Stand dynamics in undisturbed and selectively logged tropical rainforest over 18 years

Effect of logging intensity and climate extremes

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Doctoral Thesis
Swedish University of Agricultural Sciences
Umeå 2017

Acta Universitatis agriculturae Sueciae
2017:45

Cover: Rainforest silhouette
(Illustration: Daniel Lussetti and Petter Axelsson)

ISSN 1652-6880
ISBN (print version) 978-91-576-8863-7
ISBN (electronic version) 978-91-576-8864-4

Print: SLU Service/Repro, Uppsala 2017

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Abstract

Rainforests in Southeast Asia are enormously important, both ecologically and socio-economically, but their sustainability is severely threatened by various forms of disturbance that perturb the dynamics of forests here and elsewhere. To help efforts to counter such threats, this thesis focuses on two of the most important forms of disturbance that currently affect tropical rainforests: logging and extreme climatic events. It is based on research conducted in the Gunung Rara Forest Reserve, in Sabah, Malaysia (approx. 4°33´N, 117°02´E). The project started in 1992 in a mixed dipterocarp lowland rainforest, involving establishment of a long-term experiment with a 2 x 2 factorial randomized block design, where slope was the blocking factor. Two selective logging methods, supervised logging (SL) and conventional logging (CL), both with (CC) and without (NCC) pre-harvest climber cutting, and a control treatment (C), were applied to evaluate their effects on key parameters of forest dynamics, including: ingrowth of new trees ($\geq$ 10 cm diameter at breast height, DBH), growth of standing trees (survivor growth), tree mortality, and overall development of the stands. Analysis of data covering 18 years of subsequent stand development shows that SL with CC resulted in consistently higher stand volume recovery and ingrowth of dipterocarps, while suppressing establishment of pioneer species by up to 40%, compared to either CL treatment, especially at high harvest intensities In addition, CC reduced overall mortality, suggesting that it can effectively reduce negative effects of harvest operations. Using linear mixed effect models, I also found that the stand level growth rate of dipterocarps was two times higher following SL with CC than following the CL treatment. Furthermore, diversity patterns of naturally regenerating trees ($\geq$ 10 cm DBH) were studied over 10 years after selective logging, using the gradient of harvest intensity (0-16 trees ha^{-1}). Species richness peaked at intermediate levels of extraction, corroborating the intermediate disturbance hypothesis (IDH), and suggesting that moderate levels (< 8 trees ha^{-1}) of harvesting may maintain tree biodiversity. Finally, I studied the effects of El Niño Southern Oscillation events on uncut forests and found that both the intensity and duration of these events strongly influenced the forest dynamics. However, long periods of moderate-intensity El Niño-associated drought had stronger effects on tree mortality and subsequent growth of survivor trees than peak intensities. The results also indicate that cumulative effects of multiple events, rather single events, should be considered. However, although fluctuations in basal area were observed over 19 years of repeated events, the findings suggest that the uncut tropical rainforest was quite resilient and has fairly good capacity to withstand repeated extreme climatic fluctuations

Keywords: ENSO events; forest dynamics; growth models; IDH; lianas; logging damage; RIL; silvicultural treatments: sustainable forest management

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Dedication

To all those working toward the sustainable management of tropical forests, and my son Sixten, in the hope that he will find the tropical forests as interesting as I have.

Contents

List of Publications

This thesis is based on the work described in the following appended papers, referred to by Roman numerals in the text:

I Lussetti, D., Axelsson, E.P., Ilstedt, U., Falck, J., Karlsson, A. (2016). Supervised logging and climber cutting improves stand development: 18 years of post-logging data in a tropical rain forest in Borneo. *Forest Ecology and Management* vol. 381, 335-346.

II Lussetti, D., Kuljus, K., Ilstedt, U., Falck, J., Karlsson, A. Using linear mixed models to evaluate stand level growth rates for dipterocarps and *Macaranga* species following two selective logging methods in Sabah, Borneo. *Manuscript*.

III Lussetti, D. Axelsson, E.P., Hasslequist, N., Ilstedt, U., Falck, J., Karlsson, A. Intensity and duration of extreme climatic events affect the dynamics of lowland tropical rainforest in Sabah, Borneo. *Manuscript*.

IV Axelsson, E.P., Lussetti, D., Gustafsson, M., Karlsson, A., Ilstedt, U. The effect of logging practises and harvest intensity on patterns of dominance and diversity of tree ingrowth in a tropical forest. *Manuscript.*

Paper I is reproduced with the permission of the publishers, *Journal of Forest Ecology and Management*.

The contribution of Daniel Lussetti to the papers included in this thesis was as follows:

I Lussetti contributed to the data collection in the field and interpretation of the results. Lussetti was also mainly responsible for the data analysis and writing the text.

II Lussetti contributed to the data collection in the field and analysis. Lussetti was also mainly responsible for extracting data from the database used, interpreting results and writing the text.

III Lussetti contributed to the data collection in the field, and was mainly responsible for analysing the data, interpreting the results and writing the text.

IV Lussetti conceived the basic idea with the main author, led the work with the database, and contributed critically to drafts.

1 Introduction

1.1 Background

The rainforests of Southeast Asia (SEA)—spread across Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, The Philippines, Singapore, Thailand and Vietnam (Figure 1) (Kästle, 2013)—are among the oldest and most diverse ecosystems on Earth (Gaveau *et al.*, 2014). They have even greater diversity and richness than the Brazilian Amazonian and African tropical rainforests (Sodhi *et al.*, 2010; Edwards *et al.*, 2011). However, they are under intense pressure from anthropogenic disturbances, and losing coverage faster than forests in any other tropical region in the world (Sodhi *et al.*, 2004). Thus, the region's forests are severely threatened, especially by both legal and illegal selective logging (Fox *et al.*, 2009), and conversion to oil palm plantations (Fitzherbert *et al.*, 2008; Wilcove and Koh, 2010). Moreover, fluctuating climate conditions are increasingly affecting the forests' structure (Stenseth *et al.*, 2002; Condit *et al.*, 2004; Engelbrecht *et al.*, 2005), species composition and dynamics (Wright, 2005; McPhaden *et al.*, 2006; Corlett, 2011).

Today, most of the remaining forests of SEA are within logging concessions, and timber extraction rates are among the highest globally (Cleary *et al.*, 2007). Forestry exports are vital sources of income for developing countries, and within SEA, the countries of Indonesia, Malaysia and the Philippines together exports more than 80 % of today's global tropical timber (Berry *et al.*, 2010). Forests outside conservation areas are likely to have been logged at least once, commonly leading to severe pressure for conversion to oil palm plantations or other agricultural land uses (Laurance, 2007; Putz *et al.*, 2012). With current demands for forest products and the rapid increase of human populations in tropical regions, it is essential to change from pure exploitation of tropical forest to more sustainable forest management practices to maintain the supply of raw materials to the forest industry while sustaining the forests' important social and environmental functions, such as protection of soil and water resources, biodiversity and wildlife (Kleine and Heuveldop, 1993).

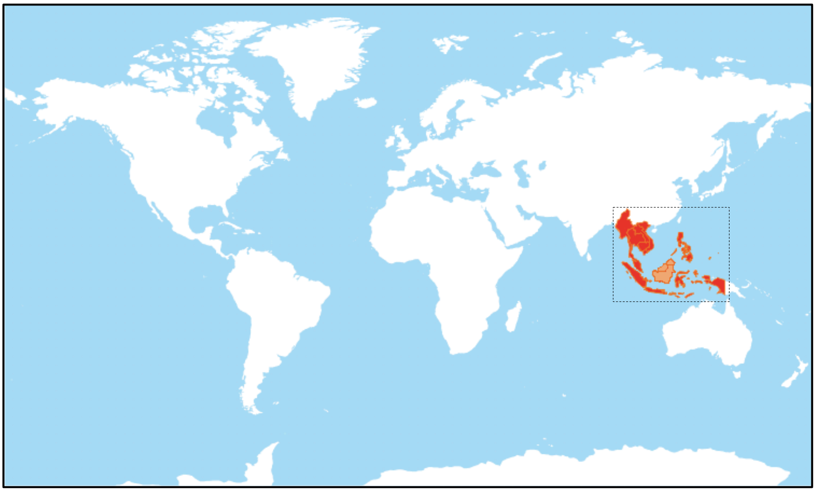

Figure 1. Location of Southeast Asia countries (framed and highlighted in red, except the island of Borneo, which is highlighted in orange).

The island of Borneo, politically divided between the countries of Indonesia, Malaysia and Brunei, is the third largest island in the world (Figure 1). Several genera of the family *Dipterocarpaceae* dominate the canopy of forests on the island, the region hosts more than 250 species of the family (Ashton and Kettle, 2012), and most of them are considered to have high commercial value (Ghazoul, 2016). Common traits of Dipterocarps include synchronized mass flowering and fruiting at irregular intervals, often triggered by droughts (Appanah, 1985; Sakai, 2002; Williamson and Ickes, 2002). Due to high stocking of valuable timber trees, the island has seen some of the most intensive selective logging ever recorded in tropical forest, with extractions commonly exceeding 150 m^3 per hectare (Pinard and Putz, 1996; Bertault and Sist, 1997; Sist *et al.*, 2003c; Sodhi *et al.*, 2004). Today, the remaining forests of Borneo are just a shadow of the legendary forests that once covered the entire island, and are continuously threatened by the growing palm oil market (Fitzherbert *et al.*, 2008; Bruhl and Eltz, 2010). Today, Malaysia is one of the largest producers of palm oil, from plantations covering areas up to 5 million hectares, representing almost half of Malaysia's cultivated lands (Malaysian Palm Oil Board, 2012). Conservation is an urgent priority for Borneo's forests, especially in biologically diverse regions that have escaped intensive logging so far. Besides setting forests aside for protection, sustainable management of the remaining secondary forests under logging concessions is essential to meet future demands for forest products (Figure 2). To facilitate this transition, more research is urgently needed to develop sustainable management techniques.

1.2 Selective logging systems

In Borneo, the logging industry began with the arrival of European colonizers in the middle of the 19th century (Dawkins and Philip, 1998). At that time the logging intensity was relatively low (Nicholson, 1979), but after the Second World War extraction of timber increased dramatically, due to increasing global demand for wood products together with widening use of machines such as crawler tractors and chainsaws, which greatly eased the work in the forests (Dawkins and Philip, 1998). Initially, timber extractions were restricted to a few species and were usually carried out in coastal forests. However, harvesting gradually increased and larger forest areas were designated for logging, and today most of the remaining forests in Borneo are classified as production forests (Gaveau *et al.*, 2014) and are thus open for logging. On the island of Borneo, almost 50% (approx. 26.3 M ha) of the original forest cover has been lost and another 25% approx. 13.6 M ha) has been selectively logged, while an additional 42% (approx. 6.6 m ha) of the remaining primary forest cover is expected to be logged in the near future (Gaveau *et al.*, 2014).

Selective logging regimes, usually involving the harvest of valuable timber trees exceeding a specified threshold stem diameter at breast height (diameter at 1.3 m; DBH), with prescriptions designed to maintain the forest cover, are usually applied in Borneo today (Sodhi *et al.*, 2010). Such regimes, intended to allow the remaining stands to regenerate and revert to old-growth stands (Figure 2), are considered better than clear-cutting regimes, and embraced as suitable approaches to protect forest integrity while allowing appropriate use of resources (Rametsteiner and Simula, 2003; Gatti *et al.*, 2015). Selective, however, is something of a misnomer: in Borneo's dipterocarp forests, nearly all the large commercial trees are typically removed, leaving only smaller or less desirable trees to form the next harvestable crop (Tuomela *et al.*, 1996; Huth and Ditzer, 2001). In Sabah, selective logging, often referred to as conventional logging (CL), involves use of chainsaws and crawler tractors. Before harvesting an area, crawler tractor operators and fellers walk around it and determine approximate locations of harvestable trees, roads and skid trails (Tay *et al.*, 2013). During harvests, fellers locate commercial > 60 cm DBH trees to be cut, leaving fruit trees and trees with visible defects. Trees that are felled are trimmed to logs about 6 m long, then crawler tractors are called in to extract the logs to the roadside (Tay *et al.*, 2013). The logging intensity is usually high, 8 – 15 trees are often harvested per hectare (Sist, 2000; Sist *et al.*, 2003b; Zimmerman and Kormos, 2012), leaving behind a degraded secondary forest with large gaps caused by felling trees to naturally regenerate (van Gardingen *et al.*, 1998). Depending on market demand and other factors, most trees remaining after a first logging may be harvested less than 35 years later (Sist *et al.*, 2003b) or converted to other land uses (Lasco, 2002; Adachi *et al.*, 2011). Such degraded forests have dramatically altered structure, with low, open canopies and high densities of pioneer species and climbers (Edwards *et al.*, 2011). Furthermore, degraded secondary forests are also frequently lost through transitions to other forms of land uses (Kammesheidt, 2002), including shifting cultivation, tree plantations, agricultural fields and livestock husbandry (Brown and Lugo, 1990) (Figure 2).

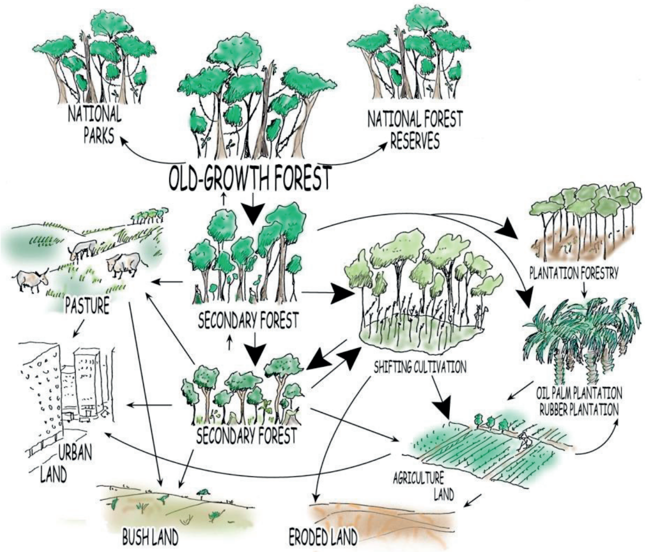

Figure 2. The landscape in many tropical countries today is a mosaic reflecting diverse land uses, some of which are leading to future land degradation and land conversions. Some changes (arrowed) can be reversed, e.g. secondary forest can be converted to old-growth forest, but once bush-land or eroded land stages have been reached, forests are unlikely to recover naturally. Published with kind permission from Jan Falck and Olle Forshed.

1.3 Sustainable forest management (SFM)

In many countries, most of the tropical forests are government-owned (Agrawal *et al.*, 2008). The timber is often harvested under concession agreements awarded to private logging companies, which are often reluctant to invest in long-term forest management (Boscolo and Vincent, 2000). In the absence of any regulations, logging companies may ignore the negative environmental impacts associated with forestry, as they derive little or no financial benefit from mitigating them. Thus, despite great progress in recent years in the development of more sustainable management policies, logging as generally practised in the tropics today still has substantial negative environmental impact (Putz *et al.*, 2000a; Sist *et al.*, 2003c). However, in recent decades there has been increasing pressure globally to improve the quality of tropical forest management systems. Concerns about the environmental, economic and social issues linked to forestry, such as threats to biodiversity and alarming potential effects of climate change, have led to international agreements and several programmes for improving forest management practices (ITTO 2005; UNFCCC, 2008; FAO, 2009).

Sustainable forest management (SFM), the management of forests according to principles of sustainable development, has been widely promoted by several international communities as a key mechanism to reduce tropical deforestation (Holvoet and Muys, 2004). SFM was designed to increase incomes and conserve forests simultaneously (Salafsky and Wollenberg, 2000; Pearce *et al.*, 2003), but various organizations and authors have applied various definitions of SFM and included various objectives (Reid and Rice, 1997). Early definitions concentrated mostly on the timber resources, with management aimed to sustain future yield of a limited number of wood products. More recently, the importance of other forest products and services has been increasingly recognized and definitions have been amended accordingly. The International Tropical Timber Organization (ITTO) defines SFM as: *"the process of managing forest to achieve one or more clearly specified objectives of management with regard to the production of a continuous flow of desired forest products and services without undue reduction of its inherent values and future productivity and without undesirable effects on the physical and social environment"* (ITTO, 2005). Basically, this means that forest activities should not damage the forests so much that their future capacity to provide products and services (timber yields, biodiversity conservation etc.) is significantly reduced. Such definitions could be perceived as rather vague, leaving forest managers wide discretion to decide what levels of forest reduction are acceptable and what forest values to sustain (Zimmerman and Kormos, 2012). A more robust and complete description of SFM, by Bruenig (1996), states that forest management should aim to sustain forest structures that retain rainforest ecosystems' viability, productivity and resilience, while satisfying human needs. To do so, Bruenig recommended practices such as limiting gap sizes to those of natural gaps, minimizing soil disturbance, and applying sufficiently long felling cycles to mimic nature as closely as possible and reduce both risks and costs. However, despite scattered successes, silvicultural practices in the tropics have not changed significantly, and adoption of SFM has remained limited (van de Laar, 2004).

When developing and implementing techniques intended to mimic natural processes and other elements of SFM regimes for these forests it is important to consider the optimal length of logging cycles. Short logging cycles will supress natural regeneration processes (Huth and Ditzer, 2001), and exacerbate degradation of the forests between logging operations (Zimmerman and Kormos, 2012). Current cutting cycles are widely suspected to be too short to maintain yields (Sist *et al.*, 2003b; van Gardingen *et al.*, 2003). For example, cycles of 25 – 40 years are common in Malaysia according to Peh *et al.* (2005) and Zimmerman and Kormos (2012). However, in simulations of logging cycles ranging from 20 to 100 years over 400 years by Huth and Ditzer (2001), conventional logging with 60-year cutting cycles resulted in significantly higher wood outputs than < 40-year cycles. Moreover, to promote the conservation of species, Huth and Ditzer (2001) suggested that logging cycles of 60 – 80 years were required. The results clearly indicate that forests' ecosystems cannot fully recover if logging cycles are too short.

One forest management concept widely promoted as an essential component of sustainable timber harvesting is reduced-impact-logging (RIL) (Pinard *et al.*, 1995; Marsh *et al.*, 1996; Pena-Claros *et al.*, 2008; Putz *et al.*, 2008; Rivero *et al.*, 2008). RIL is commonly defined as carefully planned and controlled timber harvesting conducted by trained workers to minimize logging-associated damage (Dykstra and Heinrich, 1996; Pinard and Putz, 1996). It incorporates a series of pre- and post-logging guidelines, such as climber cutting, directional felling and planning of skid trails (Sist *et al.*, 1998). Several studies have concluded that RIL techniques effectively reduce overall damage (Bertault and Sist, 1997) and promote better stand development in terms of increasing the growth of trees and seedlings (Pena-Claros et al. 2008; Edwards *et al.,* 2012) and reducing damage from creating skid trails (Sist *et al.,* 2003c). However, although RIL can successfully reduce damage related to logging in the tropics, it is very seldom practised as intended (Putz *et al.*, 2000a; Sist *et al.*, 2003c; Sist and Ferreira, 2007). Reasons for its inappropriate use are often connected to the perceived costs and lower felling intensities associated with RIL (Pinard *et al.*, 2000a; de Blas and Perez, 2008). Evidence for these drawbacks is mixed. For example, Medjibe and Putz (2012) found that in three, one and six of 10 studied cases RIL was less expensive, as costly, and more expensive than conventional logging, respectively. Furthermore, although RIL systems have been evaluated in more than 200 papers (Schwarb *et al.*, 2001), the reasons for its effects on forest dynamics are still not well understood, at least partly due to a lack of long-term evaluations of RIL's effects on stand development, including mortality, ingrowth and growth of trees.

1.4 Low-impact harvesting techniques

Several studies have reported significant levels of forest damage and weak regeneration after conventional logging operations (Boscolo and Vincent, 2000; Holmes *et al.*, 2000; Pereira *et al.*, 2002; West *et al.*, 2014). To ensure that regeneration levels are acceptable, and reduce damage during logging operation, more use of "low-impact" harvesting treatments before, during and after felling has been advocated. Such techniques typically include directional felling of trees, pre-harvest climber cutting and pre-planning of extraction roads and skid trails (Schwarb *et al.*, 2001; Forshed *et al.*, 2006; Putz *et al.*, 2008).

In directional felling, trees are felled in a predetermined orientation to minimize damage to the remaining stand and potential crop trees. Directional felling has been successfully tested (Pinard *et al.*, 1995; Cedergren *et al.*, 2002), and can significantly decrease damage during felling. Cedergren *et.al.* (2002) found that up to 78% of trees could be felled within 20 degrees of the marked direction at a site in Sabah, enabling 94% of the remaining trees selected for retention to be saved. Furthermore, accurate tree felling allows trees to be directed to fall into existing skid trails, thereby potentially further reducing damage to standing trees. Another important advantage of directional felling is that it can increase safety for the forest workers during logging operations, which is a known problem in tropical forestry (Dykstra and Heinrich, 1996).

Climbers are common in tropical lowland forests of Borneo and can have both positive and negative effects on forest diversity and ecosystems (Schnitzer *et al.*, 2011; Tang *et al.*, 2012). For instance, some climbers provide food resources for seed dispersers, thereby promoting maintenance of tree species' diversity (Bongers *et al.*, 2005). However, climbers compete intensively with trees for both below- and above-ground resources (Dillenburg *et al.*, 1993; Schnitzer *et al.*, 2005), and can thus suppress tree growth and increase mortality (Schnitzer *et al.*, 2011). Below ground, climbers and trees compete for nutrients and water resources (Tanner and Barberis, 2007), and above ground, leaves of climbers displace tree leaves and thus reduce trees' photosynthetic capacity (Ingwell *et al.*, 2010). For example, Schnitzer *et al.*

(2000) showed that high climber abundance in natural tree-fall gaps in Panama could supress tree regeneration for more than 13 years.

Furthermore, infesting climbers often tie crowns of large trees together. This can cause major problems when felling trees, as adjacent trees may be pulled down by the entangled climbers, resulting in larger than intended forest openings and unsafe environments for forest workers (Appanah and Putz, 1984; Putz, 1985; Vidal *et al.*, 1997; Gerwing, 2001; Parren and Bongers, 2001' Schnitzer *et al.*, 2004). Several logging experiments have included climber removal, but they have often not separated effects of climber cutting (CC) from those of other types of logging treatments, making it difficult to evaluate. However, some experiments that have separated effects of climber treatment indicate that CC prior to felling is a promising technique to reduce damage during felling operations (Appanah and Putz, 1984; Schnitzer, 2002; Alvira *et al.*, 2004). Moreover, César et al. (2016) found that cutting climbers in a secondary forest with enrichment plantings in Southeast Brazil increased the biomass of smaller trees and shrubs by up to 51% and enhanced survival of the planted seedlings. Marshall *et al.* (2016) reported that after 5 years, they found greater recruitment, stem growth and net biomass rates, where either lianas were absent or removed in a lowland tropical rainforest of Tanzania.

In contrast, other studies have found no evidence that climber cutting reduces logging damage. For instance, in a Cameroonian forest highly infested by climbers, Parren & Bongers (2001) found no evidence that climber removal reduced gap sizes, tree mortality or damage levels. Similarly, Cedergren et.al. (2002) concluded that climber cutting in a hilly tropical forest of Sabah had no impact on either damage to stands or the orientation of felled trees.

Soil compaction caused by the creation and use of skid trails is also regarded as a major form of damage associated with logging, restricting growth and reducing productivity in tropical forests (Pinard *et al.*, 2000b; Jackson *et al.*, 2002; Sidle *et al.*, 2004). This compaction (due to use of heavy forestry machines, such as crawler tractors and bulldozers) can reduce water and air movement into and through the soil profile, thereby restricting root growth and increasing surface runoff and erosion (Williamson and Neilsen, 2000). The problems caused by conventional logging can be severe, as no specific measures are taken to optimize the layout of skid trails. Instead, crawler tractor operators simply search the area for commercial trees to harvest (Pinard *et al.*, 2000b). Hence, previous studies have shown that up to 50% larger areas of forest ground may be damaged during CL operations that when RIL methods are applied (Bertault and Sist, 1995; Pinard *et al.*, 2000b).

Several skid trail systems have been applied in various parts of the tropical belt (Forshed *et al.*, 2006; Pena-Claros *et al.*, 2008). For instance, in Sarawak, Malaysia, Mattson-Mårn and Jonkers (1981) used a skid trail network with fixed distances between tracks of 100-150 m. They also allowed secondary skid trails up to 50 m long to reach felled trees inside the plot area. Results showed that the system could reduce damage to the residual stand by 33% compared to CL operations. Furthermore, use of a skid trail system during RIL operations, with skid trails following predetermine routes based on topographical maps and positions of target trees (Sist, 2000), can reportedly reduce soil damage in stands by up to 40% compared to conventional logging protocols (Sist *et al.*, 2003c).

The single most important feature when arranging skid trails are that they are pre-planned before harvest operation (Dykstra and Heinrich, 1996). By systematically align skid trails with fixed distance; avoiding areas prone to severe erosion, steep slopes and ravines, mortality of trees can be lowered (Forshed *et al.*, 2006).

1.5 Disturbance and tree diversity

Tropical forests are subjected to diverse disturbances of highly variable duration, intensity and frequencies (Burslem and Whitmore, 1999). Such disturbances, anthropogenic or natural, change the forest landscape's species composition and structure (Chazdon, 2003). Given the challenges already mentioned, it is becoming increasingly important to elucidate the main determinants of current diversity patterns and the likely effects of environmental changes (Sheil, 1999; Bongers *et al.*, 2009). For instance, disturbance associated with heavy logging can strongly affect forest structure, leaving a poor residual stand that is strongly dominated by pioneer species during subsequent succession (Pinard *et al.*, 1996). In contrast, low-intensity selective logging that closely mimics natural disturbances can significantly reduce damage associated with logging operations and promote natural regeneration of a much richer, more productive and desirable residual stand (Pena-Claros *et al.*, 2008; Rivero *et al.*, 2008). Such limited disturbances are likely to promote climax species, suppress pioneers and thus support ingrowth of multiple species, thereby retaining species diversity (Slik *et al.*, 2003), but the mechanisms involved and the interactions between silvicultural and climatic factors are far from fully understood.

The intermediate disturbance hypothesis (IDH) predicts that local species diversity is maximized at an intermediate level of disturbance, although it remains largely untested for highly diverse rainforest tree communities

(Molino and Sabatier, 2001). In forest ecosystems, disturbances such as tree-falls and logging can create large gaps, resulting in increased light penetration and induced growth of light-demanding pioneer species (Pinard *et al.*, 1996) thereby adding to the overall species diversity. However, excessive disturbance can cause high dominance of early succession species that eliminate late-succession species and thus suppress tree diversity (Bongers *et al.*, 2009). Although IDH presents an attractive theoretical framework, results of many empirical studies apparently conflict with it (Hubbell *et al.*, 1999; Mackey and Currie, 2001) and the discrepancies have generated much debate (Sheil and Burslem, 2003; Pierce, 2014).

1.6 Climate change in tropical forests

There is growing awareness that both the frequency and magnitude of extreme climate events are increasing in the tropics (Malhi and Wright, 2004; Yeh *et al.*, 2009; Corlett, 2011; Cai *et al.*, 2015). These events are known to have severe effects on ecosystems (Nakagawa et al., 2000; Siegert et al., 2001; Engelbrecht et al., 2005; Lee and McPhaden, 2010), so there is increasing interest in improving understanding of how these events may influence future ecological dynamics. Of particular interest in a climate change context are El Niño Southern Oscillation (ENSO) events (Karl *et al.*, 1995; Wang *et al.*, 1999; Moy *et al.*, 2002; Corlett, 2011), which are currently the strongest sources of inter-annual climate variation in the tropics (Wright and Calderon, 2006). ENSO events have two phases, El Niño and La Niña, which are governed by the periodic variation in winds and sea surface temperatures over the eastern Pacific Ocean (McPhaden *et al.*, 2006). El Niño events (characterized by warm ocean surface temperatures) induce dry, hot conditions that can lead to severe drought periods, while La Niña events (characterized by cooler surface temperatures) usually result in colder, wetter conditions. Thus, both phases strongly affect terrestrial vegetation around the tropical belt (Tyree *et al.*, 1998; Holmgren *et al.*, 2001; Engelbrecht *et al.*, 2005). Most published evaluations of effects of ENSO events focus on a particular event, the historically severe El Niño in 1997-1998 (Wolter and Timlin, 1998; Nakagawa *et al.*, 2000; Williamson *et al.*, 2000; Aiba and Kitayama, 2002; Fuller *et al.*, 2004; Slik, 2004). During this event a severe drought, accompanied by unprecedented biomass burning, struck large parts of western Borneo (Siegert *et al.*, 2001; Page *et al.*, 2002). Several studies have reported massive increases in tree mortality (Williamson *et al.*, 2000; Condit *et al.*, 2004; Slik, 2004) associated with the drought. However, some studies have suggested that El Niño-induced drought mortality mostly affects > 30 cm DBH trees

(Williamson *et al.*, 2000; Nepstad *et al.*, 2007), while others have found that mortality rates of smaller (< 20 cm DBH) trees are highest (Nakagawa *et al.*, 2000; Potts, 2003). In addition, Slik (2004) found that during the El Niño event in 1997 tree mortality was higher in logged forests than in undisturbed forests.

However, despite growing awareness of the importance of extreme events for ecosystem processes, we still know little about long-term effects of variations in such events' characteristics (such as their duration, intensity, intervals and frequency) on the dynamics of terrestrial ecosystems. This is a serious deficiency because in reality trees will experience a wide variation of climatic conditions during their lifetimes, e.g. in tropical regions extreme climatic events typically recur every 2 – 7 years (McPhaden *et al.*, 2006). Thus, it is not realistic to extrapolate results of a single event, as multiple events could have complex cumulative effects (synergistic, conflicting or a mixture of both). Thus, long-term studies are required to improve understanding of effects of these events and their interactions. Such studies are rare but essential for better understanding of probable effects of climate change on future forest dynamics (Gergis and Fowler, 2005).

2 Objectives

The main objectives of the studies this thesis is based upon were to increase understanding of tropical secondary forest succession following anthropogenic and natural disturbances, such as selective logging and extreme climatic events. I investigated (with co-authors of Papers I-IV; hereafter we) effects of two selective logging methods, conventional logging (CL) and supervised logging (SL), both with (CC) and without (NCC) pre-harvest climber cutting, and extreme ENSO events, on key variables of forest dynamics (particularly ingrowth of new trees of various species, growth of live standing trees and tree mortality) that govern post-logging stand development. The specific objectives of Studies I – IV, reported in Papers I-IV, were to:

- Investigate the impact of two selective logging methods (SL and CL), with (CC) and without (NCC) pre-harvest climber cutting, on forest dynamics (net standing basal area, tree ingrowth, tree survivor growth and tree mortality) using data covering 18 years of post-logging stand development. (Paper I).

- Describe and develop stand-level growth rate models for dipterocarp and *Macaranga* species using data covering 18 years of stand development following logging with two selective methods (CL and SL), with (CC) and without (NCC) pre-harvest climber cutting. (Paper II).

- Evaluate responses of uncut tropical rainforest dynamics and stand development to repeated extreme climatic events over 19 years, and effects of variations in the intensity and duration of such events. (Paper III).

- Study effects of two selective logging methods (SL and CL), both with (CC) and without (NCC) pre-harvest climber cutting, and levels of logging disturbance on the diversity of ingrowing trees 10 years after logging in tropical rainforests using the intermediate disturbance hypothesis (IDH) as a conceptual framework (Paper IV).

3 Methodology

3.1 Study area

All the research this thesis is based upon (reported in Papers I – IV) was carried out in the Gunung Rara forest reserve on the island of Borneo (approx. 4°33′N, 117°02′E; Figure 3A), run by the Yayasan Sabah group, Sabah, Malaysia. It was part of the SUAS project, started in 1992 in a virgin mixed dipterocarp forest, where trees of the *Dipterocarpaceae* family accounted for at least 50% of the basal area. About 230 species representing 60 families (trees ≥ 10 cm DBH) have been identified in the Gunung Rara Forest Reserve. The allocated site for the experiment covered roughly 3000 ha in total. A clay-rich Orthic Acrisol, associated with humid tropical climates and sedimentary bedrocks, covers the forest floor (Cedergren, 1996). The altitude within the site ranges between 300 – 610 m a.s.l., the slope ranges from 4.1 to 24.7°, and the climate is typical wet tropical. Average rainfall at the study area ranges from 2700 to 3400 mm per year (WorldClim, 1950-2000), mainly falling in two distinct rainy seasons, and the mean annual temperature is 27 °C. The area around the experimental site has been selectively logged for the past 30 years, and today large parts have been converted to oil palm plantations (Figure 3B and C).

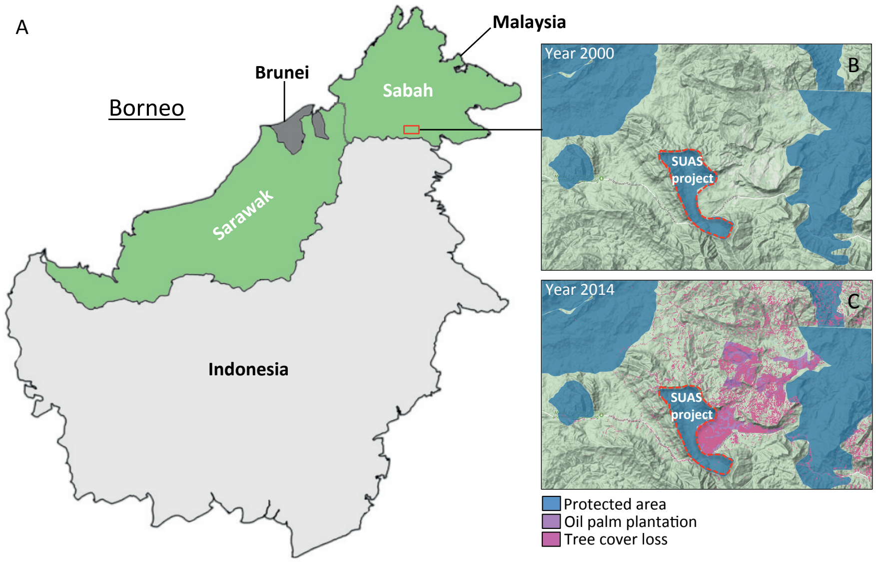

Figure 3. Map of Borneo, showing the state boundaries and location of the experimental site [A]. Change in forest loss and expansion of oil palm plantations between the years 2000 and 2014 [B] and [C], derived from the Global Forest Watch website (www.globalforestwatch.com).

3.2 Study design

The experiment was set up in 1992 as a randomized 2 x 2 complete factorial design, with four blocks in which the average slope within each plot was 22°, 11°, 8° and 6°. In each block five gross plots of 5.76 ha (240 x 240 m) were established (Figure 4), and in the centre of each gross plot a net plot of 1 ha (100 x 100 m) was established to create buffer zones and minimize edge effects of treatments. The net plots were further divided into 100, 10 x 10 m subplots and marked on the ground for easy reference. Four combinations of treatments, described below, were applied, one to each of the four gross plots in each block, while the other gross plots were untreated and used as controls (C) (Figure 4). Thus, each treatment combination was repeated four times, once in each block.

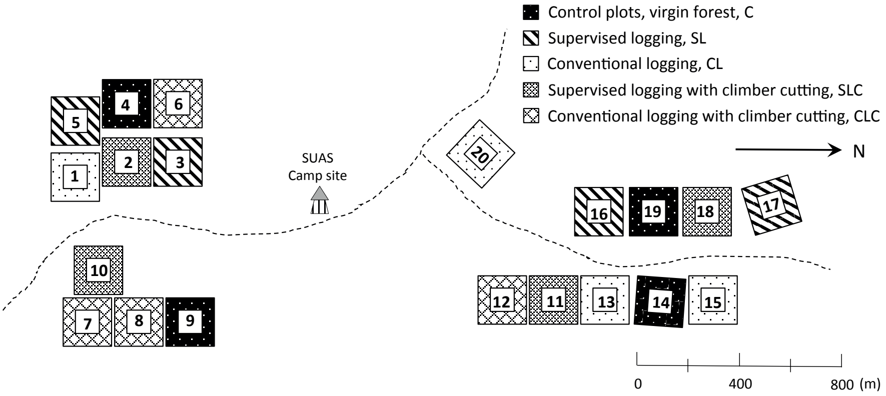

Figure 4. Overview of the experimental design and plot layout. Full squares represent gross plots (5.76 ha) and white squares within each gross plot represent the 1 ha experimental net plots.

The logging methods in the experiment that were studied (Papers I, II and IV) were conventional logging (CL) and supervised logging (SL) (Forshed *et al.*, 2006). The CL followed conventional practices in Sabah, involving use of chainsaws and crawler tractors. Prior to harvesting, fellers and crawler tractor operators search the area to determine approximate locations of commercial trees, roads and skid-trails. All trees with ≥ 60 cm DBH are supposed to be felled, except fruit trees and trees with visible defects (Tay *et al.*, 2013). However, trees exceeding cutting limits are often left in the logging area due to environmental factors such as steep slope. Timber fellers have no formal education and complete freedom to choose the direction of felling. Felling intensities depend on the availability of large trees in the forest. Commonly, 8-15 trees ha^{-1} are skidded out during conventional logging in Sabah (Pinard and Putz, 1996). After trees are felled, logs are extracted to roadside by crawler tractors.

In SL, the contractors had more detailed instructions. Skid trails were systematically aligned parallel to each other at a fixed distance of about 60 m, starting 30 m from a natural border. The distance between skid trails was based on assumptions that tractors had a winching distance of about 25 m, and were allowed to reverse up to 5 m into a plot if necessary. Thus, crawler tractors could winch out all logged trees between two skid trails. In addition, crawler tractor operators were not allowed to open up new tracks or leave pre-planned skid trails when skidding logs. The skid trail system also allowed skidding of trees both uphill and downhill. All skid trails were established before felling operations and potential crop trees (PCTs), with DBH in the range 40-59 cm, along the skid trails were marked with paint to avoid damaging them. Furthermore, SL included directional felling. Trees were felled by professionally educated tree fellers towards skid-trails, sometimes even at the expense of PCTs, preferably at an angle of 45^o to the skid-trail. Trees close to existing skid-trails were felled into the adjacent skid-trail. Tree crowns were directed to fall into skid-trails to minimize gap creation and damage to PCTs. Trees that could not be felled into skid-trails were felled in a direction that caused least problems when winching out the logs. Separate teams of forest operators working for the same contractor applied the two logging treatments in the experiment. During logging operations in 1993 these teams received instructions separately and lived in two separate camps to avoid affecting each other's practices. Thus, different crawler tractor operators created and used the planned and unplanned skid trails.

The logging treatments (CL and SL) were combined with (CC) and without pre-harvest climber cutting (NCC). Climber cutting was performed one year before the logging operations and involved cutting of all woody climbers of ≥ 2 cm diameter with a machete, except climbers of the genus *Ficus*.

The logging methods (CL and SL) followed forestry laws and regulations applied in Sabah at that time. Diameter cutting limit was 60 cm, and all trees of commercial value larger than this were to be harvested, except for fruit trees and trees of rare species according to registrations at that time.

The plot establishment procedures, including pre-harvest climber cutting and first measurement of trees with ≥ 10 cm DBH were conducted between March and June in 1992, then trees were harvested in June – August 1993. The first measurement of trees after the harvest operations was conducted during September – December in 1993, and all trees with ≥ 10 cm DBH were subsequently re-measured biannually during the months of September – November until 2011. Thus, data covering 18 years of post-logging stand development were available.

3.3 Field measurements and climate factors

During biannual fieldwork periods, every tree within the net plot with ≥ 10 cm DBH was measured and marked with an individual ID-tag that was buried at its base. Recorded data for each tree were: tree ID-number, distance and bearing from a reference point giving the coordinates for each tree, DBH if possible, otherwise 0.3 m above the highest buttress, tree status (Alive, Dead, New) and tree species. Trees were identified to species level if possible, otherwise to family, by professional inventory rangers. Trees that could not be identified were classified as other timbers (OT). The diameter (DBH) of trees was measured with a diameter measuring tape in mm, and metal detectors were used to relocate tree ID-tags. The distance from the centre point of each sub plot was measured with a measuring tape in mm and bearing was measured with a 360° compass. All trees measured were further grouped into functional tree groups, depending on specific characteristics (Appendix 1, Paper II). The functional groups evaluated in Studies I-IV were: complete stand (ALL) including all tree species; Dipterocarps, trees of the *Dipterocarpaceae* family (DIPT); and pioneer *Macaranga spp.* (MAC).

The ENSO-index used in Study III was derived from monthly Equatorial Southern Oscillation index measurements at Indonesia (Indonesian sea level pressure, standardized anomalies) compiled by the National Weather Service (www.cpc.ncep.noaa.gov). Other climate data were collected from Danum Valley Field Centre climate station, run by the Royal Society SE Asia Rainforest Research Programme, which has records of rainfall, temperature and humidity from 1985 to present.

3.4 Data analysis

In Study I, basal areas of all trees in the plots ($m^2\ ha^{-1}$) were converted to volumes ($m^3\ ha^{-1}$) using equations obtained from the STREK-project in East Kalimantan, Indonesia (Bertault and Kadir, 1998). Generalized additive models (GAMs) were then used to explore effects of the logging (SL and CL) and climber cutting (CC and NCC) treatments on post-harvest ingrowth of new trees (≥ 10 cm DBH), growth of trees (survivor growth) and tree mortality over 18 years post-logging. The GAM structure can be written as:

$$g(E(Y)) = \alpha + S_1(X_1) + \dots S_p(X_p),$$

where Y is the dependent variable, $E(Y)$ is the expected value, and $g(Y)$ is the function linking the expected value to the predictor variables $X_1 \dots, X_p$. The terms $S_1(X_1), \dots, S_p(X_p)$ denote smooth, non-parametric functions. The dependent variables were survivor growth, ingrowth and mortality. Predictor variables were logging treatments (SL and CL), climber cutting practice (CC or NCC), time (years) and harvested volume ($m^3 ha^{-1}$) as normal cubic splines. The model initially included all possible interactions, but was simplified by backward stepwise regression, sequentially removing insignificant ($P > 0.05$) interactions in order of insignificance (Bolker *et al.*, 2009).

Two-sample *t*-tests were used to investigate whether randomization resulted in significant differences in stand volumes between treatments prior to harvest and if harvested volume (m^3ha^{-1}) differed between treatments. With one-tailed paired *t*-tests, I tested the increase in standing volume after logging from the initial post-harvest value in 1993. This was done individually for the four different treatments (CL, CLC, SL and SLC).

Linear mixed models (LMMs) were used to analyse tree growth data and construct growth rate curves of dipterocarp species and *Macaranga* species in Study II. These models are suitable when modelling longitudinal data, i.e. repeated measurements over time (Verbeke and Molenberghs, 2000). LMMs have a fixed functional part and a random component, and take into account the correlation detected among observations coming from the same sampling unit by defining non-diagonal variance-covariance matrices, which are used to obtain the best unbiased estimates for the models' fixed parameters (Ibid.). Furthermore, the models permit definition of a covariance structure for the random effects and residual terms, and the best linear unbiased prediction for the random components specific to each unit (Ibid.). The following model was generated for basal area growth of trees of dipterocarp species:

$$Y_{ij} = \beta_0 BA95_i + (\beta_1 CL_i + \beta_2 SL_i + \beta_3 CLC_i + \beta_4 SLC_i)\, t_{ij} + b_{i1} + b_{i2} t_{ij} + \varepsilon_{ij}$$

where Y_{ij} is the basal area of dipterocarps in plot i at time j, and CL_i, SL_i, CLC_i and SLC_i denote indicator variables defined as one when the plot belongs to the corresponding logging treatment group and zero otherwise. Thus, β_1, β_2, β_3 and β_4 are average growth rates following logging treatments CL, SL, CLC and SLC, respectively. The fixed part of the intercept was modelled using the basal area in 1995 (when growth curves changed from negative following the logging disturbance to positive). Therefore, we modelled growth during the years 1997-2011. We tested both Gaussian serial correlation and Toeplitz banded serial correlation for modelling the residual serial correlation, and found that the Gaussian approach explained the most.

Growth curves of pioneer species were not linear. Therefore, we included a quadratic time effect in this model. To decide what random effects should be included in the model, we compared the average trend of the ordinary least squares (OLS) residuals with fitted variance functions for several options. The results indicated that a LMM with random intercepts and random slopes for both linear and quadratic time effects was most plausible. The following model was estimated for growth of *Macaranga* basal area in plot i at time point j:

$$Y_{ij} = \beta_0 BA93_i + (\beta_1 CL_i + \beta_2 SL_i + \beta_3 CLC_i + \beta_4 SLC_i)\ t_{ij} + (\beta_5 CL_i + \beta_6 SL_i + \beta_7 CLC_i + \beta_8 SLC_i) t^2_{ij} + b_{i1} + b_{i2} t_{ij} + b_{i3} t^2_{ij} + \varepsilon_{ij}$$

Here: Y_{ij} is the basal area of *Macaranga* species in plot i at time j; $\beta_0 BA93_i$ is the fixed intercept (the point when basal area growth started to be positive); CL_i, SL_i, CLC_i and SLC_i denote indicator variables defined as one when the plot belongs to the corresponding logging treatment group and zero otherwise; and $\beta_1,\ldots,\beta_4$ and $\beta_5,\ldots,\beta_8$ give the average linear and quadratic time effects of the logging treatments CL, SL, CLC and SLC, respectively. The plot-specific growth curves are quadratic, with plot-specific intercepts as well as slopes for the linear and quadratic time effects (b_{i1}, b_{i2} and b_{i3}, respectively). The average growth rates decrease with time and especially for the first years after logging, the *Macaranga* growth rates are mainly determined by the coefficient of the linear time effect.

All results from growth models of dipterocarps were tested using Wald and t-tests, and results from *Macaranga* growth models were tested with Wald tests. For complete model description used in Study II, please se Appendix 2 (Paper II).

In Study III, general linear regression models (GLMs) were used to investigate effects of the intensity and duration of ENSO-events (independent variables) on tree ingrowth, tree survivor growth and tree mortality in the plots. Since the assumption of equal variance was violated, Kruskal-Wallis non-parametric tests were used to test for differences between effects of El Niño, La Niña and neutral events on forest dynamics.

In Study IV, one-way analysis of variance (ANOVA) was used to address effects of the treatments on ingrowth of the 15 most abundant tree species (trees ≥ 10 cm DBH) and overall tree biodiversity (species richness, rarefied species richness and Simpson's index of diversity (Simpson´s *D*)), where treatment was set as the predicting factor, as well as including the block factor to account for environmental variability. Assumptions were evaluated with residual and histogram plots. In some analyses the assumption of equal variance was violated and transformations provided insufficient correction. Therefore, ranked responses were used as dependent variables, an approach that enables evaluations that are equivalent to non-parametric tests, but in this context also allow inclusion of the blocking factor. Results from ANOVAs were subsequently explored with Tukey's honestly significant (HSD) test. To test the diversity-harvest intensity relationships and population growth of individual tree species, regression analyses were used. Linear, logarithmic and polynomial fits were tested, and we chose the more complex model only if the additional polynomial parameter was significant ($P < 0.05$). Regressions on the population growth rates included the 15 most abundant species to ensure there were sufficient observations for the analyses.

All analyses described in the studies I - III were implemented in the statistical programs R (version 3.1.2; 2014) and R studio (version 0.99.489) using the unified graphical user interface Deducer (version 0.7-7), JGR (version 1.7-16), the nlme-package (version 3.1-120) and the mgcv-package for GAM-structures (version 1.8-6). However, in Study II, the ‘mixed’ procedure in SAS (version 9.4) was applied, and the analysis reported in Paper IV was implemented in JMP 11 pro (version 11.2.0).

4 Results and discussion

The major findings from the studies included in the thesis is presented and discussed with the purpose to link results from individual studies to each other, as well as to the main objectives of the thesis. Particular emphasis is placed on discussing the effects of different anthropogenic and natural disturbances on forest ecosystem development after two selective logging practices; supervised logging (SL) and conventional logging (CL) combined with- (CC) or without (NCC) pre-harvest climber cutting practice.

4.1 Effects of supervised logging and climber cutting on stand development

In Study I, we analysed data covering 18 years of post-logging stand development to evaluate effects of two selective logging methods (SL, including use of pre-aligned skid trails and directional felling; and CL, where trees were felled then crawler tractors were called in for skidding) on net stand volume recovery, survivor growth (growth of standing trees), ingrowth (of trees with ≥ 10 cm DBH) and mortality of trees. Effects of the logging treatments with (CC) and without (NCC) pre-harvest climber cutting were also examined. Before the treatments, stem density in the plots ranged from 428 to 594 ha^{-1} and the standing volume (m^3ha^{-1}) from approx. 467 to 686 m^3ha^{-1}. No significant differences in pre-harvest density between stands assigned to different treatments were found ($P \geq 0.133$). In total, 133 trees were harvested and yarded out to landing, of which 122 were members of the *Dipterocarpaceae* family. Harvest intensity ranged from 1 to 16 trees ha^{-1} (12.5 – 234 m^3ha^{-1}) and averaged 8 trees per ha^{-1} (106 m^3ha^{-1}). No significant between-treatment differences in harvested volume were found ($P > 0.200$). We investigated not only overall effects of the treatments on all trees in the stands, but also effects on the commercially dipterocarp species (*Dipterocarpaceae*), and fast-growing pioneer (*Macaranga*) species.

The results revealed that standing volume development was substantially enhanced by a few relatively simple management practices. For instance, SL with directional felling, use of pre-aligned skid trails and combination with CC resulted in consistently higher stand volume recovery of dipterocarps than conventional logging protocols over 18 post-logging years (Figure 5).

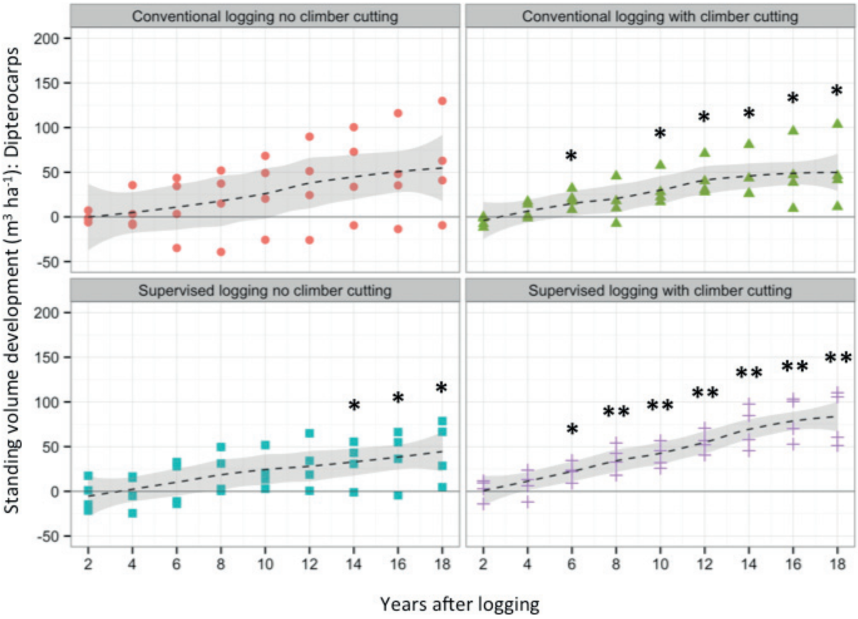

Figure 5. Loess-smoothed curves showing standing dipterocarp volume (m^3ha^{-1}) development, relative to the volume immediately after logging, in plots subjected to the indicated logging and climber cutting treatments. Grey areas indicate 95% confidence intervals. Significant increases in standing volume from the initial year are indicated by asterisks: * ($P \leq 0.05$), ** ($P \leq 0.01$) or *** ($P \leq 0.001$) according to one-sided paired t-tests.

Survivor growth was strongly influenced by the logging intensity (Table 1). When harvest intensities were high, the survivor growth of *Macaranga* species was more than twice as high following the CL treatment than following the SL treatment, while survivor growth of dipterocarps was higher following the SL treatment than following either CL treatment (Figure 6). In addition, when harvest intensities were high the survivor growth of *Macaranga* species was about 40% lower following treatments with climber cutting (CC) than without climber cutting (NCC), showing that CC may be an important silvicultural

Table 1. Results from GAM (Generalized additive models) on survivor growth (m^3 ha^{-1} $year^{-1}$) on trees (≥ 10 cm DBH), i.e. growth of trees alive at both the initial and terminal inventories of each measurement cycle of two years, for complete stand (all trees), dipterocarps species and *Macaranga* spp, respectively, for 18 years of post logging data (1993-2011), following selective logging in 1993. Treatment is the fixed effect of logging method (supervised logging or conventional logging) and climber is the fixed effect of pre-harvest climber cutting or no climber cutting. Harvested volume is the covariate showing the effect of harvest intensity. Significant results ($P \leq 0.050$) are marked in bold.

	All trees				**Dipterocarps**				**Macaranga**			
	R^2 adj = 0.49				R^2 adj = 0.19				R^2 adj = 0.70			
Factor	**Estimate**	**Std. Error**	**t-value**	**P-value**	**Estimate**	**Std. Error**	**t-value**	**P-value**	**Estimate**	**Std. Error**	**t-value**	**P-value**
Treatment	0.660	0.735	0.898	0.371	- 1.954	0.807	- 2.420	**0.017**	0.847	0.559	1.515	0.132
Climber	2.807	0.737	3.807	**< 0.001**	0.684	0.447	1.533	0.128	- 1.424	0.566	- 2.514	**0.013**
Harvest volume	0.028	0.004	6.833	**< 0.001**	0.001	0.004	0.321	0.749	0.028	0.004	7.263	**<0.001**
Treatment*Climber	- 4.049	1.053	- 3.845	**< 0.001**	-	-	-	-	-	-	-	-
Harvest volume*Treatment	-	-	-	**-**	0.022	0.007	3.353	**0.001**	- 0.019	0.005	-4.165	**< 0.001**
Harvest volume*Climber	-	-	-	-	-	-	-	-	0.017	0.005	3.487	**< 0.001**

-indicate insignificant ($P > 0.05$) interactions removed by backward stepwise regression.

technique to reduce the ingrowth of *Macaranga* species. The survivor growth varied among the studied tree groups, and (as expected) the *Macaranga* species grew faster than the dipterocarp tree species (Pena-Claros *et al.*, 2008). The higher growth of standing trees observed in this study are most likely attributed to the increase of resources availability; when more volume is extracted, more resources such as light and nutrients become available to the residual stand (Ingwell *et al.*, 2010).

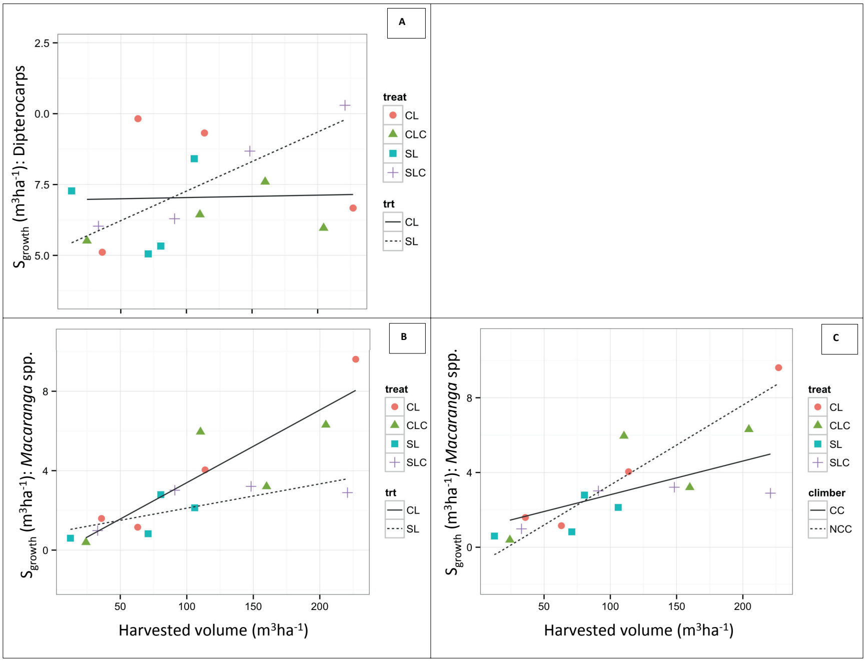

Figure 6. Growth (m^{3}ha^{-1}year^{-1}) of surviving trees (≥ 10 cm DBH), i.e. growth of trees alive at both the initial and terminal inventories of the nine biannual measurement cycles following selective logging in 1993, in relation to harvested volume, following conventional logging (CL) and supervised logging (SL), with (CC) and without (NCC) climber cutting. Effects are shown for dipterocarp species [A] and *Macaranga* spp. [B and C].

Several studies have stressed the need for better understanding of effects of combinations of silvicultural treatments on forest growth to design more sustainable forestry practices (Fredericksen and Putz, 2003; Dauber *et al.*, 2005). In this study, we were able to separate effects of CC *per se*, and its interactions with the cutting treatments, on several key parameters of forest dynamics (ingrowth, survivor growth and mortality of trees). Combining CC with SL had the positive effect of increasing ingrowth of dipterocarp species, but interactions between harvest intensity and CC treatment also had important effects, as increases in ingrowth rates and reductions in overall mortality associated with CC strengthened with increases in harvest intensity. Moreover, growth rates of *Macaranga* survivor growth were lower when CC was applied, relative to rates without it, at high harvest intensity, suggesting that the interaction between CC and harvest intensity has contrasting effects on the growth of pioneer and climax species. It is unclear what mechanisms that underlies the contrasting effects of CC seen in our study. However it is possible that the removal of climbers influence abiotic factors and/or change the competitive interactions between the two species groups, and thus could promote dipterocarp and suppress *Macaranga* spp. development. Information and understanding of such mechanisms would be valuable for management of tropical rainforest regeneration.

High harvest intensity was also associated with higher rates of appearance of new trees, in accordance with previous studies (Parrotta *et al.*, 2002; Sist and Nguyen-The, 2002). In addition, tree mortality was strongly influenced by harvest intensity, being highest (with either SL or CL treatments) at high harvest intensity. The positive effects on ingrowth of new trees (with ≥ 10 cm DBH) of removing climbers in combination with the SL treatment, especially when harvest intensities were high, supports the idea that climber cutting treatments are effective for reducing negative effects of forest operations in tropical forests (Parren and Bongers, 2001; Sist and Ferreira, 2007; Pena-Claros *et al.*, 2008). The effects of CC were also long lasting, and the results could contribute to the development of long-term sustainable forest management practices. The results are consistent with previous findings that the presence of climbers can reduce stand-level biomass growth by 10% (van der Heijden and Phillips, 2009) and net biomass accumulation by up to 18% (Schnitzer *et al.*, 2014) in Panama and Peru, respectively.

4.2 Growth models for dipterocarps and pioneer species

Growth models can be highly valuable for identifying the main factors affecting the long-term behaviour of tropical rainforests, and elucidating their effects and interactions. Such models can assist forest researchers and managers in many ways, notably when predicting future yields and identifying suitable silvicultural options (Vanclay, 1994). Thus, in Study II we assessed long-term consequences of SL and CL, with (CC) and without (NCC), pre-harvest climber cutting, using LMMs to analyse tree growth data and model the basal area growth of both dipterocarp species and *Macaranga* species.

During logging operations, 126 trees (in total) were logged and skidded out from the 15 experimental 1 ha^{-1} plots. Of these 126 trees, 115 were dipterocarps and the harvest intensity ranged from 1 to 16 trees ha^{-1} (0.59 – 10.8 m^2ha^{-1}), and averaged 8 trees ha^{-1} (5.2 m^2ha^{-1}).

Growth rate coefficients derived from LMMs for dipterocarp species indicated that the SLC and CL treatments gave the highest and lowest growth rates (0.2552 ± 0.0437 SE and 0.1249 ± 0.0504 SE, respectively). Thus, dipterocarp growth rates were twice as high following the SLC treatment. A Wald test confirmed that the dipterocarp growth rate significantly differed following these treatments ($P = 0.0481$). Hence, in 2011 (18 years after logging) the standing dipterocarp basal area had recovered to approx. 93 and 84% of the initial level in SL and SLC plots, respectively, but to just 72-73% of the initial level in CL and CLC plots.

After 18 years of post-logging, basal area of dipterocarp trees ≥ 60cm DBH had recovered between 56 – 94% in the different treatments. Highest recovery was found for the SL treatment, and the lowest for the CLC treatment. The time required for full recovery of the basal area of dipterocarps of this size remains unknown, but it is important to consider in future studies since it may affect sustainable yields and cutting cycles (Sist et al. 2003b; van Gardening et al. 2003). Growth of such big trees is known to increase with increasing size (King *et al.*, 2005), and higher growth rates have been reported for canopy trees than understorey trees (Sterck *et al.,* 2001). Thus, when interpreting results based on total basal area recovery from either a financial or ecological perspective, it is important to consider differences in diameter distribution as well as species composition.

The growth dynamics of *Macaranga* species completely differed from those of the dipterocarp species. These pioneers did not grow linearly with time; their growth rates peaked after 15-18 years then levelled out, and the basal area of *Macaranga* species tended to be twice as high at the end of the study period in CL and CLC plots than in SL and SLC plots. However, no statistically significance between-treatment differences were found in the growth model for *Macaranga* spp., probably due to large within-treatment variation.

4.3 Effects of repeated extreme climatic events in uncut forest

In Study III, repeated extreme climatic ENSO (El Niño and La Niña) events over 19 years and their effects on forest dynamics (ingrowth, survivor growth and mortality) on pristine tropical lowland rainforest was studied. Understanding effects of large climatic events is crucial as these forests not only provide numerous ecosystem services such as wood production and carbon sequestration, but are also globally important hotspots of biodiversity and endemism (de Bruyn *et al.*, 2014). Furthermore, studies on ENSO events predict that the most important consequences of anticipated climate change may be increases in the frequency and magnitude of such events (Karl *et al.*, 1995; Schar *et al.*, 2004).

During the study period (1992-2011), three El Niño periods, four La Niña periods and three "neutral" periods with relatively normal climate conditions, occurred (with various intensities and durations). During the first seven years (1992-1999), mostly characterized by repeated El Niño events, the overall basal area slightly decreased, largely due to peaks in mortality in 1993 and during the historically severe El Niño event of 1997-1998 (Figure 7A). In contrast, during 2000-2009 (characterized by repeated La Niña events and periods with relatively normal conditions) stand basal area continuously increased relative to the initial basal area in 1992. The variation observed in basal area development seemed to be driven mostly by mortality and to a lesser extent by ingrowth of new trees (with ≥ 10 cm DBH), and survivor growth (Figure 7B – D). This conclusion was supported by the connection between the fluctuations in standing basal area and basal area mortality observed during the first part of the study period. The detected importance of mortality for stand development is consistent with previous findings that severe single droughts alter the structure and function of tropical forests in several ways (Woods, 1989; Harrison, 2001; Phillips *et al.*, 2010; Corlett, 2011). For instance, El Niño events reportedly increase tree mortality (Williamson *et al.*, 2000; Van Nieuwstadt and Sheil, 2005), but also either increase (Condit *et al.*, 2004) or reduce (Engelbrecht *et al.*, 2005) seedling mortality. Study III and the cited studies clearly highlight the importance of climatic-driven mortality for dynamics of tropical forests and suggest that increases in frequency of such disturbances may threaten their persistence, or at least severely change their structure and composition.

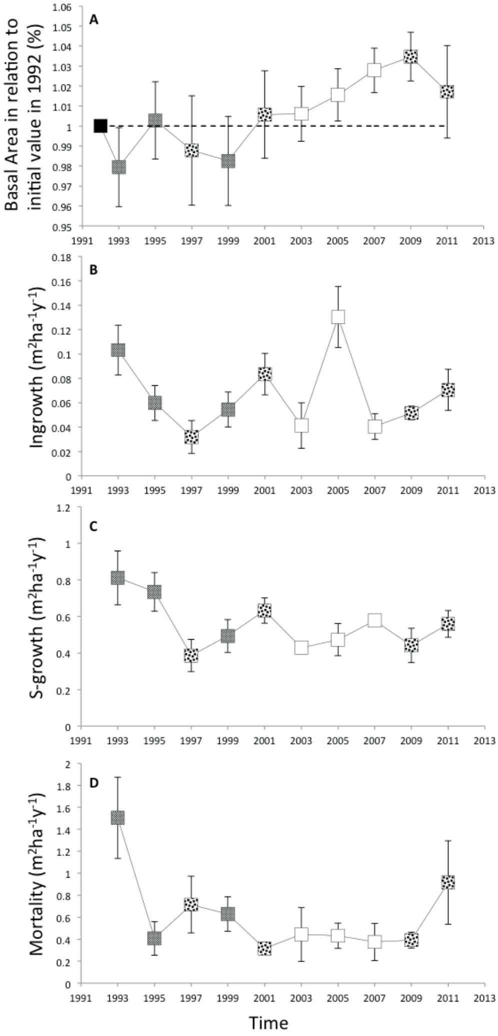

Figure 7. Changes in basal area relative to initial values in 1992 (%) in an untreated mixed dipterocarp rainforest in Sabah, Borneo [A], and changes in basal area due to: ingrowth of new trees (≥ 10 cm diameter at breast height) [B], survivor growth (S-growth, living trees) [C], and tree mortality [D]. Basal area data were normalized with respect to initial values measured in 1992 (black dashed lines), whereas ingrowth, S-growth and mortality show growth or reduction rate in basal area (m^2 ha^{-1} $year^{-1}$). Colours of boxes indicate categories based on mean ENSO values during the indicated period; grey boxes indicate El Niño years (Enso > 0.5), dotted boxes La Niña years (Enso < -0.5) and white boxes years with relatively neutral conditions (-0.5 < ENSO < 0.5). Black box represent initial mean values of basal area in 1992 (≈ 36 m^2 ha^{-1}). Error bars indicate standard error (SE).

Although massive ingrowth in 2005 contributed to the increase in basal area development during the second part of the study period (Figure 7B), it seems unlikely to have been due to conditions at the time. Instead, it was probably connected to an earlier mast fruiting event (possibly before the study period or after the 1992-1993 or 1997-98 El Niño events). Such fruiting events are characterized by marked peaks in flowering and subsequent fruit production (Wich and Van Schaik, 2000), and are commonly synchronized with El Niño drought events in SEA (Curran et al., 1999; Wich and Van Schaik, 2000; Wright and Calderon, 2006). Despite the fluctuations in basal area observed over the 19 years of development, this uncut forest seemed fairly resilient to repeated extreme climatic events.

Furthermore, the results showed that effects of ENSO events on forest development were strongly influenced by their duration and intensity, i.e. responses in tree mortality, ingrowth and survivor growth all depended on both of these variables of ongoing events (Figure 8). However, duration was the most important factor driving forest development during El Niño events, as mortality and survivor growth increased linearly during long periods of drought (Figure 8D and F). In contrast, the intensity was negatively related to survivor growth, as the basal area growth of standing living trees declined with increasing intensity of El Niño events (Figure 8C). Increases in mortality during drought events are well documented (Nakagawa *et al.*, 2000; Williamson *et al.*, 2000; Potts, 2003; Niklas and Spatz, 2004) and could explain the increase in growth in the basal area of survivors observed in Study III, as increases in basal area mortality will release resources due to the associated reductions in canopy cover and increases in decomposition, thereby favouring growth of living standing trees (survivor growth).

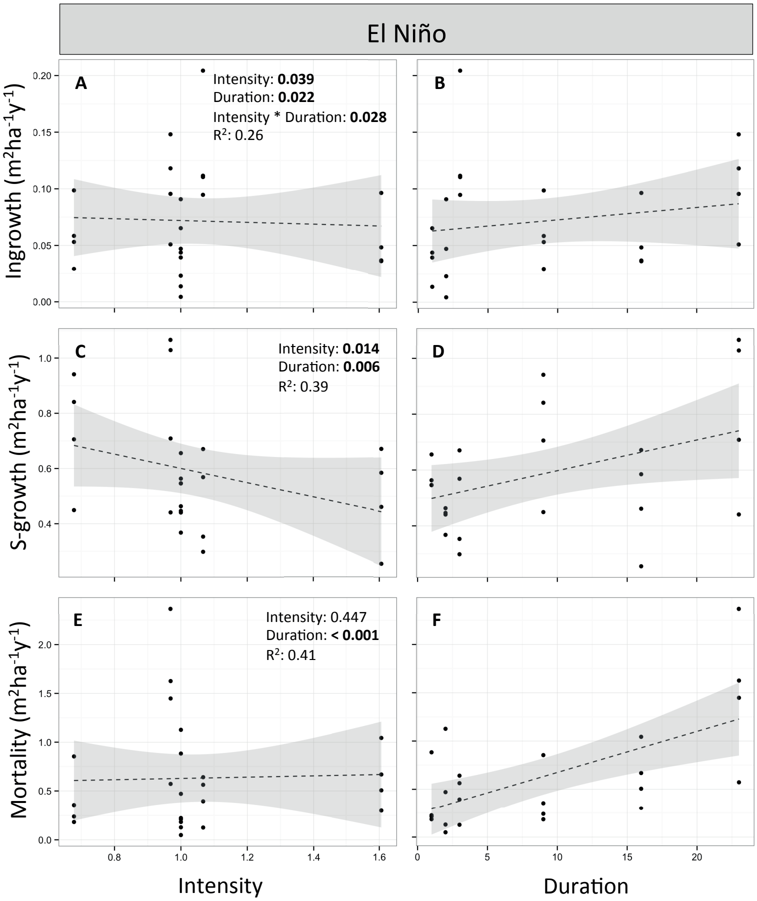

Figure 8. Relationships of the duration (months) and intensity (ENSO-index) of El Nino events with: the basal area growth of ingrowing trees (with ≥ 10 cm diameter at breast height) [A] and [B], the basal area growth of surviving trees (S-growth) [C] and [D], and the reduction in basal area due to tree mortality [E] and [F]. These relationships were tested using linear regression models implemented in R software, with loess smoothing. If the interaction between duration and intensity was non-significant the model was simplified by backward stepwise regression. Shaded areas represent 95 % confidence intervals, and R2-values are values from the final model. Results from the analyses deemed significant (P ≤ 0.05) are marked in bold.

Ingrowth of new trees (≥ 10 cm DBH) was affected by a two-way interaction between intensity and duration, indicating that growth of small trees was promoted most strongly by El Niño events with intermediate intensities and intermediate to long durations, although long droughts can obviously cause limitations in soil water availability, thereby restricting trees' growth and increasing their mortality (Burslem et al., 1996). A possible explanation is that short or intermediate drought events trigger adaptive mechanisms in tropical trees, such as leaf shedding and utilization of soil water reserves, that can reduce the impact of drought and increase their capacity to withstand periods with low rainfall (Borchert, 1998; Gibbons and Newbery, 2003).

Despite a relatively small-scaled study, we believe the results from this study could be useful for future evaluations of extreme climatic events and their effects on forest dynamics, as variations in the duration, intensity and frequency of such events could have cumulative effects (synergistic, conflicting or a mixture of both). Thus, long-term studies covering repeated extreme events may be crucial for robust predictions. The results also suggest that the current classification of El Niño and La Niña events does not cover important parameters for forest ecology.

4.4 Effects of logging disturbance on tree diversity

Study IV examined long-term consequences of anthropogenic disturbance (logging practices) on tree diversity; more specifically effects of SL and CL both with (CC) and without (NCC) climber cutting and controls (C) and a gradient of logging intensity on tree ingrowth, diversity and species composition for almost 20 years after logging. The results show that practices during harvest operations and logging intensity can significantly affect both rates of ingrowth post-logging and the diversity of ingrowing species in tropical forests.

Logging induced a range of responses that need to be considered when evaluating the causes and consequences of logging induced disturbance in tropical rainforests. For instance, harvest increased ingrowth of new trees (trees ≥ 10 cm DBH) from ~6.0 ± 1.1 trees ha^{-1} $year^{-1}$ in uncut forests, to ~25.0 ± 1.8 trees ha^{-1} $year^{-1}$ in forests that were subjected to harvest, and the proportion of ingrowth belonging to the *Macaranga* species increased with higher levels of disturbance. Furthermore, disturbance decreased rarefied species richness and Simpsons index of diversity (Simpson´s *D*), but increased species richness and *Macaranga* dominance of ingrowing trees (Figure 9). Previous studies have shown that anthropogenic disturbance such as selective logging can increase the diversity of trees in tropical forests (Plumptre 1996; Sheil 2001). Part of this effect can be explained by the increased number of trees growing in after harvest, e.g. as the number of trees increase, so does the probability of finding new species (Gotelli & Colwell 2001).

The regression analyses on the effect of the disturbance gradient on tree ingrowth commonly revealed best explanatory power when using a logarithmic fit, suggesting that large part of the variation is explained in the low end of the disturbance gradient, i.e. the treatment per se. However, even when control plots were omitted it was apparent that the gradient of disturbance affected many aspects of the ingrowth, e.g. the gradient of disturbance increased overall ingrowth of *Macaranga* spp. and decreased Simpson´s *D* (thus implying

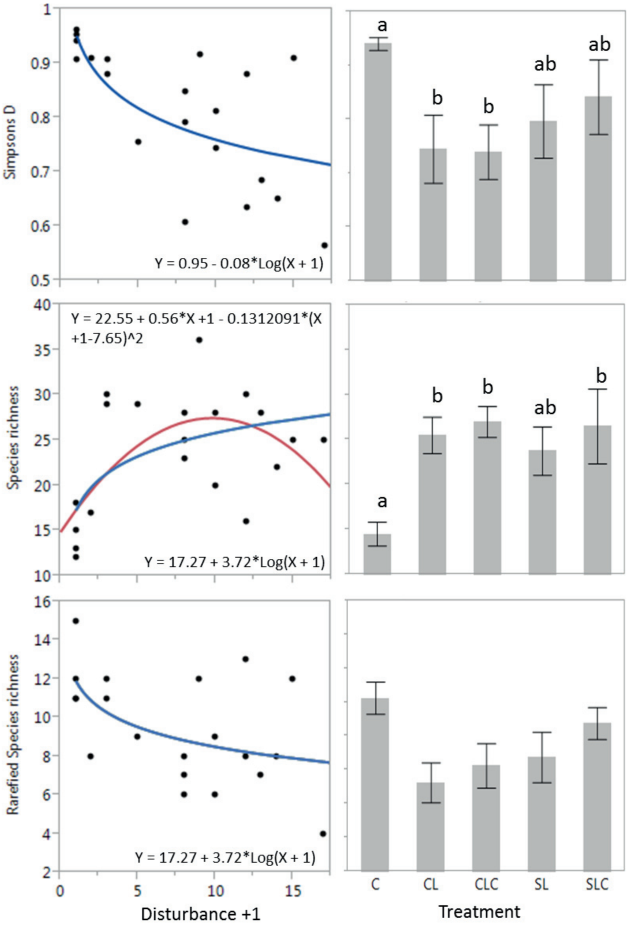

Figure 9. Simpsons index of diversity, species richness and rarefied species richness of trees growing into the tree strata (diameter at breast height ≥ 10 cm) in a tropical rainforest, in Borneo, as a function of disturbance level (number of trees harvested ha^{-1}), 10 years after conventional (CL) and supervised (SL) logging without climber cutting (CL and SL, respectively) and with climber cutting (CLC and SLC, respectively), or no harvesting (controls, C) Error bars show SE and bars with different letters denote significant differences (Tukey's HSD, P < 0.05).

increased dominance by some species). Furthermore, analyses of ingrowth of the 15 most common species revealed the strongest response from one pioneer species (*M. gigantea*) and as a consequence, that dominance of *Macaranga* spp. increased to constitute about 50 % of the stems growing in at the high end of the disturbance gradient. This effect was not only explained by harvest per se, but dominance continued to increase towards the end of the disturbance gradient. This dominance also coincided with rarefied species richness and Simpson´s *D* that decreased and was lowest when *M. gigantea* ingrowth and *Macaranga* spp. dominance was the highest.

The effects of disturbance on species richness were equally well explained by a model with logarithmic and polynomial fit. In this context the distinction is critical, as logarithmic models do not support a drop in species richness at the end of the disturbance gradient (thus dispute the IDH), whereas a polynomial model do (thus support the IDH). The logarithmic fit is supported by less model complexity but a polynomial fit is supported from ecological arguments and observations, e.g. the positive effect of stem density on species richness (Gotelli & Colwell 2001) are likely to go down with increased dominance (such as shown here). Despite being statistically undistinguishable from a logarithmic model there are thus reasons to argue for a model that can support a decrease in species richness with the level of disturbance such as the polynomial. For example, there are evidence that disturbance in these kind of forests cause both an increase in ingrowth and affect the species composition of ingrowth and that highly disturbed forests tend to be dominated by a few species (Woods 1989; Lamb, Erskine & Parrotta 2005). This would logically result in a reduced chance of finding new species in communities characterised by high dominance. Furthermore, a polynomial pattern is also supported by the analyses of long term effects that revealed strong polynomial pattern of the change in species richness in relation to disturbance intensity, both in the mid-sized class trees and in the stand as a whole. The same arguments supporting a polynomial pattern of diversity also suggest that diversity of tree ingrowth should be highest at intermediate levels of disturbance (here around logging intensities of 8 trees ha^{-1}). In this study the species richness of trees growing into the tree strata was about 30% higher at intermediate levels of disturbance compared with higher or lower levels of disturbance.

The findings in this study have clear management implications as they conclude that logging intensities should not exceed more than 8 trees per ha^{-1} (here, approx. 100m^{3}ha^{-1}) in order to promote highest possible species diversity of tree ingrowth, but the levels might have to be adjusted downwards to restrict pioneer species ingrowth and dominance. However, *Macaranga* spp. ingrowth could potentially also be restricted by applying logging practises causing less disturbance to the residual stand. By employing pre-planned skid trails, directional felling and climber cutting, as carried out during supervised logging (SLC) and reduced impact-logging practices (RIL), to restrict ingrowth of pioneer species, could possibly restrict the negative impacts from harvest operations on biodiversity patterns of the residual stand.

5 Conclusions

The overall conclusions of this thesis are that supervised logging in combination with climber cutting can promote better stand development than conventional logging practices by increasing ingrowth and reducing both the mortality of valuable commercial timber species and the ingrowth of *Macaranga* species. Furthermore, it provides evidence that the current classification of ENSO events does not cover important parameters for forest ecology, by omitting their intensity and duration, which strongly influence forest dynamics during such events.

Specific conclusions and recommendations drawn from each study can be summarized as follows.

I At high harvest intensity (> 8 trees ha^{-1}), supervised logging (SL) in combination with climber cutting (CC) consistently resulted in greater stand volume recovery, higher ingrowth of commercially valuable tree species, and lower establishment of pioneer species than the other treatments. Furthermore, climber cutting improved the survivor growth of dipterocarp species and reduced the overall mortality rate at high harvest intensities, suggesting that cutting climbers can improve post-harvest development.

II After eighteen years of post-logging data following two selective logging methods (SL and CL) combined with- (CC) or without (NCC) pre-harvest climber cutting, SL and SLC had recovered 93 and 84% respectively of initial standing basal area, in comparison to CL and CLC treatments that recovered 72 and 73%. The results also showed that during the study period stand basal area growth rates of dipterocarps were two times higher following the SLC treatment than following the CL treatment, revealing a faster basal area recovery following SLC.

III The duration and intensity of extreme climatic events are important factors to consider when evaluating effects of such events on forest dynamics. Results showed that mortality and survivor growth increased linearly with the duration of El Niño events. Results could be useful for future evaluation of extreme climatic events and their impact on forest ecology, as variation in events and their intensity and duration could mediate the effects of single events and therefore lead to better future predictions of such events. However, despite the fluctuations in basal area observed over the 19 years of development, this uncut forest seemed fairly resilient to repeated extreme climatic events.

IV Intermediate levels of disturbance resulted in the highest species richness of ingrowing trees. The findings have clear management implications as they indicate that harvests should be restricted to a few trees per hectare ($\leq$ 8 trees ha^{-1}) to promote the highest possible diversity.

6 Future research directions

Understanding the ecological processes in tropical rainforests following selective logging and climate-induced disturbance is extremely important for improving predictions of forest development and guidelines for sustainable forest management. Thus, there are clear needs for more long-term evaluations of silvicultural management methods and effects of extreme climate events use of the acquired information to formulate robust strategies to improve harvesting techniques and promote sustainable future yields of tropical rainforests. Furthermore, understanding disturbance regimes is crucial for understanding changes in ecosystem properties and stability. Interactions between forest landscape fragmentation and parameters of forest dynamics such as ingrowth, and rates of tree growth and mortality rates must be elucidated to improve knowledge of ecosystem controls. Stronger links among researchers and between researchers and forest managers are also required, to improve the quality of monitoring studies and ensure that the results of such programs are incorporated into management practices.

In summary, I believe that the research described in this thesis could contribute to better understanding of tropical rainforests' responses to different levels of anthropogenic and natural disturbance and their potential consequences for ecosystem functions.

One research priority is to evaluate effects of repeated extreme climatic events on forest ecosystems subjected to different selective logging regimes. Adaptation of forest management to climate change requires understanding of the effects of climate on forest and predictions of likely changes in these effects over time. This requires multiple forms of knowledge and new approaches to forest management decisions. Therefore, I suggest that multi-disciplinary research is needed, incorporating (*inter alia*) climatological, forest management, ecological, governance and socio-economic analyses.

Furthermore, I believe more long-term studies of selectively logged secondary forest management are needed. The emphasis should be on developing and improving silvicultural techniques aimed to reduce the damage associated with logging operations. Various authors have examined overall logging effects (Oliviera and Braz, 1995; Putz *et al.*, 2000b; Villegas *et al.*, 2009; Vinson *et al.*, 2014), but relatively little is known about the long-term effects. Further research on these effects, and associated factors, could help efforts to understand and reduce negative impacts of selective logging on forest dynamics and biodiversity. However, management interventions must also be critically evaluated with regard to ecological viability and cost-benefit ratios.

The possible utility of setting species-specific cutting limits should also be investigated. Currently, only trees with a DBH of at least 60 cm can be cut in Sabah. More evaluation of the ecology, growth rates and wood properties of specific tree species of commercial value are required, as I believe that several of those species rarely, if ever, reach the DBH cutting threshold. A management system including cutting limits for specific tree species and appropriate silvicultural techniques could potentially reduce overall damage associated with harvesting, especially for trees with > 100 cm DBH (Sist *et al.*, 2003a), as well as leaving more multi-sized stands to naturally regenerate.

Finally, I recommend more efforts to generate robust models to predict growth rates of trees in different DBH-classes following specific logging practices. Prediction models of long-term effects of various silvicultural treatments have received more attention recently, and several authors have highlighted the importance of modelling tropical rainforests to improve predictions (Chave *et al.*, 2014; Ruslandi *et al.*, 2017). However, it is still extremely important to back up model predictions with long-term data collection to validate the outcomes when modelling tropical forest dynamics.

With the recommendations for future research mentioned above, I believe that the dataset used in the studies this thesis is based upon could be highly important. The trees in the experimental plots have been inventoried biannually since 1993, and hopefully the surveys will continue. Such long-term datasets are rare, but extremely valuable for studying tropical ecosystems.

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Acknowledgements

First and foremost, I would like to express my gratitude to my group of supervisors: Anders Karlsson, Ulrik Ilstedt and Petter Axelsson. Thank you all for all the great support and guidance during these years, for always having patience and kindness, for always pushing me forward during hard moments and helping me through this project. You have all enriched my life, both personally and professionally, and for that, I am very grateful.

Jan Falck, without you, I would never have had the opportunity to experience the wonders of Sabah's tropical rainforests. I can't thank you enough for fearlessly inviting me to Sabah back in 2009, but also believing that I, a biologist with an unhealthy interest in amphibians and reptiles, could contribute to the fantastic forestry project you set up over 25 years ago. You are a true inspiration and I will never forget our enthralling discussions out in the SUAS-camp. I hope we get the opportunity to experience this again in the near future.

Great thanks are also due to all of my colleagues at the Department of Forest Ecology and Management. Special thanks to Göran Hallsby, Björn Erhagen, Linda Gruffman, Martin Ahlström, Jaime Uria Diez, Kristi Kuljus, Bo Ranneby, Olle Forshed, Malin and Viktor, Aida and Naxto, Javier and Anna, Michael and Kelley Gundale, Niles and Eliza Hasselquist, Rosa Goodman, Lunkan, John Marshall, Tommy Mörling, Ann Dolling, Pjodd, Gert Nyberg, Göran Spong, Hans Sjögren, Ida Taberman, Erik Valinger, Waffe, Sandra Jämtgård, Mats Öquist, Anand Roopsind, Ruslandi, Thales West, Ulf Renberg, Elisabeth Degerstedt, Gun-Marie Johansson and Ann-Kathrin Persson.

Projek ini tidak mungkin terlaksana tanpa bantuan dari rakan dan teman sekerja kami di Sabah, Borneo. Saya dengan ini ingin berterima kasih kepada Dr. Waidi Sinun dan Dr. Yap Sau Wai di Yayasan Sabah diatas perbincangan

menarik di antara kami dan kesemua bantuan yang telah diberikan kepada kami selama kami berada di Sabah. Terima kasih juga kepada Gideon Peter Joitol dan David Alloysius diatas kesemua bantuan dari segi logistik dan kerja lapangan. Seterusnya, saya ingin berterima kasih kepada Pn. Rita Sundangkit dan Cik Jenifer Chua untuk semua yang telah anda aturkan termasuk hotel dan pengangkutan semasa saya berada di Sabah. Terima kasih kepada Francis Totu, Brahim, Ibrahim, Fred, Victor dan Sairul Azlan kerana menjadikan persinggahan saya di Luasong indah, terutamanya "perjumpaan kecil" kami di rumah Victor atau di Luasong Forestry Center. Terima kasih kepada wanita di rumah rehat Luasong, Habibah, Mama Lina, Jenna dan Ida untuk teman yang baik dan masakan yang sedap. Ateng, terima kasih kerana sentiasa mengatur penginapan saya di rumah rehat Luasong.

Tidak dapat disangkal lagi, orang yang paling penting untuk projek kami ialah semua yang telah terlibat membantu kami semasa tempoh kerja lapangan intensif di dalam kem SUAS. Saya tidak akan lupa saat indah kita di dalam hutan dan anda semua adalah saudara lelaki saya dan sahabat yang hebat. Dengan ini, saya mengucapkan terima kasih kepada anda: Thomas Rolling, Jakariah Ahmad, Simon Lagundi, Albert Lojingi, Ramsah Mahalan, Juniansah Selamat, Rojita Samat, Raziansyah Juma, Krisnos Maung, Rasidy Igau, Nelson Suntik, Azire Mumin, Herry Basang, Juspin Balungking, Suhari Sapari, Wonson Tuil, Dizolkeply Sundolon, Rosli Meging, Lawrence Tinkol, Idris Arsan, Fadilis Mujih, Wilfred Alexander Abbas, Jeffry Battin, Johpin Jaalif, Masliadi Asri, Staincen Kari, Nicholas Dain, Azwan dan Azman Tahil, Azman besar, Rosley Damit, budak-budak lelaki Kalabakan, Arik Jeffrin abang besar saya, Amshari “Komando” Agimin, Yapdi Tajab, Amat lelaki “chainsaw”, dan banyak yang saya malangnya terlupa nama-nama mereka. Tiada ucapan terima kasih yang lebih hebat lagi di dunia ini yang dapat menggambarkan usaha yang telah anda sumbangkan. Kamu betul-betul adalah wira sebenar di dalam projek kami. Saya berharap jalan yang kita lalui akan bertemu lagi dalam masa terdekat di masa hadapan.

Slutligen, till Mor och Far, Robert och Camilla, Anna-Lena, Sabina och Lars-Göran, Sara, Janne och Ulla, Andreas och Ulrika, Andreas och Emma, “lillebror” Daniel *Besar*, Anders Hildeman, Bent och Pernilla, Per-Anders och Johanna, Petter och Eva, Linnea och Jonas, Micke och Christer, Henrik och Jessika, Henrik Hedenås och Ruaridh Hägglund, av ett stort antal skäl, TACK!

Christina och Sixten