species and the absence of harvested climax species in a logged forest (Okuda *et al.*, 2003). It is possible that these explanations are responsible for some part of the differences observed in the NLPSF. *C. rotundatus*, *Ilex hypoglauca*, and *Syzygium spp.* were all more abundant in the selectively logged forest, with *C. rotundatus* and *I. hypoglauca* completely absent from the relatively undisturbed forest. These three species have previously been identified as pioneer or secondary forest species (Graham and Page, 2012; Mizuno *et al.*, 2016). Therefore, their increased abundance in the selectively logged forest may be the result of logging, supporting the idea that an influx of previously excluded species changes the tree species composition of a degraded forest. However, of the species known to be commercially valuable and widely logged, *Shorea spp.*, *Gonystylus bancanus*, *Cratogeomys spp.*, *Callophylum spp.*, and *Tetramehista glabra* (Giesen, 2009; Husson *et al.*, 2018), only *Callophylum spp.* and *Tetramehista glabra* are more abundant in the relatively undisturbed forest. Therefore, it is unlikely that the absence of harvested species is leading to the observed differences in species composition. Additionally, vector-fitting analysis identified 9 species significantly correlated with the ordination, however, as the ordination did not show clear clustering these species are not representative of either forest condition. Furthermore, the low r^2 value associated with the

PERMANOVA, roughly 6%, shows that forest condition is not explaining much the variation in species composition. Therefore, to gain a better understanding of how, and why, species composition differs greater sampling and a more comprehensive knowledge of the historic logging is required.

Conversely to the tree species composition, the structure of the selectively logged forest is highly similar to the relatively undisturbed forest, with no differences in tree density or DBH. Yet, the mean tree density reported in this study, for both forest conditions, is considerably lower than previously reported for the undisturbed mixed swamp forest habitat in the Sebangau forest (Page *et al.*, 1999). This is most likely due to differences in the classification of a tree as the previous study included trees with a minimum DBH of 7cm, compared to 9.87cm (circumference 31cm) in this study. These additional small trees were responsible for as many as half of those previously counted as the 7cm-12cm DBH category contained on average 57.5% of all trees recorded (Page *et al.*, 1999). Therefore, the tree density of both the selectively logged forest and relatively undisturbed forest, reported in this study, are likely to be equal to or possibly greater than those previously reported for undisturbed tropical peat-swamp forest. Additionally, in the Gunung Palung National Park, West Kalimantan, tree density was reported as being higher in logged forest than unlogged forest, yet, the number of trees with a DBH >35cm was significantly lower in logged forest (Felton *et al.*, 2003). This lack of larger trees in logged forest was not observed in this study and, oppositely, the selectively logged forest contained the largest tree recorded in this study.

Whether or not the upper canopy tree species have successfully regenerated in the selectively logged forest is less clear. The number of trees over 16m tall was found to be significantly lower in the selectively logged forest, than the relatively undisturbed forest, however when converting height categories to midpoints this difference was not identified. Additionally, the modal tree height class, $11\text{m} \leq h < 16\text{m}$, and profile of tree heights identified in this study is generally consistent with multiple other studies in undisturbed areas of NLPSF (Shepherd *et al.*, 1997; Page *et al.*, 1999). Although, both the relatively undisturbed forest and selectively logged forest appear to lack the tallest trees, >30m, found in historically logged Malaysian tropical peat-swamp forest (Wong *et al.*, 2018). If the tallest trees are truly missing from the selectively logged forest, it is not entirely unexpected as the tallest trees would have been more intensely targeted by loggers (Hamard *et al.*, 2010) and limited regeneration of upper-storey tree species has been previously observed in Sumatran tropical peat swamp forest (Gunawan *et al.*, 2012). As with species composition, a greater sample size is needed to further investigate any tree height differences between the two forest conditions.

Conclusion

With such extensive implications, the loss of tropical peat-swamp forests is of huge importance not just for local biodiversity but for global carbon emissions, public health, and the economies of Southeast Asia (Tan *et al.*, 2018). As habitat degradation and severe weather phenomena are set to worsen, there will be an increase in fire prone land (Alamgir *et al.*, 2019; Cai *et al.*, 2014; Gaveau *et al.*, 2013). With this expectation it is vital to have a solid understanding of what will be left in place of current tropical peat-swamp forests. The results of this study suggest that areas of burned tropical peat-swamp forest may be unable to regenerate naturally. Therefore, these sites will have to be the focus of active restoration schemes and further studies will be necessary to identify the site by site requirements of fire degraded peatlands. More positively, the vegetation in selectively logged forests appears to be capable of reaching diversity levels found in undisturbed forest. Therefore, if further degradation can be prevented these areas may be a refuge for the region's faunal diversity.

Chapter One Appendix

Table 1: The tree species recorded in the Natural Laboratory of Peat-Swamp Forest. The table shows the conversion of local species name to scientific names as well as the abundance and location of each tree. RUF = Relatively Undisturbed Forest, SLF = Selectively Logged Forest, OBS = Old Burn Site, NBS = New Burn Site.

Tree local name	Species	Abundance				
		Total	RUF	SLF	OBS	NBS
Alulup	<i>Maasia (Polyalthia) hypoleuca</i>	2	2	0	0	0
Blawan	<i>Tristaniopsis sp.</i>	1	0	1	0	0
Ehang	<i>Diospyros siamang</i>	1	1	0	0	0
Gandis	<i>Garcinia sp.</i>	1	0	1	0	0
Gantalang	<i>Garcinia sp. 3</i>	1	1	0	0	0
Geronggang	<i>Cratoxylum glaucum</i>	11	2	9	0	0
Hangkang	<i>Palaquium leiocarpum</i>	6	5	1	0	0
Irat	<i>Santiria laevigata</i>	3	2	1	0	0
Jambu Barung DK	<i>Syzygium spp.</i>	1	0	1	0	0
Jambu Jambu	<i>Syzygium spp.</i>	16	4	12	0	0
Jangkang Kuning	<i>Xylopiya fusca</i>	11	5	6	0	0
Jelutong	<i>Dyera polyphylla</i>	6	3	3	0	0
Jinjit	<i>Calophyllum hosei</i>	12	9	3	0	0
Kajalaki	<i>Aglaia rubiginosa</i>	2	2	0	0	0
Kapurnaga	<i>Calophyllum sclerophyllum</i>	2	2	0	0	0
Katiau	<i>Madhuca mottleyana</i>	3	0	3	0	0
Kelumun buhis	<i>Nephelium maingayi</i>	1	0	1	0	0
Kempas	<i>Koompassia malaccensis</i>	1	1	0	0	0
Kemuning putih	<i>Syzygium sp.2</i>	3	2	1	0	0
Kenari	<i>Blumeodendron tokbrai (elateriospermum)</i>	9	8	1	0	0
Lalas DK (kayu lalas daun kecil)	<i>Syzygium sp.5</i>	2	1	1	0	0
Mahadingan	<i>Calophyllum spp.</i>	2	1	1	0	0
Mahadingan M	<i>Calophyllum spp.</i>	1	1	0	0	0

Malam Malam	<i>Diospyros areolata</i>	12	9	3	0	0
Manggis	<i>Garcinia spp.</i>	9	7	2	0	0
Mangkinang	<i>Elaeocarpus mastersii</i>	20	12	8	0	0
Medang	<i>Litsea sp. 1 cf. resinosa</i>	4	3	1	0	0
Medang dua	<i>Litsea spp.</i>	9	1	8	0	0
Medang limo	<i>Magnolia bintulensis</i>	1	0	1	0	0
Medang M	<i>Litsea spp.</i>	3	0	3	0	0
Mendarahan daun besar	<i>Horsfieldia crassifolia</i>	11	9	2	0	0
Mendarahan daun kecil	<i>Gymnacranthera farquhariana</i>	2	1	1	0	0
Meranti	<i>Shorea teysmanniana</i>	8	8	0	0	0
Meranti Sumut	<i>Shorea teysmanniana</i>	22	4	18	0	0
Mertibu	<i>Dactylocladus stenostachys</i>	1	0	1	0	0
Nonang	<i>Xylopia coriifolia</i>	2	1	1	0	0
Nyatoh babi	<i>Palaquium pseudorostratum</i>	1	1	0	0	0
Nyatoh burung	<i>Palaquium ridleyii cf. xanthochymum</i>	1	1	0	0	0
Nyatoh gagas	<i>Palaquium cochlearifolium</i>	3	2	1	0	0
Nyatoh Palanduk	<i>Isonandra lanceolata</i>	1	1	0	0	0
Pampaning	<i>Lithocarpus spp.</i>	2	1	1	0	0
Pampaning bitik	<i>Lithocarpus sp. 1 cf. dasystachys</i>	9	1	8	0	0
Papong	<i>Sandoricum beccanarium</i>	9	4	5	0	0
Pisang Pisang	<i>Mezzetia spp.</i>	3	3	0	0	0
Pisang Pisang Besar	<i>Mezzetia parviflora (leptopoda)</i>	9	4	5	0	0
Pisang pisang K	<i>Mezzetia umbellata</i>	1	1	0	0	0
Ponak	<i>Tetramerista glabra</i>	5	4	1	0	0
Pupuh palanduk	<i>Neoscortechinia kingii</i>	15	9	6	0	0
Rambai hutan	<i>Baccaurea bracteate</i>	3	2	1	0	0
Rambangun	<i>Tetractomia tetrandra</i>	20	12	8	0	0
Rambutan hutan	<i>Nephelium lappaceum</i>	14	6	8	0	0

Ramin	<i>Gonystylus bancanus</i>	1	1	0	0	0
Rasak	<i>Cotylelobium lanceolatum</i>	1	1	0	0	0
Sumung	<i>Ilex hypoglauca</i>	6	0	6	0	0
Tabaras akar tinggi	<i>Mesua sp.1</i>	11	9	2	0	0
Tabaras biasa	<i>Stemonurus scorpiodes</i>	2	0	2	0	0
Takal	<i>Calophyllum soulattri</i>	5	0	5	0	0
Tampang	<i>cf. grandis var. rufofusca (cf. rufofusca)</i>	5	2	3	0	0
Tarantang	<i>Camptosperma coriaceum</i>	7	6	1	0	0
Tatumbu	<i>Syzygium havilandii</i>	8	3	5	0	0
Tumih	<i>Combretocarpus rotundatus</i>	20	0	2	17	1

Chapter Two: Assessing the Biodiversity of Degraded Tropical Peat-Swamp Forest by Surveying the Fruit-Feeding Butterfly Community

Abstract

The degradation of tropical peat-swamp forests is continuing to occur at an alarming rate, with few areas of pristine forest remaining in Southeast Asia. As these forests are global hotspots of biodiversity and act as refuge for significant populations of critically endangered species, it is vital to better understand the consequences of all degradation types for the region's fauna. Lepidoptera populations are regularly surveyed to indicate the wider habitat condition but are, additionally, deserving of attention due to their diversity and importance in an ecosystem. This study investigated the effect of historical logging and forest fires on fauna by survey the fruit-feeding butterfly population in the multiply degraded Sebangau Forest, Kalimantan. From August 2018 – July 2019, 1370 butterfly trappings were recorded from a total of 17 species. The burned forest area was almost entirely devoid of butterflies, with only 12 recorded across the year. In contrast, the population recorded in the historically selectively logged forest showed equal abundance, species richness, and species composition to the relatively undisturbed forest. Additionally, abundance and species richness significantly increased during April, May, and June, highlighting the importance of year-round studies. When considering the biodiversity indicator application of Lepidoptera, this study suggests that burned tropical peatlands are uninhabitable for forest fauna, emphasising the importance of fire prevention. However, recovering selectively logged forests can be highly valuable for conservation if these areas receive the necessary protection and future degradation can be prevented. These secondary forests could provide a vital lifeline to species dependent on tropical peat-swamp forests.

Introduction

The tropical forests of Southeast Asia are among the most biodiverse ecosystems on the planet and are rightly recognised as a conservation priority (Myers *et al.*, 2000). Borneo, part of the Sundaland hotspot, contains the largest area of intact forest in Southeast Asia and is comprised of a vast array of different forest ecosystems (Alamgir *et al.* 2019). One such ecosystem is the tropical peat-swamp forest, which is widely distributed across the lowland coastal regions as well as up to 200km inland along river valleys (Rieley *et al.*, 1996; Page *et al.*, 2006). These forests harbour a great diversity of flora and fauna and, in particular, are vital refuges for populations of the threatened primates and felids, as well as a high number of endemic freshwater fish (Jackson *et al.*, 2009; Posa *et al.*, 2011; Husson *et al.*, 2018).

Despite growing recognition of their importance, the destruction of these forests is continuing to occur on a colossal scale (Miettinen *et al.*, 2016). This initially began in the early 1980s as peat-swamp forests were largely unclaimed and historically assigned biologically unimportant (Husson *et al.*, 2018). As a result, the forests were widely logged or converted for agriculture and plantations in an effort to reclaim the land (Posa *et al.*, 2011; Murdiyarso *et al.*, 2019). The most severely degraded sites then became vulnerable to fire resulting in further uncontrolled destruction (Turetsky *et al.*, 2015). As of 2015, only 6.4% of peatlands across Peninsular Malaysia, Sumatra, and Borneo remained covered by pristine peat-swamp forest (Miettinen *et al.*, 2016). Roughly 22.8% are classified as degraded forest, with the remainder of peatland sites varying from industrial plantation to entirely burnt open areas (Miettinen *et al.*, 2016). Given such small areas of pristine forest remain, the regeneration and protection of degraded peatland is essential for the conservation of tropical peat-swamp forests and the ecosystem services they provide.

Little is known about the faunal biodiversity of degraded tropical peat-swamp forests as most efforts so far have focussed on the recovery of hydrological conditions and the regeneration of vegetation (van Eijk and Leenman, 2004; Blackham *et al.*, 2014; Graham *et al.*, 2017). Of the few published studies exploring faunal diversity, decreases in butterfly diversity have been observed (Houlihan *et al.*, 2013) as well as reductions in the density of primates and other large mammals (Posa *et al.*, 2011). Although, logged forests may still be capable of supporting diverse fauna populations as evidenced by the presence of high bird diversity (Hawa *et al.*, 2016) and 4 of the 5 Bornean felid species (Cheyne *et al.*, 2011). Whilst high biodiversity, and significant conservation potential, has been recognised in the secondary forests of other tropical forest ecosystems (Dent, 2010), considerably more attention is required to determine if the same can be said for tropical peat-swamp forests.

In order to do this, well defined and scientifically underpinned long-term projects are required to fully understand the extent of degradation and regeneration (Lindenmayer and Likens, 2009). One commonly adopted technique is to survey butterfly populations to infer the health of the wider habitat (Bobo *et al.*, 2006; Nyafwono *et al.*, 2014). Known as indicator species, the high mobility, high habitat sensitivity, and short generation time of butterfly species allows them to be highly responsive to changes in the environment (Thomas, 2005; Bonebrake *et al.*, 2010). In addition to biological justifications, surveying well-identified populations is both time and cost-effective, with multiple successful methods well established (Sparrow *et al.*, 1994; Purwanto *et al.*, 2015).

However, even with its wide usage, there is a lack of clarity surrounding the capability of butterfly populations to accurately indicate habitat quality as positive correlations between butterfly species richness and other taxonomic groups do not always hold true (Lawton *et al.*, 1998). Furthermore, two review papers, assessing 40 individual studies, concluded that habitat degradation across the tropics has resulted in increases, decreases, and no effect on Lepidoptera richness or diversity (Koh *et al.*,

2007; Bonebrake *et al.*, 2010). Importantly though, neither of these review papers includes a single study carried out in a tropical peat-swamp forest and therefore butterfly surveys may still provide a potentially effective mechanism for understanding wider habitat biodiversity. Additionally, this highlights the significant lack of scientific attention peat-swamp forest populations have received in comparison to dipterocarp forests (Houlihan *et al.*, 2013), and more significantly temperate regions (Bonebrake *et al.*, 2010). Previous studies suggest it is likely that tropical peat-swamp forest butterfly populations will be highly impacted by habitat disturbance as species richness and diversity are positively correlated with canopy cover and individuals are highly capable of flying multiple kilometres to more favourable conditions (Houlihan *et al.*, 2013; Marchant *et al.*, 2015). Moreover, the understudied butterfly populations are themselves deserving of scientific attention and should not only be studied within the indicator framework (Bonebrake *et al.*, 2010). This is due to their role in pollination, nutrient cycling, and as an important food source at both larval and adult life stages (Bonebrake *et al.*, 2010; Basset *et al.*, 2011).

Therefore, the main aim of this study is to assess the biodiversity within a degraded tropical peat-swamp forest to gain insight into their conservation potential. By surveying the butterfly population, the study hopes to draw wider inferences into the total faunal biodiversity of the selectively logged and burned forest areas within the Sebangau forest, Central Kalimantan, Indonesia. The Sebangau forest provides an excellent opportunity as the fruit-feeding butterfly population is well identified and threatened by multiple types of current and historic degradation (Houlihan *et al.*, 2012).

Specifically, this study will investigate two main questions: (1) How do the species richness and abundance differ between the burned, selectively logged, and relatively undisturbed forest conditions? It is hypothesised that the burned forest will contain the fewest species and smallest abundance. The selectively logged forest will contain a greater number of species and increased abundance, compared to the burned forest, but still fewer than the relatively undisturbed forest. (2) How does the species composition differ among the three forest conditions? It is hypothesised that all three forest conditions will contain significantly different species compositions. The burned forest will be dominated by generalist species and lack forest specialists. The logged forest will contain a mixture of both generalists and forest specialists, but at a reduced abundance compared to the undisturbed forest. The undisturbed forest will only contain forest specialists, including specialist species not recorded in the undisturbed forest.

Methods

Survey Period and Trap Layout

Fruit-feeding butterfly surveys were conducted in three forest conditions within the mixed-swamp forest habitat of the NLPSF: the relatively undisturbed forest (RUF), the selectively logged forest (SLF), and the new burn site (NBS). In the relatively undisturbed forest and selectively logged forest surveys were conducted for a full year from August 2018 – July 2019. However, the final month of surveying was not completed in the new burn site and, therefore, data was only collected for 11 months, August 2018 – June 2019.

Three transects were established within each forest condition, which were separated by 100m and ran parallel from east to west. A total of 10 traps were hung on each transect, with 5 in the understory, 1m-2m above ground, and 5 in the canopy, roughly 15m depending on the forest structure. Understory and canopy traps were hung in pairs to capture the full community of fruit-feeding butterflies in the NLPSF (Houlihan *et al.*, 2013). Therefore, trap pairs were hung in 5 locations along each transect with 50m between each pair. In the selectively logged forest and relatively undisturbed forest, traps were suspended from tree branches using nylon string and tied off around the tree trunk to secure the trap. In the new burn site, where the canopy is no longer present, traps were hung at an equivalent height using bamboo poles to suspend the trap.

Trap Set-Up

The butterfly population was surveyed using fruit baited traps as it is a highly reliable and unbiased technique (Bonebrake *et al.*, 2010). Whilst this technique predominantly traps fruit-feeding butterflies in the Nymphalidae family, it is a widely used technique as these species make up a significant proportion of the butterfly species in tropical forests (DeVries *et al.*, 2012). The trap type and bait used in this study were consistent with those used in previous research (Houlihan *et al.*, 2013). The traps are a cylindrical shape, roughly 1m in height and 30cm in diameter, made from a polyester mesh. They have a closed top and open base, with a bait tray hanging below the open base. The bait was a mixture of sugar, fermenting bananas, and Malaga, a locally sourced liqueur.

Trap Monitoring

A single survey period consisted of five consecutive days of trap monitoring, with the traps being placed the day before the first monitoring day and taken down on the fifth monitoring day. On monitoring days each trap was checked once daily between 8 am and 12 pm. All trapped butterflies were identified to species level, when possible, using a local species guide (Houlihan *et al.*, 2012). The genera *Tanaecia* and *Euthalia* require microscopy of genitalia to separate species so individuals were only recorded to genus level (Hill *et al.*, 2001). Unique identification codes were written on the underside of every butterfly's wing to allow for the recording of any recaptures. All individuals were subsequently released, and traps were re-baited daily to prevent drying out and replenish any missing bait.

Statistical Analysis

All trappings, including recaptures, were treated as separate data points and included in all sections of the analysis. This is because butterflies were found to cross between forest conditions, as well as being recaptured across multiple months, and therefore a recaptured individual can be an important component of multiple butterfly communities, justifying their inclusion. Additionally, recapture percentages were low overall, indicating butterflies were not “trap happy” and recaptures are unlikely to overinflate abundances.

Species accumulation curves were produced to visually assess the completeness of butterfly species sampling in each forest condition. In addition, the Chao 1 species richness estimator was used to estimate each condition’s true total species richness.

To identify differences in species richness and number of trappings, per trap pair in each forest condition, Generalised Linear Mixed Effect Models (GLMM) were constructed using the maximum likelihood estimation. Forest condition was modelled as a fixed effect and month, transect, and trap pair were included as random effects. Trap pair was nested within transect. Uniformity, overdispersion and zero-inflation were checked to allow for the identification of the correct distribution family. As a result, the Poisson distribution, with a long link function, was chosen for species richness whilst negative binomial was used for butterfly abundance.

The butterfly species composition of each forest was compared visually by performing non-metric multidimensional scaling (nMDS) using the Bray-Curtis dissimilarity index. A dummy species was added to species composition matrix in order to reduce the Bray-Curtis coefficient’s erratic behaviour when analysing datasets with highly, or entirely, denuded samples (Clarke *et al.*, 2006). Permutational multivariate analysis of variance (PERMANOVA) was then used to test for significant differences among each condition’s species composition. An ANOVA was used to test the homogeneity of each forest condition’s multivariate dispersion, a key assumption of PERMANOVA.

All analysis was performed using R studio 3.6.3 (R Core Team, 2019). GLMMs were constructed using ‘lme4’ (version 1.1-23: Bates *et al.*, 2015) and all assumptions checked using ‘DHARMA’ (v0.3.2.0: Hartig, 2016). Multivariate analysis was performed using ‘Vegan’ (v2.5-6: Oksanen *et al.*, 2019). All figures were produced using ‘ggplot2’ (v3.1.1: Wickham, 2016).

Results

A total of 1370 butterfly trappings were recorded over 175 survey days between August 2018 – July 2019. This comprised of 1191 separate individuals of which 144 individuals were recaptured at least once (Total recaptures: 179; Single recapture: 117; Double recapture: 20; Triple recapture: 6; Quadruple recapture: 1). At least 17 species of butterfly were trapped in total, however, only 15 could be identified to species level. Individuals of the *Tanaecia* and *Euthalia* genera were only identifiable to genus level as species identification requires microscopy of genitalia (Hill *et al.*, 2001).

Across the entire study only 12 butterfly trappings occurred in the new burn site, 10 *Melanitis leda* and single individuals of *Tanaecia spp.* and *Zeuxidia aurelius*. As a result, the new burn site was excluded from statistical analysis. On the contrary, 687 and 671 butterfly trappings were recorded in the relatively undisturbed forest and selectively logged forest, respectively. Both forest conditions contained 15 species, 13 of which were shared. Species accumulation curves for both the relatively undisturbed forest and selectively logged forest begin to approach the asymptote and therefore increased sampling effort would likely only marginally increase the number of species recorded in either forest condition (Figure 8). This is supported by the Chao 1 richness estimator which estimates the true number of species in the relatively undisturbed forest to be 17.2 (SE \pm 3.31) and 22.8 (SE \pm 11.3) in the selectively logged forest.

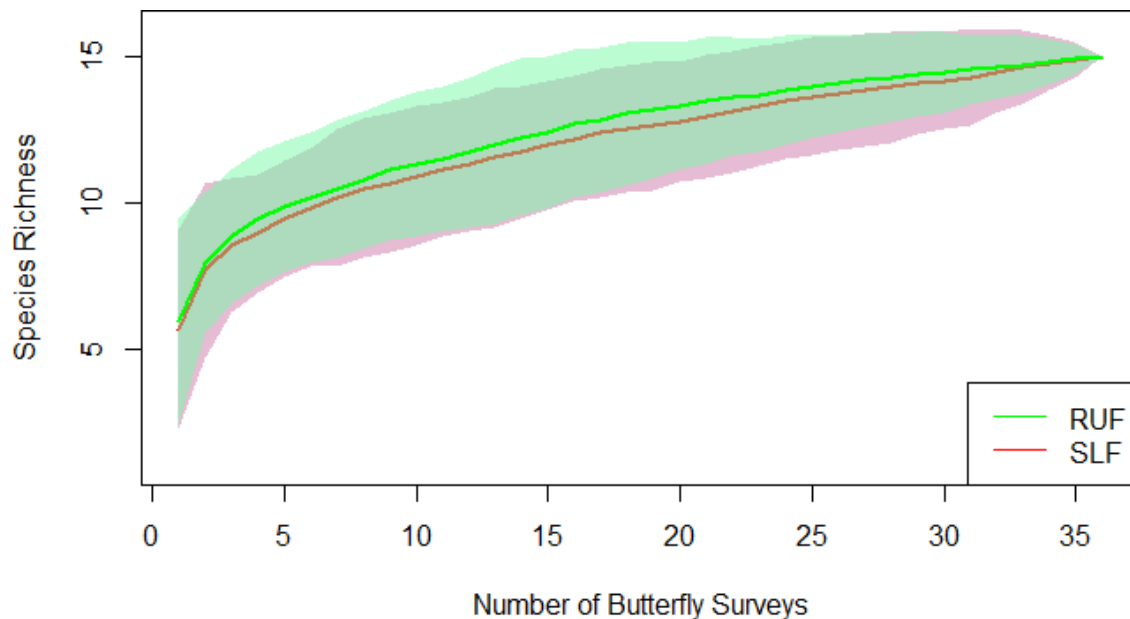


Figure 8: Mean species accumulation curves for the butterfly species richness of the relatively undisturbed RUF: green) and selectively logged (SLF: red) forest areas in the NLPSF. A single survey was defined as the accumulation of trappings from all 5 trap pairs per transect, for the 5 consecutive days of monitoring each month. Random permutations = 100 and shaded areas represent a 95% confidence interval.

Abundance

Overall, the number of butterfly trappings across the whole of the selectively logged forest and relatively undisturbed forest remained relatively equal throughout the course of the study, with peaks and falls occurring in the same months (Figure 9). From August to April the total number of butterfly trappings was greater each month in the relatively undisturbed forest, however, during May, June and July, the opposite was found. The greatest difference occurred in February when the twice as many butterfly trappings were recorded in the relatively undisturbed forest, 32 compared to 16. However, the difference in number of trappings per condition per month was typically small, with a mean difference of 12.3 butterflies, just 10.8% of the average total. Much greater differences in the number of butterfly trappings are seen when comparing across months, with considerable increases in April, May, and June (Figure 9). The combined abundance of all trappings in both forest conditions from August to March varied from 48 to 132. Whereas April, May, and June averaged 207.3 total trappings which then decreased again July back to 79. The least abundant month was February with 48 total butterfly trappings and the most abundant was May with 242. The observations were confirmed by the results of a GLMM which found that the abundance of butterflies recorded in trap pairs did not significantly differ between the selectively logged forest and relatively undisturbed forest ($Z = -0.047$, $p = 0.962$).

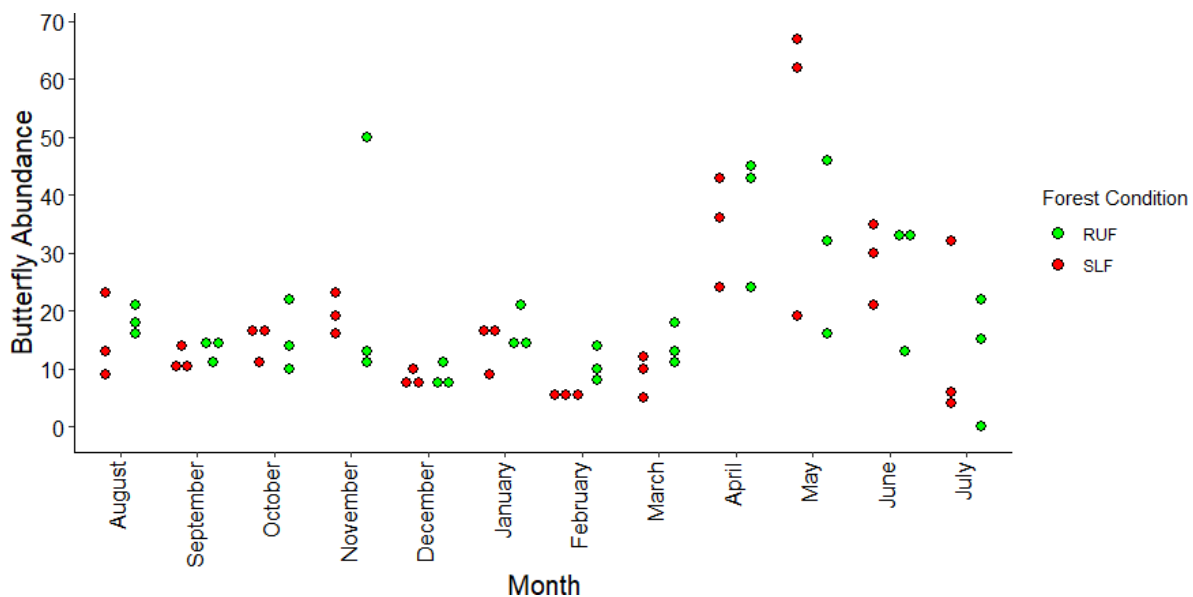


Figure 9: The abundance of fruit-feeding butterflies in the relatively undisturbed (RUF: green) and selectively logged (SLF: red) and forest areas of the NLPSF. The abundance values presented are the total number of trappings recorded across all 5 trap pairs per transect per month, from August 2018 – July 2019, with each forest condition containing three transects.

Species Richness

The species richness of fruit-feeding butterflies in the NLPSF follows the same patterns described above for abundance. The total species richness of the two forest conditions is roughly each month and, again, a greater difference is apparent when comparing between months (Figure 10). In 5 of the 12 months the two conditions contained the same species richness, when trappings from all transects in each condition were combined (September = 9; November = 9; February = 8; March = 8; April = 12). April was the most species rich month with both forest conditions containing 12 species and a total of 16 different species when combined. This was twice the number of species recorded in August, December, January, March, and July when only 8 species were recorded in total across both the selectively logged forest and relatively undisturbed forest. The greatest variation between forest conditions occurred in December as the selectively logged forest contained 7 species compared to 4 in the relatively undisturbed forest. Again, these observations were confirmed by GLMM as the species richness of trap pairs did not significantly differ between the two forest conditions ($Z = -0.199$, $p = 0.843$).

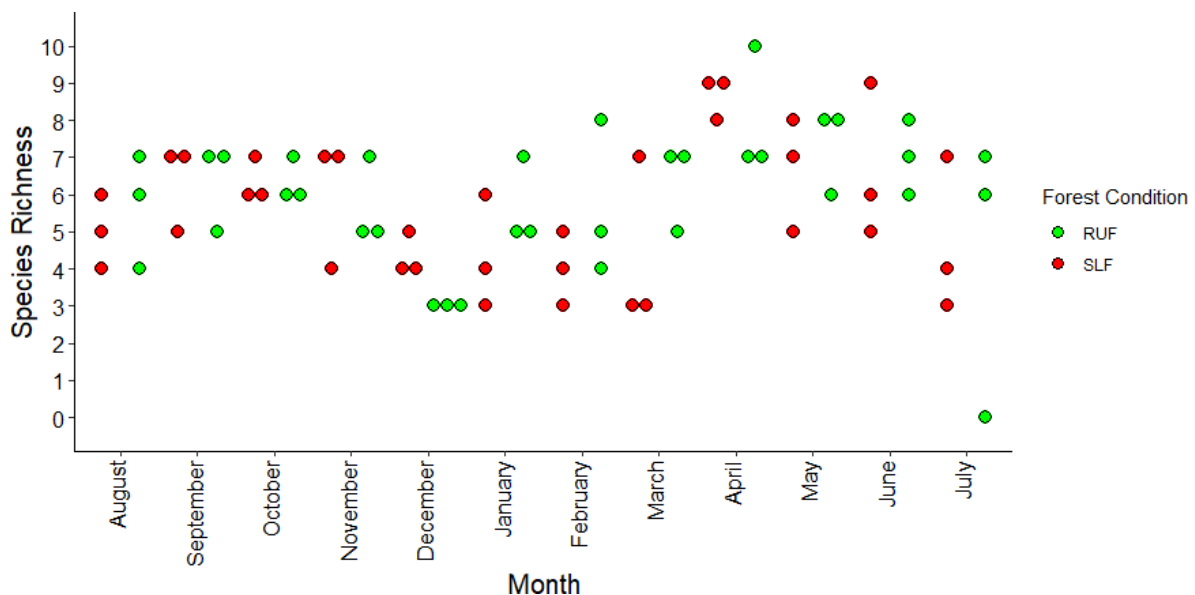


Figure 10: The species richness of fruit-feeding butterflies in the relatively undisturbed (RUF: green) and selectively logged (SLF: red) forest areas of the NLPSF. The species richness values presented are the total number of species recorded across all 5 trap pairs per transect per month, from August 2018 – July 2019, with each forest condition containing three transects.

Species composition

Over the course of the study 17 species were recorded in total, 13 of which were shared between the selectively logged forest and relatively undisturbed forest conditions. Only two species were exclusive to the relatively undisturbed forest, *Mycalesis patiana* and *Faunis stomphax*. Likewise, two species were recorded only in the selectively logged forest, *Euthalia* sp. and *Lexias canescens*. However, these four species were the least abundant across the study with only single trappings of *Euthalia* sp. and *L. canescens* and 2 trappings of *M. patiana* and *F. stomphax*. Additionally, the five most abundant species in each of the two forest conditions were the same, indicating that their respective species compositions are highly similar (RUF: *Agatasa calydonia* (142), *Dophla evelina* (127), *Prothoe franck* (102), *Lexias pardalis* (81), *Tanaecia* sp. (74). SLF: *A. calydonia* (145), *L. pardalis* (113), *P. franck* (95), *D. evelina* (87) and *Tanaecia* sp. (85)).

Visual comparison, by nMDS, of the composition of the fruit-feeding butterfly communities shows no separation in the clustering of points by forest condition (Figure 11, $k = 2$, stress = 0.207). This further supports the observation that the selectively logged forest and relatively undisturbed forest contain the same species, at the same abundances, in their respective forest areas. Furthermore, a PERMANOVA test found that the species compositions did not significantly differ between the two forest conditions ($F_{1,71} = 0.533$, $p = 0.800$, $R^2 = 0.005$). Species composition was found to significantly vary between months ($F_{11,71} = 4.08$, $p = 0.001$, $R^2 = 0.441$), however, as no significant interaction was identified between habitat and month it would indicate that month is affecting the species composition of both forest conditions in the same way ($F_{11,71} = 0.757$, $p = 0.931$, $R^2 = 0.082$).

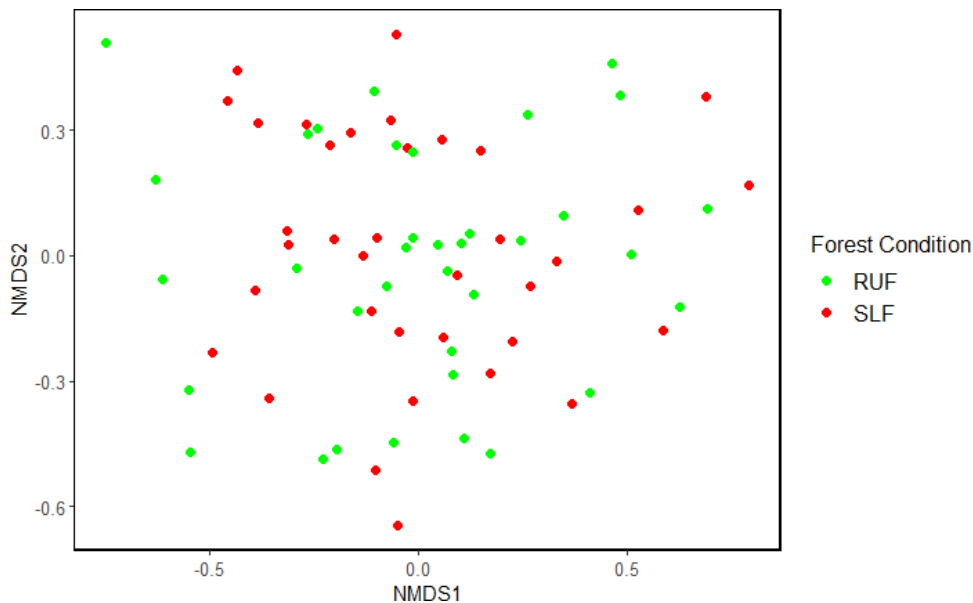


Figure 11: Non-metric multidimensional scaling of the Bray-Curtis dissimilarity matrix of the fruit-feeding butterfly species composition by forest condition. Each point represents a pooling of all butterfly recordings per transect per month. Forest conditions included are the relatively undisturbed forest (RELATIVELY UNDISTURBED FOREST: green) and the selectively logged forest (SELECTIVELY LOGGED FOREST: red). NMDS1 and NMDS2 display the two dimensions of the nMDS ($k = 2$, stress = 0.207, random starts = 50, iterations = 999).

Butterfly Recaptures

In total 144 individuals, from 10 species, were recaptured at least once across the entire survey period, totalling 179 recaptures. All recaptures occurred in the relatively undisturbed forest and selectively logged forest, and none of the 12 butterflies recorded in the new burn site were recaptured. Of the 144 individuals recaptured 39 were found to have crossed between the selectively logged forest and relatively undisturbed forest conditions. The direction of crossing was roughly equal as 16 individuals moved from the selectively logged forest to relatively undisturbed forest, 19 moved from relatively undisturbed forest to selectively logged forest, and 2 individuals crossed between the conditions multiple times. These 39 individuals came from 9 of the 10 recaptured species, only *Faunis stomphax* was recaptured and did not cross forest conditions. However, it is difficult to compare *Faunis stomphax* to the other recaptured species as it was only recorded twice across the whole survey, a single individual captured on two consecutive days on the same transect.

Table 2: A summary of fruit-feeding butterfly recaptures in the NLPF. Total heading shows the respective species' abundance across the whole survey. Recapture heading additionally shows how many times an individual was recaptured (1, 2, 3 or 4). Recapture rate = (Number of individuals recaptured/Total number of Individuals) * 100 (e.g. *Agatasa calydonia* (35/245)*100 = 14.3%).

Species	Total		Recapture						
	Trappings	Number of Individuals	Total Recordings	Number of Individuals	1	2	3	4	Rate (%)
<i>Agatasa calydonia</i>	287	245	42	35	29	5	1	0	14.3
<i>Dophaevelina</i>	214	177	37	28	21	5	2	0	15.8
<i>Prothoe franck</i>	197	150	47	31	20	7	3	1	20.7
<i>Lexias pardalis</i>	194	176	18	17	16	1	0	0	9.66
<i>Tanaecia</i> spp.	160	148	12	12	12	0	0	0	8.11
<i>Charaxes bernadus</i>	128	120	8	7	6	1	0	0	5.83
<i>Melantis leda</i>	88	79	9	8	7	1	0	0	10.1
<i>Zuexidia aurelius</i>	66	62	4	4	4	0	0	0	6.45
<i>Lexias cyanipardus</i>	12	11	1	1	1	0	0	0	9.09
<i>Faunis stomphax</i>	2	1	1	1	1	0	0	0	100

Discussion

The results of this study show that the type of degradation is critically important in determining how the fruit-feeding butterfly population recovers in the years following the degradation, in a tropical peat-swamp forest. This study observed an almost entire loss of the butterfly community in a burnt area of the Sebangau forest, roughly four years after the fire occurred. However, the butterfly community in the forest area that was historically selectively logged is now indistinguishable from the relatively undisturbed forest, indicating that these degraded forests are of considerable conservation value. As with chapter one, it is again important to note that the surveys conducted in this study were all within a single tropical peat-swamp forest and traps representing each forest condition were located within a single area of that condition. Therefore, it is possible that pseudo-replication may reduce the confidence in the significance of these results as spatial autocorrelation limits the independence of butterfly traps.

Whilst species richness and abundance were expected to be reduced, the near total absence of a butterfly community in the new burn site presents a more severe loss than hypothesised by this study. Across the entire study only 12 individuals were recorded, which is just 2% of the abundances recorded in the other forest conditions. Furthermore, these 12 individuals were comprised of only three species, *Melanitis leda*, *Zuexidia aurelius*, and *Tanaecia* sp., which is a loss of 80% of the species recorded in the relatively undisturbed forest. Previous studies in dipterocarp forest have also reported significant decreases in abundance and richness after forest fires, yet still recorded more than 500 individuals from over 50 species (Cleary, 2003; Cleary and Genner, 2004; Hirowatari *et al.*, 2007). Comparing the two forest types further highlights the fragility of the population surveyed in this study as the loss of even a few species has a proportionally greater impact when the butterfly community is already less diverse.

Interestingly, 10 of the 12 individuals trapped in the burned forest were *Melanitis leda*, a wide-ranging generalist species (Hirowatari *et al.*, 2007). Whilst the species composition of the NEW BURN SITE could not be statistically analysed in this study, multiple previous studies have identified significant composition changes due to high abundances of *M. leda* and other generalist species from the Satyrinae and Charaxinae subfamilies (Cleary and Genner, 2004; Hirowatari *et al.*, 2007; Widhiono, 2015). This is because species such as *M. leda* can utilise a wide range of host plants and the larvae can successfully develop on a vast array of plant species, typically grasses (Larsen, 2005; Molleman *et al.*, 2020). These grass species are early colonisers in a burnt tropical peat-swamp forest (Blackham *et al.*, 2014), which suggests that if any butterfly community is to establish in the new burn site it will be dominated by relatively few generalist species.

Additionally, the loss of forest specialists observed in the new burn site is another regular observation with regards to composition changes in degraded areas (Koh, 2007). Forest specialists are unable to survive in burned forests due to their greater thermal sensitivity, making them unable to tolerate harsh altered conditions, and high host-plant specificity, which increases the likelihood of insufficient larval resources (Koh, 2007). These species also tend to be endemic or have narrow ranges (Posa *et al.*, 2008), and as such are at a particular risk of extinction (Charrette *et al.*, 2006). Furthermore, forest specialist species are characteristically less opportunist, with reduced dispersal capabilities, therefore they will take a much longer time to return to fire degraded sites (Cleary and Genner, 2004).

Contrary to the burned forest, the fruit-feeding butterfly community in the selectively logged forest is largely indistinguishable from that of the relatively undisturbed forest. This study found no difference in richness, abundance, or composition of the butterfly community, as well as a greater number of fruit-feeding butterfly species than previous surveys in the NLPSF (Houlihan *et al.*, 2013; Tremlett, 2014). This similarity in composition was not hypothesised due to the findings of previous studies in both the

logged areas of the NLPF (Houlihan *et al.*, 2013; Tremlett, 2014; Bennett, 2015) and other tropical forest ecosystems (Koh, 2007; Bonebrake *et al.*, 2010). These previous studies found a wide variety of results, including increases in richness and diversity which are often explained by the “Intermediate Disturbance Hypothesis” (Connell, 1978). This hypothesis states that moderate disturbance levels result in a greater number of species by increasing habitat heterogeneity and preventing competitive exclusion by dominant species (Connell, 1978). In a logged forest this equates to the creation of canopy gaps which increases the level of light reaching the understory and is typically a preference of generalist species previously excluded from closed-canopy forests (Hamer, 2001; Hamer, 2003). Alternatively, any decreases in abundance or richness in a logged forest are, again, due to the loss of specialist, narrow-ranged, or endemic species which are more highly impacted by disturbance (Koh, 2007).

However, these explanations do not apply to the results found in this study as a high similarity was observed between the two communities. Instead, a possible explanation may be that the additional years of vegetation regeneration has continued to alter the butterfly community in the selectively logged forest and allowed the community to return to its original composition. Evidence for this is the presence of *Charaxes borneensis*, *Faunis stomphax*, *Prothoe franck*, and *Mycalesis patiana*. These species were not previously recorded in the logged forest (Houlihan *et al.*, 2013) and are all recognised as forest specialists or even indicators of undisturbed forest (Hirowatari *et al.*, 2007; Cleary, 2004). Additionally, a return to the original butterfly composition, after additional years of regeneration and multiple intermediate populations, has been observed in a Brazilian tropical forest (Sant’Anna *et al.*, 2014).

Whilst this study did not explicitly seek to understand seasonal variation in the butterfly population, it is important to consider when comparing the results of this study to others. This study surveyed the butterfly population for a full year, compared to other butterfly surveys in tropical peat-swamp forests which surveyed for only a few months (Houlihan *et al.*, 2013; Tremlett, 2014). This is important because this study found that both abundance and richness were considerably greater from April to June and, therefore, previous studies may not have recorded the full variety of species. However, the explanation for the apparent seasonality is not entirely clear as tropical peat-swamp forests do not experience the supra-annual mast-fruiting events seen in dipterocarp forests and instead show greater consistency in fruit availability year-round (Cannon *et al.*, 2007; Harrison *et al.*, 2010). Therefore, seasonal changes in fruit-feeding butterfly populations may not be due to the availability of food resources but possibly the large variation in climatic conditions associated with the dry and wet seasons (Houlihan *et al.*, 2013). Additionally, whilst this study found no interaction between month and forest condition on the butterfly composition, it has been observed in Bornean lowland evergreen forest where diversity was higher in an undisturbed forest during the dry season but then switched to the logged forest during the wet season (Hamer *et al.*, 2005). Further multi-year surveys would be required to better evaluate the importance of seasonality on the butterfly populations in the degraded areas of the Sebangau forest.

Lastly, in the selectively logged forest, 75% of recaptured individuals were originally recorded either on the same transect or another transect within the same forest condition, with equivalent finding for the relatively undisturbed forest being 72%. This indicates that the surveys were recording a localised population as recaptured individuals were more likely to be from the same forest condition. Additionally, the average recapture rate across all species was 11.8% suggesting that recorded fruit-feeding butterflies were not “trap happy” (Houlihan *et al.*, 2013). However, despite the apparent existence of localised communities, individual butterflies were recorded to be moving between the selectively logged forest and relatively undisturbed forest. This finding further confirms that the selectively logged forest is equally capable of supporting a diverse population as if it were unsuitable

the movement of butterflies from the relatively undisturbed forest to the selectively logged forest would not be observed (Schultze and Crone, 2001; Scriven *et al.*, 2017).

Conclusion

Overall, the results of this study show that widespread fires in tropical peat-swamp forests are leading to the loss of fruit-feeding butterfly species, which indicates a loss of total faunal diversity. Additionally, this study is the first assessment of a butterfly community in a burnt tropical peat-swamp forest, to the author's knowledge, which further emphasises the necessity to understand how species are responding to vast areas of burnt forest. However, this study additionally indicates that protecting the historically logged areas of forest from further degradation could provide an essential lifeline for the region's biodiversity.

General Discussion

The degradation of tropical peat-swamp forests in Southeast Asia has globally significant ramifications (Page *et al.*, 2002). The loss of forest habitat is causing extinctions and threatening the populations of many more species (Posa *et al.*, 2011). Anthropogenic land-use change is driving the conversion of peatlands from carbon sinks to carbon sources, emitting staggering quantities of greenhouse gases (Miettinen *et al.*, 2017). Furthermore, yearly forest fires that burn millions of hectares of forest accelerate these carbon emissions and contribute towards thousands of premature deaths by producing toxic transboundary smoke-haze (Heil, 2007; Hu *et al.*, 2018). In order to combat these issues not only is the conservation of remaining tropical peat-swamp forest required but so too is the regeneration and protection of currently degraded forests and burnt peatlands.

The results presented in this thesis show clearly that the success of natural regeneration in a degraded tropical peat-swamp forest is highly dependent on the type of degradation the forest faces. In chapter one, vegetation surveys identified a complete loss of forest cover in both the new and old burn sites. Where there was once a diverse tree species community which formed a closed canopy, as recorded in the relatively undisturbed forest, this has now been replaced by a single tree species, *Combretocarpus rotundatus*, occurring in very low densities. Additionally, the two burn sites contain significantly altered understory vegetation communities. In the new burn site, which burnt in 2015, pioneer fern species dominate the ground cover. However, ferns are almost entirely absent in the old burn site, burnt in 2006, which contains a considerable increase in the abundance of pitcher plants compared to all other forest conditions. In stark contrast, vegetation surveys in the historically selectively logged forest show the area is recovering well, as the understory vegetation composition, tree species richness, and forest structure were indistinguishable from those recorded in the relatively undisturbed forest. Although, the study did also find that differences are still present in tree species composition and the selectively logged forest contains a decreased abundance of tall trees.

The presence of *C. rotundatus* in both fire degraded sites was expected as it has been widely recognised as a degraded peatland specialist (Page *et al.*, 2009; Blackham *et al.*, 2014; Graham *et al.*, 2017). However, the lack of a return towards an understory vegetation community typical of a tropical peat-swamp forest, seen in the old burn site, presents a more interesting finding and it may provide an indication of the future vegetation composition in the new burn site, over the following decade. If this lack of overall diversity persists in the new burn site, along with the addition of a high abundance *Nepenthes* species seen in the old burn site, it would suggest that the two fire degraded sites are experiencing retrogressive succession (Page *et al.*, 2009), despite this being more commonly associated with areas burnt multiple times (van Eijk and Leenman, 2004; Hoscilo *et al.*, 2008). It is, however, difficult to predict future vegetation changes as differences in the intensity of the fire, that the two sites experienced, will additionally have an impact on long-term vegetation differences (Page *et al.*, 2009). Nevertheless, this is unlikely to mean a greater vegetation recovery in the new burn site as, even though both sites burnt only once, the new burn site experienced a more intense fire, evidenced by the greater degraded area and categorisation of the fire as high severity with a relatively high propagation speed (Atwood *et al.*, 2016). The increased spatial scale of degradation will additionally result in greater barriers to natural regrowth in the new burn site (Blackham *et al.*, 2014). Therefore, the observation of unsuccessful regeneration in the old burn site, in addition to increased fire intensity and greater spatial scale of degradation in the new burn site, leads to the conclusion that fire degradation in the new burn site will result in an altered ecological state incapable of returning the original forest condition.

The considerable difference in vegetation regeneration, identified in chapter one, was then further confirmed by the biodiversity surveys in chapter two. The fruit-feeding butterfly community, surveyed due to its potential as a bioindicator, was almost entirely absent in the new burn site. Only 12 individuals were recorded, ten of which were *Melanitis leda*, a wide-ranging generalist species (Hirowatari *et al.*, 2007). Yet, the fruit-feeding butterfly community supported by the historically selectively logged forest contained the same species richness, abundance, and composition as the relatively undisturbed forest. This finding is particularly interesting as it indicates that forests with altered tree compositions can still support the same diverse fauna populations found in undisturbed forests.

These congruent findings, of chapters one and two, are logical, as the regeneration of flora and fauna in any degraded ecosystem is highly interlinked (McAlpine *et al.*, 2016). For example, a diverse array of larval host plants is essential for a butterfly population containing many forest specialists (Menendez *et al.*, 2007). This is because each tropical butterfly species can be dependent on a narrow range of plant species to successfully produce offspring (Dyer *et al.*, 2007). The cruciality of available larval host plants can be seen when considering the results of chapters one and two alongside one another. *Agatasa calydonia*, *Dophla evelina*, *Prothoe franck*, *Lexias pardalis* and *Charaxes bernardus* were the five most abundant species recorded in chapter two. All of which were recorded in both the selectively logged and relatively undisturbed forest areas. However, each of these species relies on 11 or fewer genera of larval host plant, with only a single host plant, *Desmos chinensis*, identified for *A. calydonia* (Robinson *et al.*, 2010). Five of these larval host plant genera were recorded in both the selectively logged and relatively undisturbed forest areas in chapter one, *Aglaia*, *Litsea*, *Diosyprus*, *Lithocarpus* and *Cratoxylum*. However, none of these plant genera were recorded in the burnt area and as such none of the five most abundant butterfly species recorded in this thesis were recorded in the burnt area, despite having the dispersal capabilities to cross into the area from the forest (Benedick *et al.*, 2007). Furthermore, *Melanitis leda* can utilise a much broader range of larval host plants, 25 genera have identified of which many are grasses typical in burnt peatlands (Larsen, 2005; Robinson *et al.*, 2010; Blackham *et al.*, 2014), and therefore the species accounted for 10/12 trappings recorded in the burnt area in chapter two.

In addition to larval host plants, a variety in the composition, age, and size of trees is important for a diverse butterfly community. This is because Nymphalidae butterflies, the family of all butterfly species recorded in chapter two, require a consistent production of fruit as a food resource (Ribeiro *et al.*, 2010). This is more likely to be produced by a diverse community of large and mature trees (Wright *et al.*, 2005; Minor and Kobe, 2019). This further explains the lack of butterflies recorded in the burnt area in chapter two as, in chapter one, only a single tree of the *Combretocarpus rotundatus* species was recorded in the new burn site. Furthermore, this species is a wind-dispersed coloniser and as such produces small seeds which can be transported by the wind (Blackham *et al.*, 2013), not the fleshy fruits on which Nymphalidae feed. This dependency additionally holds true the other way around, as a diverse flora community requires a diverse fauna community for essential ecological processes such as seed dispersal (Blackham *et al.*, 2013; Munoz *et al.*, 2017) and pollination (Albrecht *et al.*, 2012).

As well as this interdependency, the regeneration of tropical peat-swamp flora and fauna can be inhibited by the same regeneration barriers, such as increased light intensity which is a common feature of degraded peatland (Page *et al.*, 2008). This light intensity makes the site inhospitable for mature forest tree species as the seedlings are unable to compete with the light-loving rapid-growing pioneer species which are normally excluded from the heavily shaded understory of a mature peat-swamp forest (Blackham *et al.*, 2014). Likewise, forest specialist butterflies exhibit a restricted thermal tolerance and, therefore, are also unable to survive under the intense sunlight in degraded peatlands

(Koh, 2007). Moreover, some butterfly species have been shown to actively avoid unfavourable conditions by modifying their movement behaviour when in close proximity to the habitat boundary (Ries and Debinski, 2001).

To understand why the selectively logged forest and burnt sites differ in their regeneration ability it is important to consider the magnitude and severity of these regeneration barriers (Graham *et al.*, 2017). The results of this thesis support previous studies that suggest regeneration barriers present in a burnt site are considerably more difficult to overcome than those in a selectively logged forest (van Eijk and Leenman, 2004; Gunawan *et al.*, 2012). Again, this is logical as selective logging targets a specific set of tree species yet still maintains at least some level of forest cover (D'Arcy and Page, 2002). Therefore, fauna can still inhabit the forest and contribute towards natural regeneration. Contrarily, peatland forest fires are indiscriminate and considerably more destructive (D'Arcy and Page, 2002). Therefore, the natural regeneration of a peat-swamp forest is considerably less likely in a burnt site due to the complete change in abiotic conditions (Graham *et al.*, 2013), rendering the area inhospitable for the species that are characteristic of this forest type (van Eijk and Leenman, 2004)

Thesis conclusions and further research

The findings presented in this thesis lead to two main conclusions: Firstly, historically selectively logged forests provide an important lifeline for the conservation of tropical peat-swamp forests. This thesis has identified that both the flora and fauna are highly similar to that of an undisturbed forest, roughly 15 years after the cessation of logging. Therefore, if further degradation can be prevented, the 4.6Mha of degraded peat-swamp forest, in Southeast Asia (Miettinen *et al.*, 2016), may be able to naturally regenerate, vastly expanding the size of this important habitat. It is also recognised that greater a sample may result in different conclusions regarding the tree species composition of the selectively logged forest. Therefore, further research should focus on expanding the area surveyed within the Sebangau forest as well as other logged forests to better clarify the conclusions of this thesis.

The second conclusion drawn from this thesis is that severely burnt sites are likely to require active restoration as the results presented here show that natural regeneration is unlikely to restore the floral or faunal composition. Additionally, these sites are more likely to experience repeated fires and as such the regeneration barriers may be too severe (Page *et al.*, 2009). As active restoration can be very costly it is important that implemented techniques are effective (Hansson and Dargusch, 2017). As a result, future research should focus on identifying site-specific regeneration barriers and preventing further degradation before turning to costly restoration techniques. One important factor in regenerating the forest composition will be restoring a closed canopy as this will prevent recurrent fires (Graham *et al.*, 2017). Even if diversity is initially very low, in comparison to an undisturbed forest, a closed canopy will improve the hospitability of degraded peatlands for mature forest species and overtime diversity will increase. As such, identifying which tree species are capable of forming this closed-canopy may be the first step to restoring burnt peatlands.

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