The impacts of selective logging and restoration on trees in a lowland tropical forest in Sabah, Malaysia

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December 2021

A thesis submitted for the degree of
Doctor of Philosophy
Faculty of Natural Sciences
University of Stirling

General abstract

Selective logging has degraded large areas of tropical forest. However, disturbed forests are important refugia for biodiversity and recover biomass over time, especially when aided by active restoration. Yet we know relatively little about the effects of logging and restoration on long-term seedlings dynamics and future tree communities. Here, I investigate differences in forest structure and tree community composition at different life-stages across unlogged, naturally regenerating (NR) and actively restored (AR) forests in Danum Valley, Malaysian Borneo, 23-39 years after logging and 12-28 years after restoration.

Basal area (all stems ≥2 cm DBH) was greatest in unlogged and did not differ between NR and AR forests. However, mean DBH was greater in AR than NR forest, suggesting that restoration accelerated the return of larger stems. Species diversity was equal across forest types but community composition differed and did not converge over time since logging.

After mast fruiting in 2019, seedling density was greater in unlogged and AR forests than in NR forest. However, seedling density in AR forest also declined fastest so, after 1.5 years, AR forest supported fewest seedlings – 0.85% of the original cohort. Larger seedlings established before mast (recorded over 2.5 years) also had greatest mortality in AR forest, but had higher relative growth rates. Masted seedling community compositions diverged over time and dipterocarps exhibited particularly high mortality in AR forest.

Differences in forest structure, community composition and recruitment processes therefore persist up to 40 years after logging. These findings may result from: differences in seed and seedling predation, viability, and differing microclimates between forests with different disturbance histories. I highlight the need for further observations of early tree life-stages in recovering forests and their drivers, which ultimately constrain the species pool of future canopy communities, and should guide decision-making in forest restoration.

Thesis Rationale

Selective logging is prevalent throughout the tropics and there is now more tropical forest regenerating post-harvest than there is unlogged forest (Asner et al., 2009, Laurance et al., 2014). As such, there is considerable interest in how forests are able to recover from logging and the potential for active restoration techniques to accelerate that recovery (Zahawi et al., 2014, Latawiec et al., 2016, Crouzeilles et al., 2017, Crouzeilles et al., 2020). While many studies provide evidence that animal biodiversity is retained post-logging (Edwards et al., 2011, Wearn et al., 2017, Yano et al., 2021), less is known about the long-term fates of tree communities and their trajectories of recovery (Brown and Gurevitch, 2004, Baraloto et al., 2012, Cazzolla Gatti et al., 2015, Ewers et al., 2015, Shima et al., 2018). Studies of early life stages (seedlings and saplings) of logged forest tree communities are sparse but suggest that seedlings in logged forest – particularly of late successional and timber species – may be more vulnerable to both abiotic and biotic pressures (e.g., drought and herbivory) than in unlogged systems (Curran et al., 1999, Bagchi et al., 2011, Qie et al., 2019). If late successional and threatened species – such as dipterocarps in Southeast Asia – are thereby unable to recruit in logged forest, there could be long-term reductions to forest ecosystem functioning, stability, and successional status, affecting the ability of forests to naturally regenerate. It is therefore important that we understand not only the long-term effects of selective logging on established trees but also the mechanisms operating at early life stages to drive future recruitment, allowing us to inform management of logged forests during recovery.

Restoration interventions (e.g., weed control, climber cutting, liberation thinning, enrichment planting) are commonly used to accelerate forest recovery post-logging. Further research is required to understand how active restoration might mitigate the effects of forest disturbance or whether, through focus on short-term carbon capture or timber production, restoration might divert successional trajectories so that species composition does not converge on old-growth. Trees planted during active restoration efforts in the late twentieth century are now reaching maturity within logged forests, enabling us to study the production of seeds and recruitment of seedlings. The pressures faced by the progeny of planted trees, and the ability of different taxa to withstand those pressures, are key to understanding the long-term success of restoration practices. Knowledge of the successes and limitations of past active restoration strategies across different life stages can be used to guide future restoration strategies, allowing them to avoid pitfalls, such as low genetic diversity of enrichment planting (Nef et al., 2021), and to best mitigate the lasting effects of selective logging in tropical forests.

Declaration of Authorship

I, Robin Hayward, declare that this thesis has been composed by myself and that it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of the work carried out in collaboration with others. I confirm that the research undertaken as part of this thesis has received ethical approval from the University of Stirling.

Signed ………………………………………………

Date ……………21/12/21……………………

Acknowledgements

I am grateful to so many people for their support during my PhD that thanking them all sufficiently would take up more space than this thesis itself. I hope that, through my actions and words outside this text, they know how much they have meant to me.

Foremost amongst those I need to thank is Daisy Dent, who has worked tirelessly to ensure not only the quality of my research but also my personal happiness within it. Daisy’s insights and encouragement have reenergised me whenever my enthusiasm has wavered and I am deeply appreciative of all her efforts to make this project a success. I have been privileged to work with an amazing team of supervisors and Lindsay Banin, Dan Chapman, and David Burslem have all given tremendous support and dedication of their time. Through their inputs, the research and perspectives of this thesis have been vastly improved and I have been delighted to learn from their experience.

This project has benefitted immensely from a number of collaborators. My thanks go to Chris Philipson, Mark Cutler, and Glen Reynolds for their willingness to share data, as well as their comments on chapter two during peer review. I am also grateful for input from Reuben Nilus and two anonymous reviewers.

Institutional support from the University of Stirling, the UK Centre for Ecology & Hydrology in Edinburgh, the Sabah Biodiversity Centre, the Danum Valley Management Committee, and the South East Asia Rainforest Research Partnership (SEARRP) has been vital to the success of this project. My PhD was funded by the UKRI Natural Environment Research Council via the Iapetus doctoral training partnership and I am grateful for the many opportunities they have provided. I would like to extend particular thanks to John Wainwright, the director of Iapetus, who provided a friendly face throughout the PhD and was a driving force for student support when the Covid-19 pandemic disrupted and delayed our projects. My PhD received additional funding from the Arnold Arboretum Ashton Award, which was of great help to support fieldwork costs. My thanks to Peter Ashton for establishing the award and for a brief but insightful chat in the coffee room at Kew.

I am grateful to the herbarium staff at Kew, the Natural History Museum, the Royal Botanic Garden Edinburgh, and the Danum Valley Field Centre for welcoming me, training me, and trusting me to use their collections.

During my PhD I was privileged to spend six months conducting fieldwork in Sabah, Borneo, and I owe thanks to everyone living and working in Danum Valley. I am endlessly grateful to Tambi Karolus, whose experience and hard work kept us safe and productive while we navigated the depths of the forest. For their support of my research and their friendship in the field, I thank Yoel, Sabide, Cco, the monkey king, Dede, Ahmat, Adam, and the entire 50 ha team. For their wealth of herbarium knowledge, I thank Ica, Alex, and Bill, and, for their logistical support, I thank Johnny and Ivy. My thanks to all the friends I made at Danum, who may not have joined me in the forest or ever seen my data but who nonetheless made my time there worthwhile; to Cindy, Chris, Simone, Paddy, Gianluca, Tanith, Peter, Suzanne, Nadine, Ingrid, Josie, Sarah, and Rahman, thank you. I will treasure fond memories of barbecues by the river, songs sung by campfires with karaoke microphones, and the many adventures we shared.

Although the Covid-19 pandemic prevented a second field season at Danum, I received follow-up data from my seedling plots thanks to the efforts of Tambi and the 50 ha team, co-ordinated by Mikey O’Brien. I am massively grateful to them all for juggling the hard work of data collection with safe adherence to local public health guidelines.

I am immensely fortunate to have been supported throughout this PhD by family and friends, new and old. Thanks to my mum, to my dad, and to Matt and to Caz for being there whenever I needed to procrastinate. Thanks also for giving me the occasional nudge to get back to work. To all the friends who have supported me through the ups and downs of life over the last few years, both online and in person, I am unceasingly grateful and it is my ongoing pleasure to support you in turn. My thanks go to Alex, Elliot, and Myrini; to Matt, David, Mia, Paulo, Théo, Xavi, Sarah, Alex and Robbie; to Lucy, Allan, Erin, John, Nina, Kirsten, Jazz, Jess, Doug, Craig, Finley, Hazel, Lidia, and Sophie; to Ellen, James, Kris, and Laura; to Emily, Dave, Julia, and Sol; to Emily, Sarah, and Cos; to Eli; to Duncan; to Danny; and to Kezz. Thank you to everyone at Stirling, not already named above, for your support and camaraderie – particularly to Lynn (and Charlie!) for sorting out my many expenses and to the rest of the Dent Lab (Izzy, Bekah, Tom, Alex, and Adam) for fantastic chats and inspirations over the years.

Thanks, finally, to the trees for being so fascinating and to you, the reader, for being interested and/or supportive enough to take a look at my thesis. I hope I have succeeded in making it easier to read than it was to write, and at least as much of a pleasure.

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Photo: Dawn over selectively logged forest in Danum Valley

[credit: Robin Hayward]

Chapter collaborators: Robin Hayward, Lindsay Banin, Daniel Chapman & Daisy Dent.

This chapter was written by RH and all authors commented on a draft of this chapter.

1.1.0 Tropical forests

Forests cover more than 20% of the Earth's land surface and are categorised regionally, based on the taxa present and their physical environment (Hansen et al., 2010). Asia and South America each contain approximately a quarter of the global land area covered by forest (Hansen et al., 2010), including ~9.4 million km^2 of tropical forest in the Americas and ~5.7 million km^2 in Asia (Wright, 2010). Tropical wet forests (figure 1.1) are found in tropical latitudes and receive at least 60 mm precipitation month^{-1} throughout the year – typically >2000 mm year^{-1} (Woodward et al., 2004, Kottek et al., 2006) – covering ~11 million km^2 (6-7%) of the Earth's land surface (Hansen et al., 2010).

Figure 1.1 *Photographs of the tropical wet forest biome*

1.1.1 The ecology of tropical forests

Tropical wet forests are amongst the most biodiverse habitats on the planet, containing over 60% of all known species, including >40,000 tree species (Dirzo and Raven, 2003, Slik et al., 2015). They exhibit high levels of endemism, especially when located across archipelagos or elevational gradients, which are driven by stable climates that allow old taxa to persist and new taxa to emerge in regions where gene flow is limited (Mittermeier et al., 1999, Kier et al., 2009). A number of mechanisms have been proposed to maintain the high tree species richness and diversity seen in tropical wet forest flora. For example, conspecific negative density dependence (C-NDD) is thought to support diversity through selection for rare species. In C-NDD, conspecific plants at higher densities experience reduced survival due to greater pressures from predators, pathogens, and resource limitation (Connell and Connell, 1971, Comita et al., 2010, LaManna et al., 2017). Conspecific individuals in tropical wet forest ecosystems are relatively sparse to avoid these pressures, allowing a greater variety of taxa to be present within the same space.

Tropical wet forest trees form a dense canopy, intercepting the majority of light before it reaches the forest floor and shading vegetation within the understory (Poorter et al., 2005). Canopy trees are generally long lived and may themselves form habitats for diverse lianas and epiphytes along their boles and branches (Woods et al., 2015). Saplings and seedlings in Borneo can survive with suppressed growth in the forest understory for over a decade, waiting for resources and space in the canopy to become available (Delissio et al., 2002). Typically, the creation of gaps, by the death or collapse of a canopy tree, enables suppressed seedlings to recruit through to the canopy, taking advantage of the increased light availability to grow out from the understory (Brokaw and Busing, 2000). Tropical forests typically have a diverse seedbank within their topsoil, although seed density may vary with as few as 100 seeds m^{-2} in Southeast Asia (recorded in Borneo; Howlett and Davidson, 2003) to several thousand seeds m^{-2} elsewhere in the tropics (depending on levels of disturbance), waiting to germinate under more favourable conditions (Tang et al., 2006, Daïnou et al., 2011, Silva et al., 2021).

Tropical wet forest trees flower and fruit through diverse strategies that range between extremes of synchrony and asynchrony, often within the same landscape (Schaik et al., 1993, Bawa et al., 2003, Adamescu et al., 2018). Asynchronous fruiting may come at the cost of greater seed predation by granivores able to locate and feed on propagules from isolated stems (Janzen, 1971, Schaik et al., 1993). One mechanism that tropical wet forest trees have evolved to mitigate seed predation (particularly within Southeast Asia), is mast fruiting (Janzen, 1971). During masting events the majority of canopy trees synchronise to flower and fruit simultaneously, which allows for predator satiation, where there are insufficient seed predators to consume all propagules prior to their germination and so some escape predation (Curran and Leighton, 2000, Silvertown, 2008, Koenig, 2021). Masts within Southeast Asian forests are thought to be associated with warming from the El Niño Southern Oscillation, which occurs every 3-9 years, although the exact mechanisms that trigger masting remain unclear and slight asynchrony between regions suggests other variables may influence masting phenology (Curran et al., 1999, Wich and Schaik, 2000).

1.1.2 Value of tropical forests

Tropical forests have high inherent value to people globally, as natural wonders, as hosts to many charismatic species, and as regions of immense cultural importance. However, they also have quantifiable importance to environmental functioning and human populations by sequestering carbon, reducing erosion, increasing water and air quality, regulating regional and global climate, and provisioning of food, fuel and shelter (Gardner et al., 2010, Edwards et al., 2014b, Boul Lefeuvre et al., 2022).

Perhaps the most commonly cited example of tropical forest value is their contribution to global carbon stocks and ability to sequester carbon from the atmosphere, reducing the quantity of greenhouse gases forcing climate change (IPCC, 2014). Tropical forest growth is a sink of 2.7 ± 0.7 Pg C yr^{-1}, although tropical land-use change and deforestation also causes the release of 2.9 ± 0.5 Pg C yr^{-1} (Pan et al., 2011). Pantropical above-ground carbon stored in live trees is equal to 285.1 (95% CI: 251.8 - 318.9) Pg, with Africa containing 114.0 (95% CI: 96.4-131.1) Pg C, South-Central America containing 108.0 (95% CI: 101.0-114.9) Pg C, Southeast Asia containing 39.2 (95% CI: 33.7-45.9) Pg C, and North Australia containing 23.9 (95% CI: 20.7-27.0) Pg C (Feldpausch et al., 2012). On average, tropical wet forests contain 259 Mg C ha^{-1} but this can vary substantially by region (Hansen et al., 2010, Feldpausch et al., 2012), and even forests degraded by logging may contain 60-140 Mg C ha^{-1} (Asner et al., 2018).

The presence of forest may help to prevent erosion of tropical soils, and in extreme cases flooding, by regulating water flow. In Kalimantan, Indonesia, direct runoff of precipitation in old growth forest was approximately two thirds as much as in ten year old logged forest, reducing likelihood of floods (Suryatmojo et al., 2011). A pantropical meta-analysis of soil erosion suggests that the presence and management of vegetation in the humid tropics could be sufficient to prevent 99% of soil erosion, relative to bare earth (Labrière et al., 2015). Furthermore, by preventing erosion and transport of sediment into rivers, tropical forests are able to improve local water quality (Lele, 2009). Local air quality may also be improved, relative to other possible land uses, as forests in Borneo produced substantially less volatile organic compounds, NO_x emissions, and ozone than agricultural land (Fowler et al., 2011, MacKenzie et al., 2011, Pyle et al., 2011).

Across tropical wet forest landscapes, including areas outside the physical footprint of the forest, tree communities provide valuable localised climate regulation by increasing transpiration of water to the atmosphere (Wright et al., 2017). Reduced temperatures and stable precipitation regimes resulting from the presence of forest, as well as increased diversity of pollinators, have been demonstrated at sites across the tropics to increase agricultural outputs of adjacent land (Snyder et al., 2004, Blanche et al., 2006, Sodhi et al., 2010, Souza et al., 2012). Within forests, near total canopy cover results in relatively stable temperatures, shade from the sun, and high humidity (Fetcher et al., 1985, Laurance, 2004). In the canopy too, epiphytes act to control the microclimates of tree crowns, moderating evapotranspiration, reducing temperatures and creating a more stable environment for arthropod communities (Stuntz et al., 2002). The values of these ecosystem services can be significantly reduced in the event of deforestation or forest fragmentation, however, causing harm to the remaining ecology and landscape of the area (Laurance, 2004). A 50% reduction in forest cover in Borneo, for example, correlates strongly with significantly reduced precipitation (Lawrence and Vandecar, 2014). It is therefore important that these costs to ecosystem services and functioning are considered when forests are exploited and when conservation and restoration strategies for tropical forests are planned to mitigate them.

1.2.0 Land use change and degradation in tropical forests

Tropical forests face substantial threats from land-use change, resulting in extensive deforestation and degradation. Between 2000 and 2005, 286,000 km^2 of forest cover was lost in the tropics (Hansen et al., 2010) and the highest CO_2 emission rates from tropical deforestation occurred between 2005 and 2010 (1792 ± 133 Mt CO_2 yr^{-1})

(Carter et al., 2017). Deforestation and forest degradation throughout the tropics accounted for ~10% of global greenhouse gas emissions between 2000 and 2010 (IPCC, 2014).

While forests globally are threatened, tropical forests were unique in experiencing accelerating loss, with c. 2000 km^2 of increased losses each year from 2000 to 2005 (Hansen et al., 2013). On a national level, the largest contributor to this trend was Indonesia (accelerating at 1021 km^2 per year between 2000 and 2005) and, more broadly, Southeast Asia had the highest rate of deforestation relative to land area of any major region in the tropics in 2000-2015 (Achard et al., 2002, Hansen et al., 2013, Curtis et al., 2018).

Tropical forest land-use change is largely driven by conversion to agriculture, particularly amongst forests which were previously logged or otherwise degraded (Edwards et al., 2011). Conversion to agriculture represents 81.7 % of deforested tropical land; 82.5% in Africa, 88.2% in Latin America, and 65.2% in Asia; the majority of alternative land-use change being conversion to non-industrial lands, such as bare rock or soil, grassland, and early successional secondary forest (representing 14% of deforested land globally and 30.1% in Asia) (De Sy et al., 2019). Accordingly, 72% of global CO_2 emissions from deforestation, and 67% in Asia, are from deforestation driven by agriculture (Carter et al., 2017). In Latin America, over two thirds of forest land cleared for farmland is for pasture, while in Africa and Asia the majority of cleared land is used to produce crops (De Sy et al., 2019). Of the converted agricultural land in Asia, 53.7% is used for small-scale crop production and 42.8% for industrial-scale tree crops, such as oil palm (De Sy et al., 2019). In Asia, oil palm expansion has been a major driver of deforestation over the last 20 years (Wicke et al., 2011, Lawrence and Vandecar, 2014). Malaysian plantation areas, for example, increased by 890,000 ha in the six year period between 2008 and 2014 (Azhar et al., 2017).

In addition to forest clearance, land-use change in the tropics can represent a shift from old-growth forest to production forest, something which is not considered in the above statistics. Forest degradation occurs when resources are extracted, or human activity otherwise causes a level of ecosystem functioning to be lost (e.g., timber extraction or bushmeat hunting), while the overall land use of the area remains the same. At the landscape scale, forest degradation can create an additional 15-19% carbon emissions on top of emissions from deforestation (Huang and Asner, 2010). Degraded forests tend to be more vulnerable to clearance for use as agricultural land than undisturbed forest because they are not prioritised in conservation efforts (Edwards et al., 2011). Conservation tends to prioritise undisturbed forest ecosystems but degraded forest systems can retain high conservation value that increases over time if left to recover with appropriate management and connectivity with old growth forest (Whitworth et al., 2018). That degraded forest systems are regularly overlooked in conservation planning has been the subject of increasing academic concern, with recent pantropical meta-analyses and reviews highlighting the value of retaining degraded forests within tropical landscapes, where they are shown to retain high species richness and diversity, carbon stocks, regulation of local climate and soil hydrology, and high timber yields in the event of logging, relative to agricultural landscapes (Putz et al., 2012, Edwards et al., 2014b, Chaudhary et al., 2016, Bousfield et al., 2020).

The causes and extent of forest degradation can vary regionally and can range from local traditional extraction of non-timber forest products to large-scale industrial exploitation of resources. One of the most common causes of forest degradation throughout the tropics is selective logging (Asner et al., 2009) and selectively logged forest is the focal system for this thesis.

1.3.0 Selective logging

Selective logging is the systematic, low-density, removal of desirable species and stems from production forests (Edwards et al., 2014b). By harvesting the largest (typically >40 cm DBH) and most valuable individuals and only removing ~4-10 stems per hectare, much of the forest structure and diversity remains intact and, if left undisturbed, biodiversity, carbon stocks, and other ecosystem services can recover (Berry et al., 2010, Putz et al., 2012, Edwards et al., 2014b, Chaudhary et al., 2016). In this way an effort is made towards balancing conservation with the requirements of industry and local populations for resources and employment. This contrasts with clear-fell logging, in which all stems are removed and may result in conversion to other land-uses such as agriculture, where the ecosystem is entirely replaced (Sala et al., 2000, Edwards et al., 2014b, Whitworth et al., 2018).

There has been some debate regarding the exact processes and time requirements of tropical forest recovery after selective logging and how these must be considered in relation to the economic drivers for the logging industry to return and harvest again. Commonly, selectively logged forests are subject to repeat logging at a shorter interval than is required for recovery to occur, leading to cumulative impacts across logging cycles, particularly amongst reproductive adult trees (Sist et al., 2003, Lobo et al., 2007, Sebbenn et al., 2008, Hiltner et al., 2018, Yguel et al., 2019). As large and valuable stems become increasingly rare with subsequent logging cycles, the short-term profitability of conversion to agricultural land increases and therefore also the likelihood of deforestation (Edwards et al., 2014a).

Between the years 2000 and 2005, at least 20% of the tropics was selectively logged, making selective logging 20 times more common than clear-fell techniques (Asner et al., 2009). It is estimated that more of the tropics is now logged than remains unlogged, illustrating the potential scale of its environmental impact (Laurance et al., 2014). Selective logging is particularly prevalent within the Asia-Pacific region (Laurance and Edwards, 2014). Malaysia, for example, experienced declining forest cover in every state between 2000 and 2005 (Hansen et al., 2010) and the island of Borneo – the geographical focus of this thesis – comprised 8% of all tropical land designated as logging concessions over the same period (Asner et al., 2009).

Borneo was first commercially logged in the early 1970s and the state of Sabah has since been logged at approximately 20-year intervals (Reynolds et al., 2011, Gaveau et al., 2014). Initial rapid expansion from 1970-90, established over half of logging roads present in 2010, then after 1990 expansion slowed and road extension halved between 2000 and 2010 (Gaveau et al., 2014). Despite this slowing, logging road density in Borneo was 16 times greater than elsewhere in the tropics in 2010, and less than 40% of Borneo was primary forest, with 19.1% of that in the state of Sabah (Gaveau et al., 2014). Less than 60% of Bornean carbon stocks (>200 Mg ha^{-1}) are located inside maximum protected areas (Asner et al., 2018), 42% of Borneo's primary forest is designated as production forest, and a further 16% has been allocated to conversion for agriculture (Gaveau et al., 2014), highlighting the vulnerability of these forests and the importance of recognising their value.

1.3.1 Techniques for selective extraction of timber

The intensity, scale and techniques used in selective logging vary by site and region. The impacts of selective logging vary with these different logging methods, making it important to understand how these differences translate to disturbance impact and rate of recovery (Putz et al., 2001). Commonly, selective logging is carried out by means of either cable (often referred to as ‘high-lead’) or tractor logging techniques. While both practices can be adapted to suit a range of environments, efficiency usually dictates that cable logging is used on the steepest slopes of a production forest (≥17°), while tractor logging is more appropriate to a moderate terrain (Dykstra et al., 1996). These different methods can lead to fine-scale patterns of disturbance across the logged landscape related to local terrain (Marsh and Mittermeier, 1987). In the process of cable logging, ~20 ha of forest is cleared around a central ‘spar tree’ or a portable tower, which acts as the highest anchor point from which to haul cut stems during transportation to their processing point (Marsh and Greer, 1992). There is substantial damage extending outwards from this cleared area along the routes of main winch lines (Marsh and Greer, 1992). This cable logging creates predictable damage around a central point. In contrast, tractor logging results in a near random mosaic of skid tracks, broken trees, and undamaged patches, where ground-based machinery is used to drag stems to the point of processing (Marsh and Greer, 1992). This disturbance causes significantly greater soil compaction than cable logging and therefore potentially greater erosion and nutrient leaching (Marsh and Greer, 1992). Comparing these two techniques, cable logging tends to result in a remnant community with a lower diversity of mature tree and sapling species, while tractor logging reduces the richness of seedlings (Foody and Cutler, 2003). These differences likely result from differences in remnant canopy damage and ground compaction (Foody and Cutler, 2003).

In contrast with traditional extraction techniques, reduced impact logging (RIL) aims to minimise environmental impact, while also maximising long-term profits (Barreto et al., 1998, Holmes et al., 2002, Baraloto et al., 2012). RIL focuses on minimising disturbance throughout the logging process, however the specifics of RIL, and even the extent of responsibility for the forest post-logging, varies hugely by country (Putz et al., 2008). The standards of RIL always include increased worker safety, reduction of waste, and mitigation of residual damage from falling trees by directing them away from other stems with either high conservation value or potential to be logged for profit in future rotations (Putz et al., 2008). Before logging, harvesters may cut any lianas linking the selected tree mechanically to other stems, thus reducing the amount of residual damage when it is felled (Richards et al., 1996). Typically, a trained RIL work crew will, for example, conserve more of the stand's residual above ground biomass (Holmes et al., 2002, Putz et al., 2012, Lussetti et al., 2016). As a result, RIL has been observed to cause significantly fewer post-logging tree mortalities (Schulze and Zweede, 2006), and considerably less residual damage, both in terms of absolute quantity and ground area affected in Brazil (Pereira et al., 2002, Asner et al., 2004b). RIL has resulted in less disruption to animal biodiversity (especially birds) in Guyana (Bicknell et al., 2015); and lower levels of disturbance to forest structure across Borneo, due to above ground biomass (AGB) and near infra-red radiance more similar to primary forest than typical selectively logged forests across Borneo (Tangki and Chappell, 2008).

1.4.0 Impacts of logging on plant communities and subsequent recovery

While, in theory, the disturbance caused by selective logging should mimic gaps left by natural disturbances like tree fall (Webb, 1997), in practice this has rarely been shown to be the case because selective logging is typically conducted rapidly and at a landscape scale, unlike natural disturbances. The exact rates and trajectories of forest recovery post-logging vary in relation to site specific conditions such as forest fragmentation and species diversity, as well as logging technique and intensity (Putz et al., 2012, Arroyo-Rodríguez et al., 2017). For example, in Sabah and Kalimantan, Borneo, successional richness post-logging has been shown to depend on the forest's original successional status and level of pre-logging disturbance, as well as the distribution of logging across landscapes (Cannon et al., 1994, Sheil and Burslem, 2003, Berry et al., 2008), while the rate of seedling recruitment in Sabah was affected by the severity of disturbance to vegetation and soil during logging (Nussbaum et al., 1995), with gap size playing a crucial role in determining localised recovery in Brazil (de Carvalho et al., 2017). Rates of recovery can also be affected by silvicultural treatments post-logging such as vine cutting and seedling planting, although a recent review suggests that natural forest regeneration may be the best approach for recovery of many plant and animal taxa (Crouzeilles et al., 2017).

1.4.1 Physical environment

Selectively logged forests may have distinct physical environments from old-growth, as abiotic variables, including soil nutrients and structure, light levels, and humidity, are affected.

The physical process of logging, particularly the passage of bulldozers and other heavy machinery, can alter the soil's physical properties and redistribute nutrients and propagules away from skid trails. When initially creating trails, bulldozer blades displace topsoil, creating side-mounds which are comparatively fertile and allow for high seedling recruitment and survival on forest edges, while conversely decreasing fertility and growth on the trail itself (Gillman et al., 1985, Guariguata and Dupuy, 1997, Pinard et al., 2000a). As much as 40% of the surface soil can be churned by machinery on site, drastically reducing the viability of the seedbank in these areas (Nicholson, 1979, Howlett and Davidson, 2003). Furthermore, the weight of machinery and the timber being dragged out of the forest has been shown to cause long-term soil compaction on logging roads and skid trails, negatively affecting regrowth by reducing soil permeability (leading to increased surface runoff, erosion, and nutrient leeching) and making it more difficult for roots to grow (Greacen and Sands, 1980, Putz et al., 2008). Selective logging removes large canopy trees from the forest, removing substantial biomass and nutrients that would otherwise decompose on site, providing habitat and recycling essential nutrients (Dillis et al., 2017). Predictably, this, as well as several secondary factors, including change in the dominant species producing leaf litter for the area, can have a significant impact on soil chemistry of logged forests (Olander et al., 2005).

Removal of large canopy stems can substantially alter microclimates in the short term post-logging, with logged forests typically having hotter and more variable microclimates than old growth (Hardwick et al., 2015, Fauset et al., 2017, Blonder et al., 2018). While microclimate buffers in Sabah have been shown to recover approximately a decade after repeated logging, high irradiance and vapour pressure deficits may persist at macro scales (Senior et al., 2017a, Senior et al., 2017b). In studies from peninsular Malaysia and Sierra Leone, logged forests had thinner and slightly lower (<3 m difference) canopies, with larger canopy gaps (10.2% gap fraction vs 5.6%) than unlogged forests, including a greater proportion of gaps reaching all the way to the forest floor (Okuda et al., 2003, Kent et al., 2015). This reduced Leaf Area Index (LAI) in logged forest allows more solar radiation to penetrate to the understory (Hardwick et al., 2015), reduces the heterogeneity of the light environment, and increases periods of direct insolation (Yamada et al., 2014).

1.4.2 Vegetation structure

Selective logging has immediate effects on forest structure through the physical removal of both targeted trees and collateral stems. As trees are felled, their proximity to other stems can result in damage to neighbouring trees, and a pan-tropical meta-analysis suggests this is especially true for felled trees >80 cm DBH (Picard et al., 2012). Additionally, mature trees are often laden with epiphytes and lianas meaning that it is not just a single member of the plant community being removed from the canopy but instead an entire micro-community (Woods et al., 2015). Lianas may be supported by several trees in the canopy and can exert damaging mechanical stress on connected trees when a single tree is logged (Richards et al., 1996). In Brazil, these mechanisms have resulted in the mortality of as many as 10 non-target trees (DBH >10 cm) per logged individual (Costa and Magnusson, 2002).

Forest canopy structure may recover rapidly post-logging (Pfeifer et al., 2016). Studies from Brazil suggest that half of the gap area can close within the first year post-logging (Asner et al., 2004a) and canopy gaps close almost completely four years after logging (de Carvalho et al., 2017). A study from Borneo found that, in under a decade, leaf area and associated ecosystem functions can recover to pre-logging values (Pfeifer et al., 2016). Some elements of the canopy environment may take longer to recover however, and ten years after logging in French Guiana, for example, the average crown height of trees remained reduced, as well as the bole-to-crown height ratio (Rutishauser et al., 2016). The bole height was also unlikely to increase in mature trees once a crown had been established, regardless of any increase in total height (Rutishauser et al., 2016). Several decades post logging (examined up to 50 years), tree crowns in peninsular Malaysia remained both smaller and shorter than those in unlogged forest, with less variation in both measures (Yamada et al., 2014). However, the surface area of tree crowns was >1.5x greater in logged forest in the same landscape (Okuda et al., 2003).

Following initial rapid recovery of canopy structure in logged forest, tree density typically returns to near pre-harvest values within five to fifteen years at a landscape scale (Slik et al., 2002). However, a number of studies report distinct time frames for recovery. In Costa Rica and central Africa, density and total basal area of mature and sapling stems on logging tracks remained decreased 12-18 years after logging (Guariguata and Dupuy, 1997, Hall et al., 2003). In Malaysia, the regeneration of stems and root biomass was still significantly lower on skid trails than elsewhere 18 years post-logging (Pinard and Putz, 1996, Pinard et al., 2000a). After 20 years, in the Western Ghats, India, logged forest still had a lower mature stem density and, after 27 years, it had 6-45% lower stand basal area than unlogged forest (Jeyakumar et al., 2017).

Measurements taken within a year of logging in Sabah suggest conventional and reduced impact logging retain 44% and 67% pre harvest biomass respectively, with subsequent records showing net decreases in biomass several years post-logging (Pinard et al., 1996). Despite this, carbon stocks in logged forests have still been shown to increase faster than old growth in the American tropics or tree plantations in central Africa (Gourlet-Fleury et al., 2013, Poorter et al., 2016). Studies of timber recovery after selective logging suggest 50-100 year intervals between harvests are required to allow sufficient regeneration for sustainable extraction (Foody and Cutler, 2003, Nagaraja et al., 2005, Putz et al., 2012).

1.4.3 Tree and liana community composition

Selective logging does not affect all taxa equally and, unlike natural tree mortality, specifically targets slow growing, high-grade, shade-tolerant, hardwoods, shifting the overall functional composition of the plant community in a single mortality event (Richardson and Peres, 2016). Thus, immediately post logging we may see a shift in functional composition towards fast growing early successional species. Furthermore, because disturbance in selectively logged forest is centred on logging gaps and skid trails, community composition at a landscape scale may not solely be determined by amount of timber extracted and instead by the density and distribution of more localised patches of disturbance (Costa and Magnusson, 2002). The increased light and temperatures associated with logging gaps affect different species in different ways, and changes to plant growth rates are species or size specific (Soliz-Gamboa et al., 2012). Early successional stems can respond rapidly to the sudden increase of light in the understory with increased growth and recruitment (Pinard et al., 1996, Herault et al., 2010).

The majority of plant community regeneration in logging gaps and areas with significantly disturbed soil selects for early successional species, which dominate logging gaps for at least eight years post-logging in Brazil (de Carvalho et al., 2017). Early successional stems are most common in areas where structural disturbance has been greatest, and so these species regenerate unevenly across the landscape, as has been recorded in Malaysian Borneo (Howlett and Davidson, 2003). The exception to this trend of early successional species showing preference for more disturbed soil is on the skid tracks. Early successional stems can be up to twice as abundant on skid edges (where fertile soil and seeds have been pushed to the side by logging operations) than on skid tracks (where soil has been compacted by dragging cut stems and heavy machinery) (Howlett and Davidson, 2003).

Amongst early successional taxa, disturbance specialist lianas may be particularly prolific post-logging, as seen in Borneo and Cameroon (Schnitzer et al., 2004, Magrach et al., 2016, Cleary, 2017). Their capacity for rapid clonal propagation and growth allows disturbance specialist lianas to grow rapidly to fill gaps with high light levels in disturbed landscapes, often outcompeting regenerating tree taxa and limiting growth of remnant stems (Schnitzer and Bongers, 2002, Chazdon, 2014, Rocha et al., 2020). For this reason, liana thinning and removal is a common silvicultural treatment in logged forest, with the aim of reducing pressures that slow timber tree recruitment (Finegan, 2014). However, many liana species provide valuable food resources for animals, which can be necessary for supporting wildlife in disturbed forests (Bongers et al., 2005, Meijaard, 2005, Martins, 2009, Arroyo-Rodríguez et al., 2015). Following 19 years of forest regeneration post-logging in peninsular Malaysia (Addo-Fordjour et al., 2012), and 2-64 years in Ghana (Addo-Fordjour et al., 2020), lianas in logged forest had lower abundance and distinct community composition from unlogged forest.

Despite their frequent dominance in disturbed areas of logged forest, early successional taxa are not necessarily competing with desirable and late successional species (Pinard et al., 1998). In fact, early successional taxa often help in the establishment of these stems through provision of nurse-plant canopies. Early successional species can create structure and micro-climatic conditions more similar to old growth forest, and decomposition of their short-lived leaves can provide essential nutrients (Howlett and Davidson, 2003). While some early successional taxa, such as *Macaranga* in Kalimantan, may continue to recruit and persist at high densities more than 15 years after logging (Slik et al., 2002), a study from Ghana seven years post-logging suggests that most early successional taxa rapidly return to lower densities, as the forest recovers, due to their relatively brief life spans (Duah-Gyamfi et al., 2014). In contrast, studies from French Guiana and India found that shade tolerant plants and canopy taxa, usually common to these areas, had still failed to re-establish >20 years post-logging (Baraloto et al., 2012, Jeyakumar et al., 2017). Due to the declining number of early successional stems at this stage in recovery and the re-emergence but relatively low abundance of late successional species, logged forests can have higher diversity and richness than unlogged forest, while also having fewer stems (Berry et al., 2008, Jeyakumar et al., 2017). Richness per unit area increased linearly with time since logging in Kalimantan (Slik et al., 2002) but mature stems continued to be especially sparse across the landscape at 20 years post-logging in India (Nagaraja et al., 2005).

Regardless of logging history, tropical forest plant communities tend to be dominated by the same families; however, the individual species present are likely to be different, with more intermediate, and low wood-density plants in logged forests (Okuda et al., 2003). For biomass to not only recover but to return to pre-logging composition in terms of functional groups and species, a ~200 year recovery period may be required (Appanah et al., 1990). Late successional timbers especially can take centuries to recover (Chazdon, 2003) and even amongst smaller tree size-classes (2-20 cm DBH), ~80 year community recovery times have been recorded in Costa Rica for logged forest to resemble an unlogged community (Guariguata and Dupuy, 1997).

1.4.4 Seed production and seedling recruitment

Long term recovery of forest ecosystems post-logging depends on the ability of the community to successfully recruit future generations (Pillay et al., 2018). It is therefore vital that we understand mechanisms of recruitment and survival at all life stages within selectively logged tree communities.

Seed availability for recruitment of new generations is primarily determined by seed production from mature trees. Given that large reproductive trees of late-successional groups are preferentially removed during logging, seed production may be limited and taxonomically skewed by the intensity of harvest in logged forests. A study in southern Mexico suggests that fewer propagules are produced in logged forests and environmental conditions worsen in correlation with the scale, intensity, and time period over which logging was carried out, effectively reducing both recruitment and survival of seedlings (Martínez-Ramos et al., 2016). Taxa with a mast fruiting strategy (e.g. dipterocarps in Southeast Asia) may be particularly affected by reduced seed production and survival as they rely on the high density of fruits during mast to satiate predators (Janzen, 1971). In a study of mast fruiting in Indonesian Borneo, seed production in logged forests was just 23% of unlogged and while 99% of seeds escaped predation in unlogged forest, in logged forests only 92% survived (Curran and Webb, 2000). Of the remaining seeds, the proportion which are then able to germinate may also be reduced, as observed at previous masts in Malaysian Borneo, potentially due to higher light levels and increased chance of seed desiccation (Itoh et al., 1995, Oshima et al., 2015, Granados et al., 2017). Meanwhile, non-masting taxa may be better able to cope with lower seed densities, given that their reproductive strategy doesn’t rely on predator satiation – instead they are able to germinate and grow more opportunistically.

Differences amongst reproductive strategies of trees have the potential to shift the composition of tree communities in the future, based on which seedling groups are best able to survive and grow within disturbed forests. A study from India found that 20 years after selective logging, seedling diversity was higher than immediately post-logging but the seedling and sapling community was primarily dominated by earlier successional species, which require medium to large canopy gaps to grow into mature trees (Nagaraja et al., 2005). Logged forests not only have more early successional taxa than unlogged, but studies from Borneo suggest they may also recruit more seedlings of invasive species (Dillis et al., 2017, Waddell et al., 2020). This suggests that community composition of future cohorts of established trees may also be skewed towards early successional and invasive species.

1.4.5 Timber tree recovery and the case of the Dipterocarpaceae in Southeast Asia

While the recovery of plant community functioning and composition is key to understanding the long-term sustainability of selectively logged forests, the recovery of valuable timber trees is of particular interest. Commercially valuable early successional trees may be common amongst stems <10 cm DBH almost a decade post-logging, as seen in Brazil (de Carvalho et al., 2017), and commercial taxa of all successional stages have been shown to survive and recruit in selectively logged landscapes in Southeast Asia (Bischoff et al., 2005, Berry et al., 2008). In Southeast Asia, most of these commercial species are from the family *Dipterocarpaceae* and are valued for their high-quality timber (Sist et al., 2003). Dipterocarps are a typically shade tolerant family that characterises old growth forests across Southeast Asia (Appanah et al., 1998, Philipson et al., 2012). Because dipterocarp trees are selectively harvested, there is substantial interest in how this group of tree species recovers after logging and the amount of time required for the population to recover to allow for relogging.

Studies suggest that dipterocarp assemblages recover well from selective logging. In north Borneo, a greater number of dipterocarps were found in logged (15 years post-logging) than in unlogged forest, suggesting that the family is likely to recover if given sufficient time without human interference (Berry et al., 2008). This recovery can be accelerated through a mixture of silvicultural techniques, such as cutting stems of early successional tree species or lianas or planting of seedlings grown in nurseries (Finegan, 2014, Lussetti et al., 2016). Dipterocarp species have large seeds, which enable seedling establishment at low resource availability, and form ectomycorrhizal (EcM) associations, which may improve water and nutrient uptake in otherwise limited soils (Brearley, 2012, Segnitz et al., 2020). Where dipterocarps are recorded as recovering in logged forest, species level community composition may be unlike old growth dipterocarp forest since tolerance of high light intensities may be species specific within the family (Nussbaum et al., 1995). In peninsular Malaysia, approximately 14% of dipterocarp seedlings in logged forest were able to survive to their second year *versus* 17% in old growth (Appanah and Manaf, 1994).

Post-logging, the extent and intensity of dipterocarp reproduction is reduced and mast fruiting events are likely to be more sporadic than in unlogged forest (Appanah and Manaf, 1994, Curran et al., 1999). This has longer-term implications on forest regeneration and maintenance of viable dipterocarp populations. In a study in Indonesian Borneo, only 15% the number of dipterocarp seedlings recruited in logged forest eight years post-logging compared to unlogged forest (Curran et al., 1999). Furthermore, when population density is reduced, dipterocarps become more likely to self-pollinate, resulting in decreased community genetic variation and therefore greater vulnerability to subsequent decline (Obayashi et al., 2002, Nutt et al., 2016, Tito de Morais et al., 2020). Lower rates of dipterocarp seed production during mast fruiting, as has been recorded in Malaysian Borneo (Itoh et al., 1995, Oshima et al., 2015), may also make dipterocarps more vulnerable to seed predators in logged forests as there are insufficient quantities to fully satiate food resource demands (Curran and Webb, 2000). In logged forest in Borneo, seed predators are more abundant, react more quickly and more intensely to mast, and travel in larger groups, resulting in greater mortality of seeds and seedlings post-mast (Curran and Webb, 2000, Brodie et al., 2015, Davison et al., 2019).

The long-term recovery of dipterocarps after selective logging is still uncertain. Despite an increasing understanding of their short- and medium-term recovery, their long-term recovery is dependent on continued successful mast fruiting events which are, in turn, at risk from changes in faunal seed predation behaviours (Köhler and Huth, 2004).

1.4.6 Active restoration

Following logging, silvicultural techniques may also be applied to mitigate the impacts of logging on forest ecosystems, increasing ecological functioning and forest structure, and allowing shorter harvesting intervals by accelerating growth and reestablishment of valuable stems (Fredericksen and Putz, 2003, Peña-Claros et al., 2008, Gutierrez et al., 2021). Different land managers may prioritise different objectives of active restoration and the goal of ecological functioning has often been overlooked in favour of carbon sequestration or timber production, especially where logistical ease and financial constraints limit achievable seedling planting strategies (Holl and Brancalion, 2020, Chazdon et al., 2021). Within the United Nations Decade on Ecosystem Restoration (2021-2030) however, it is expected that greater focus should be directed to ecological functioning where active restoration of logged forests is attempted (Aronson et al., 2020, United Nations, 2020). Post-logging silvicultural techniques can involve management, such as cutting of unsuitable stems, or tree planting, where seedlings of valuable species are planted into the understory (Finegan, 2014, Tuck et al., 2016).

A common management technique in logged tropical forests is liberation cutting of lianas to prevent the strangulation of juvenile tree stems and ensure that thickets do not intercept too much sunlight before it can reach the understory tree community (Pérez-Salicrup, 2001, Finegan, 2014). The implementation of post-logging liana cutting is particularly valuable in the dipterocarp forests of Southeast Asia but is less beneficial in locations like Costa Rica and Guatemala, where liana proliferation is less likely to dominate logged forests (Finegan, 2014). Liana cutting experiments have shown increased tree growth, relative to untreated forest, in Tanzania (Marshall et al., 2017), Panama (van der Heijden et al., 2019), and Sabah (Lussetti et al., 2016). A tree-by-tree approach is recommended when employing liana cutting for active restoration to avoid a reduction in liana ecosystem services which might be brought about by a generalised cutting approach (Schnitzer and Bongers, 2002, Marshall et al., 2017).

Post-logging silviculture may also involve cutting of early successional tree stems to encourage canopy openness and late successional (valuable timber) stem growth (Wadsworth and Zweede, 2006, Swinfield et al., 2016) as well as to control invasive species (Kobayashi, 2007). Selective thinning of the tree community has been shown to benefit the recovery of high value species in Indonesia (Swinfield et al., 2016), Bolivia (Peña-Claros et al., 2008), and Brazil (Wadsworth and Zweede, 2006). The successful shift of community composition to high value species in forests restored this way highlights the importance of careful planning to avoid unintended compositional shifts, however. For this reason, thinning treatments must be considered on a site-by-site and species-by-species basis.

Active restoration also commonly involves the planting of juvenile stems in to degraded forests (Lamb et al., 2005). These are often species with high value to land managers, either for their capacity to sequester carbon or for the quality of their timber (Moura Costa, 1996, Sovu et al., 2010, Widiyatno et al., 2020), although managers will sometimes plant species which support other ecosystem services, such as fruit trees and natives that provide habitat but have little or no commercial timber value (Moura Costa, 1996, Osuri et al., 2019). Combined with cutting of competitive stems, planting programmes are designed to give desirable stems a head start in recruiting to the canopy, replacing the stems felled during logging. In the Amazon, effective management of logged forests over a 30 year period, produced approximately 68% more marketable timber in some cases (Barreto et al., 1998) and a recent study from Sabah suggests that carbon accumulation may be accelerated by active restoration techniques (Philipson et al., 2020). In Brazil, however a similar increase in wood production was matched by an increased rate of stem mortality so total gross primary production remained unchanged (Figueira et al., 2008).

Although active restoration can accelerate biomass accumulation in logged forest, recovery of tree community composition is relatively poorly understood and varies substantially among sites. In the Western Ghats, India, restored forest (7-15 years after restoration) showed greater community similarity to nearby unlogged forest than to forest allowed to regenerate naturally since logging ~80 years previously (Osuri et al., 2019). However, in Pará, Brazil, 30 years after logging and ~20 years after restoration, community composition was distinct across unlogged, naturally regenerating, and actively restored logged forests, with actively restored forest more dissimilar to unlogged forest than was forest allowed to regenerate naturally (de Avila et al., 2015). Furthermore, while naturally regenerating forest showed a trajectory of converging community composition with unlogged forest in Brazil, restored forest did not, suggesting restoration may have delayed or diverted the process of recovery. Variable effects of restoration on tree community composition could result from differences in initial conditions, extent of logging efforts, and/or intensity and objectives of restoration techniques. Further research is required to inform land managers of where and when active restoration is appropriate to aid logged forest recovery over natural regeneration processes (Chazdon et al., 2021).

1.5.0 Synthesis

Selective logging is pervasive throughout tropical forests, especially within Southeast Asia. While logged forests can retain many of the values attributed to unlogged forests and are expected to recover naturally over time, the mechanisms and timelines behind such recovery vary and require further study to inform conservation. While active restoration has the potential to accelerate recovery of aboveground biomass, less is understood about the long-term implications of active restoration for tree community composition. This thesis aims to investigate how selective logging and active restoration affect tree communities within a single study landscape: Danum Valley.

1.6.0 Thesis study site: Danum Valley

The Danum Valley Conservation Area (DVCA; 200-1000 m above sea level; figure 1.2) consists of 438 km^2 of primary lowland and lower montane rainforest set aside from the 10,000 km^2 Yayasan logging concession in East Sabah, Malaysian Borneo (Marsh and Greer, 1992, Howlett and Davidson, 2003). The logging concession was allocated in 1970 to generate revenue from available timber resources to fund the Yayasan Sabah Group – a foundation established by the Sabah state government to improve the livelihood of Sabahans through charitable activities and programmes, especially education and welfare (Marsh and Greer, 1992, YSG, 2020). In line with these key objectives of the Yayasan Sabah Group, ~20% of the concession is set aside as unlikely to experience logging, including the DVCA (a class 1 forest reserve and cultural

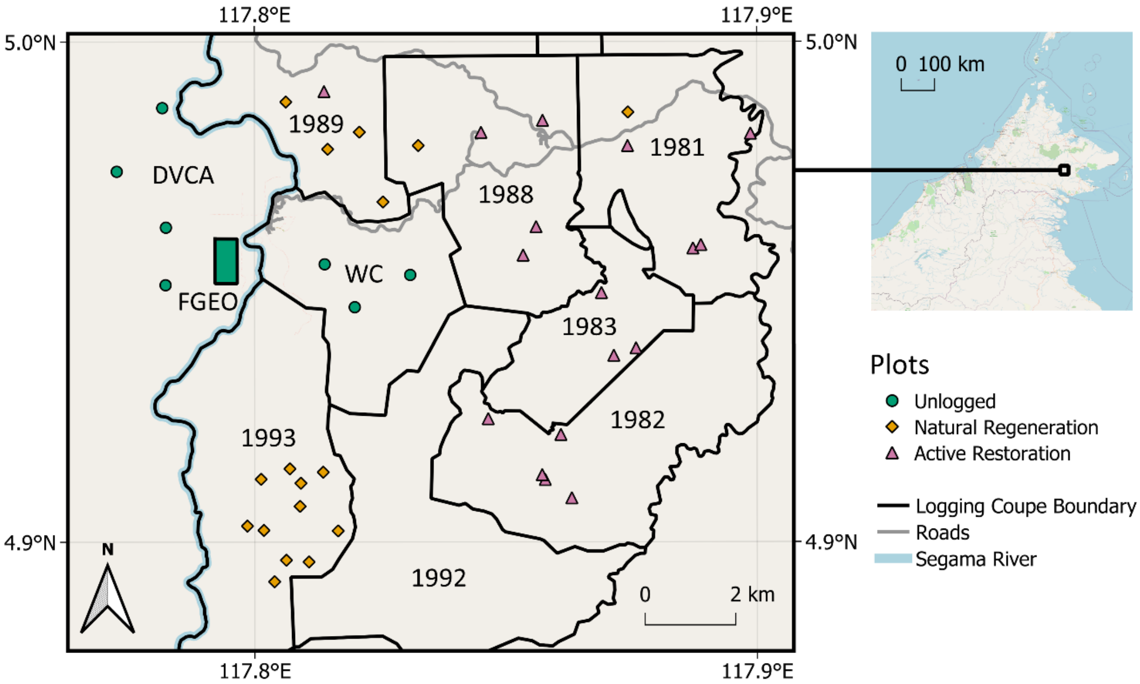


Figure 1.2 *Map of the Danum Valley Conservation Area (DVCA) and adjacent logged forest in the Ulu Segama Forest Reserve (USFR). Known locations of INDFORSUS plots are shown within logged forest coupes (labelled by the year they were logged) in the USFR, and of the ForestGEO 50 ha plot (FGEO) in the DVCA. An unlogged water catchment region of the USFR is labelled 'WC'; access roads, which have been retained since logging, are shown in grey; and the Segama River is shown in blue.*

heritage area) (Marsh and Greer, 1992).

Danum receives rain on an average of 220 days per year, amounting to ~2700 mm per year, mostly during the afternoons and evenings (Marsh and Greer, 1992, Walsh and Newbery, 1999). Daily mean temperatures at Danum range from 22.5 °C to 30.9 °C (SEARRP, 2018). The DVCA contains >15,000 plant species, including 511 species of tree across 164 genera and 59 families (Newbery et al., 1992). At least 247 of these species can grow to ≥30 cm circumference at breast height (CBH). Approximately 57% of these trees ≥30 cm CBH at the DVCA carry lianas (Newbery et al., 1992) and 90% of trees ≥10 cm CBH are in the understory (<50 cm CBH) (Newbery et al., 1999). Many trees die standing, resulting in a relatively low frequency and scale of near-ground canopy gaps, into which saplings may grow (Newbery et al., 1992). The forest is primarily dominated by trees from the family *Dipterocarpaceae*, which produce valuable timber for the logging industry and, while they are protected within the DVCA, have been selectively logged from neighbouring sites within the Yayasan logging concession (Newbery et al., 1992). Of the ≥180 species of dipterocarp known to be present in Sabah, ~30 have been recorded in the DVCA, making them the fourth most species rich plant family after *Lauraceae* (83 spp.), *Euphorbiaceae* (51 spp.), and *Meliaceae* (36 spp.) (Newbery et al., 1992). *Euphorbiaceae* is dominant within early successional communities in the area (Berry et al., 2008). Many species at Danum (primarily dipterocarps) reproduce by mast fruiting. The most recent mast fruiting event occurred in July-August 2019.

Within the DVCA is a 50 ha permanent research plot of primary forest (figure 1.2), established by the Forest Global Earth Observatory (ForestGEO) in 2010 (Anderson-Teixeira et al., 2015). Adjacent to this is a landscape of historically logged forest, hosting the INDFORSUS network of 52 plots, established in 1995 (figure 1.2; Foody and Cutler, 2003). These 0.1 ha plots were logged once between 1981 and 1993 and have since been allowed to recover naturally. An initial census of the tree community was taken in 1996, then recensused in 2016 (Foody and Cutler, 2003). The logging coupes covered by the network are typically ~27 km^2 and were established in 1970 (Foody and Cutler, 2003). Both tractor (for moderate terrain) and cable (for steep slopes) logging techniques were used in these coupes, along with the trial of a RIL coupe in 1993 (Marsh and Greer, 1992, Davis, 2000). In a study by Pinard *et al.* (2000a), the 1993 conventional selective logging coupe was found to be 17% covered by skids and roads (*vs.* 6% in RIL), with 84% of that area showing signs of subsoil disturbance. The stem size criterion used for each coupe was that all commercially viable trees >60 cm DBH should be harvested, leading to high intensity mean extraction (118 m^3 ha^{-1}), although spatial variation within and between coupes was substantial (Foody and Cutler, 2003). Subsequent to logging, a subset of logging coupes were selected for active restoration as part of the Innoprise-FACE Foundation Rainforest Rehabilitation Project (INFAPRO). From 1992 to 2004 – an average of nine years post-logging – seedlings were planted from 52 dipterocarp species and 21 non-dipterocarp species, including 16 native fruit tree species (Moura Costa, 1996, Face the Future, 2011). Seedlings were planted every 3 m in parallel lines cut 10 m apart, following 4-8 months growth in nurseries or until they reached a height of 50 cm with > 10 leaves. Planted forest sites were initially cut to reduce early successional stems, and then maintained for three years by regular weeding (Moura Costa, 1996, Face the Future, 2011). These pre-existing plot networks, knowledge of the adult tree communities and matrix of land management practices offer an excellent opportunity within a single landscape to study the trajectories of plant community change after logging and restoration, which forms the focus of my thesis.

1.7.0 Thesis outline

Thesis aim: To determine how selective logging and active restoration affect tree abundance, dynamics, and community composition across life stages.

In this thesis I will analyse the long-term effects of selective logging and active restoration on the tree community of a tropical lowland dipterocarp wet forest in Sabah, Borneo. In each chapter, I will assess a different stem demographic to consider how patterns of recruitment and tree community composition vary across forest types and life stages. This will help us to understand how selective logging and active restoration strategies can affect forest tree communities now, and in the future, and therefore how we might guide future strategies to avoid pitfalls by which recovery could be delayed.

Chapter 2: Three decades of post-logging tree community recovery in naturally regenerating and actively restored dipterocarp forest in Borneo.

In Chapter 2, I will analyse the density, richness, diversity, and community composition of saplings, poles, and established trees (2-5 cm, 5-10 cm, and >10 cm DBH, respectively) across forest types. Findings from chapter 2 will improve our understanding of long-term shifts in tree community composition in logged and restored forests, as well as providing important context for studies of seedlings in the same landscape in chapters 3 and 4. I will discuss the extent to which different metrics remain affected 23-35 years post-logging and 12-24 years post-restoration, and put these findings in the context of wider debates on the efficacy of active restoration versus natural regeneration of logged forests. Chapter 2 aims to answer the following key questions:

- *Q1. How does selective logging affect stem density, basal area, richness, and diversity of tree species when compared with neighbouring unlogged forest?*
- Q2. *Does the trajectory of recovery over time for these metrics differ between selectively logged forests that regenerate naturally compared to those that were actively restored?*

Chapter 3: Recruitment and survival of seedlings following a mast fruiting event in Borneo's old-growth and disturbed forests.

In Chapter 3, I will track survival of an in-situ cohort of 5119 seedlings for ~1.5 years, following their germination from a synchronous mast fruiting event. Results from chapter 3 will give an indication of how reproductive output varies across unlogged, naturally regenerating, and actively restored forests, and will be the first time survival of naturally propagated seedlings in an actively restored tropical forest has been tracked post-mast. I will assess the extent to which logging and active restoration explain differences in both initial seedling recruitment and subsequent rates of mortality, highlighting what this could mean for recruitment of future canopy trees across different forest types. Chapter 3 aims to address the following hypotheses:

Q1. Are germinated seedling numbers higher in unlogged than logged forests due to the greater size, density, and fecundity of reproductive adults?
Q2. Does community composition of newly germinated seedings differ among unlogged, logged, and restored forests due to differences in the adult community?
Q3. Does seedling community composition change over time, post-germination, and is this affected by logging, restoration treatment, and the established tree community?

Chapter 4: Seedling dynamics in response to logging and restoration of a lowland tropical wet forest in Borneo.

In Chapter 4, I will record growth and survival of 1506 established seedlings (>20 cm tall and <1 cm DBH) over ~2.5 years. Compared to the seedling cohort recorded in chapter 3, seedlings of this size-class are more established within the understory and will therefore give insight to the dynamics of growth and survival by which some seedlings can persist in the understory for over a decade. By revisiting tagged individuals, I will model the extent to which selective logging and active restoration determine likelihood of survival and relative growth rate of stems in this size class. I will consider how trade-offs between these metrics might influence the recruitment of different functional groups to the canopy within different forest types. Chapter 4 aims to answer the following key questions:

Q1. Do seedling densities, survival, and relative growth rates differ amongst unlogged, naturally regenerating, and actively restored logged forest?
Q2. How are seedling growth and survival related and are these relationships consistent across functional groups (EcM trees, non-EcM trees, and lianas)?

Chapter 5: General discussion

In Chapter 5, I will synthesise the findings of earlier chapters to generate a more complete picture of how tree communities are affected by selective logging and active restoration at my study site in the long-term. By drawing together key findings within the context of the academic literature, I will consider the implications of my research for future active restoration strategies in tropical forests and highlight important questions for future research.

Chapter 2: Three Decades of post-logging tree community recovery in naturally regenerating and actively restored dipterocarp forest in Borneo

Photo: sunset over selectively logged forest in Danum Valley
[credit: Robin Hayward]

A version of this chapter has been published as:

> Hayward, R.M., Banin, L.F., Burslem, D.F.R.P., Chapman, D.S., Philipson, C.D., Cutler, M.E.J., Reynolds, G., Nilus, R., Dent, D.H. 2021. Three decades of post-logging tree community recovery in naturally regenerating and actively restored dipterocarp forest in Borneo. *Forest Ecology and Management*, 488, 119036

Research ideas were formulated by RH and DD. Data were collected by DB, CP, MC, GR, and the South East Asia Rainforest Research Partnership team at Danum. RH collated and analysed data with advice from DD, LB, DC, and DB. RH led the writing of the text and all authors commented on a draft version of this chapter. This chapter version is formatted for the thesis but otherwise matches the published version.

2.1.0 Abstract

Selective logging has affected large areas of tropical forests and there is increasing interest in how to manage selectively logged forests to enhance recovery. However, the impacts of logging and active restoration, by liberation cutting and enrichment planting, on tree community composition are poorly understood compared to trajectories of biomass recovery. Here, we assess the long-term impacts of selective logging and active restoration for biomass recovery on tree species diversity, community composition, and forest structure. We censused all stems ≥2 cm diameter at breast height (DBH) on 46 permanent plots in unlogged, primary forest in the Danum Valley Conservation Area (DVCA; 12 plots, totalling 0.6 ha) and in sites logged 23-35 years prior to the census in the Ulu Segama Forest Reserve adjacent to DVCA (34 plots, totalling 1.7 ha) in Sabah, Malaysian Borneo. Active restoration treatments, including enrichment planting and climber cutting, were implemented on 17 of the logged forest plots 12-24 years prior to the census. Total plot-level basal area and pole (5-10 cm DBH) stem density were lower in logged than unlogged forests, however no difference was found in stem density amongst saplings (2-5 cm DBH) or established trees (≥10 cm DBH). Neither basal area, nor plot-level stem density varied with time since logging at any size class, although sapling and pole stem densities were lower in actively restored than naturally regenerating logged forest. Sapling species diversity was lower in logged than unlogged forest, however there were no other significant effects of logging on tree species richness or diversity indices. Tree species composition, however, differed between logged and unlogged forests across all stem size classes (PERMANOVA), reflected by 23 significant indicator species that were only present in unlogged forest. PERMANOVA tests revealed no evidence that overall species composition changed with time since logging or with active restoration treatments at any size class. However, when naturally regenerating and actively restored communities were compared, two indicator species were identified in naturally regenerating forest and three in actively restored forests. Together our results suggest that selective logging has a lasting effect on tree community composition regardless of active restoration treatments and, even when species richness and diversity are stable, species composition remains distinct from unlogged forest for more than two decades post-harvest. Active restoration efforts should be targeted, monitored, and refined to try to ensure positive outcomes for multiple metrics of forest recovery.

2.2.0 Introduction

More than 20% of tropical forests were selectively logged during the first five years of the 21st century, and recent estimates suggest that more than half of the tropical forest biome may now have been logged (Asner et al., 2009, Laurance et al., 2014). In selectively logged forests, which account for 95% of the tropical timber harvest (Asner et al., 2009), the majority of trees remain standing, retaining residual reproductive adults that provide a source of propagules for natural recovery of biodiversity and ecosystem functioning. By contrast to clear-fell logging, whereby all stems are removed, selective logging aims to remove only ~4-15 stems per hectare and targets the largest trees (usually >40 cm diameter at breast height; DBH at c. 1.3 m) and the highest quality timber species (Pinard and Putz, 1996, Edwards et al., 2014b). As such, selective harvesting performed with adequate care and at sufficiently long harvesting intervals may represent an acceptable middle-ground between high levels of timber extraction and strict protection (Meijaard, 2005, Berry et al., 2010, Putz et al., 2012, Edwards and Laurance, 2013). However, the impacts of logging on tree species diversity and community composition are still poorly understood.

While selective logging is prevalent throughout the tropics, the island of Borneo alone has generated greater exports of timber than the African and American tropics combined (Cleary et al., 2007). These high extraction volumes reflect the abundance of valuable timber, particularly species in the family Dipterocarpaceae, combined with the rapid economic development of Malaysia after gaining independence in the second half of the 20th century (Brookfield and Byron, 1990). Forests in Borneo were first selectively logged in the early 1970s and have a projected interval of 40-60 years between harvests in production forests (Sist et al., 2003), although actual cutting cycles are frequently shorter (Reynolds et al., 2011). At present, over 62% of the forest area in Malaysian Borneo is considered degraded (Bryan et al., 2013) and, of the remaining primary forest, 42% is allocated for potential selective logging and 16% for conversion to agriculture (Gaveau et al., 2014). Given the extent of forest ecosystems affected by selective logging and the potential for this area to expand, it is critical that we understand the long-term impacts of selective logging and the capacity for forests to recover over time.

Selectively logged forest has been demonstrated to provide valuable habitat for forest animals and migration corridors between areas of undisturbed forest (Edwards et al., 2011, Wearn et al., 2017). Indeed, in selectively logged forest, over half the total area is not directly disturbed by logging operations (Putz et al., 2019). There is widespread consensus that logged forests have a relatively high conservation potential for forest animals due to their functional similarity to unlogged forest habitat, although these habitats may not support all rare bird and mammal species (Meijaard, 2005, Wells et al., 2007, Edwards et al., 2011, Putz et al., 2012, Wearn et al., 2017). Research on plant communities in logged forests has shown that overall species richness and the abundance of most species tend to be resilient to the impacts of selective logging (Berry et al., 2010, Putz et al., 2012). However, shifts in the abundance of a few key species can drive notable reductions in biodiversity, as well as changes to community structure and the physical structure of the forest (Foody and Cutler, 2003, Putz et al., 2012). These abundant species, as well as metrics of community composition, can be valuable indicators of degradation and the effectiveness of biodiversity conservation efforts (Imai et al., 2014, Fujiki et al., 2016).

In Borneo, logging reduces the density of large hardwoods, predominantly from the family Dipterocarpaceae, which are targeted for harvesting, and tends to increase the abundance and basal area of early successional pioneer species (Berry et al., 2008). In terms of forest structure and biomass recovery, it is estimated that above ground biomass takes approximately 60 years to recover in logged forest (Berry et al., 2010, Philipson et al., 2020), although below ground biomass may take substantially longer (Martin et al., 2013). In contrast, the recovery time needed for tree community composition to match an undisturbed reference state may take anywhere from 50 to several hundred years (Appanah et al., 1990, Foody and Cutler, 2003, Putz et al., 2012). This time frame is generally longer than the minimum harvesting interval projected for Borneo (Sist et al., 2003, Reynolds et al., 2011), suggesting that plant community effects may accumulate through repeated cycles of logging.

Restoration strategies to mitigate the negative effects of timber extraction include rehabilitation-for-conservation and carbon capture mechanisms, and investment by the selective logging industry to enable shorter harvesting intervals by enhancing regeneration and growth of valuable stems (Fredericksen and Putz, 2003, Peña-Claros et al., 2008). Depending on which of these goals the restoration strategy targets, different actions may be taken (*e.g.* replanting a single valuable species for profit *vs* replanting a range of adversely affected native taxa for conservation), leading to distinct tree communities post-restoration. Most commonly, active restoration strategies employ a combination of enrichment planting, in which seedlings of valuable timber species are transplanted into logged forests (Kettle, 2010), and liberation thinning, which may involve cutting back stems of early successional species, and liana cutting, to increase light availability and allow target tree species to effectively compete for resources (van der Heijden et al., 2015, Marshall et al., 2017). Despite the intention of these techniques to promote growth and carbon-capture, a recent global meta-analysis casts doubt on whether active restoration techniques post-logging result in shorter recovery times, or instead whether they induce a lag in diversity and vegetation structure recovery relative to natural regeneration processes (Crouzeilles et al., 2017). Crouzeilles et al. (2017) did not assess community composition trajectories however, nor provide region-specific recovery estimates for richness and diversity, and long-term assessments of community recovery are still much needed.

Trajectories of recovery in tree community composition and diversity over time have rarely been explored in selectively logged Southeast Asian forests. Typically, studies compare species assemblages at one or two discrete time points since logging with an unlogged comparison or pre-logging record of the tree community (Okuda et al., 2003, Bischoff et al., 2005, Berry et al., 2008). While these studies provide valuable insights to community recovery, they lack information on directional trends in changing community composition with time. Here we present data across a 12-year post-logging chronosequence in Bornean lowland dipterocarp forest to explore tree community richness, diversity, and composition of neighbouring plots 23-35 years after logging, which were either left to regenerate naturally or were subject to active restoration treatments. Where plots were actively restored for improved carbon uptake, we explore the ecological co-benefits to the tree community 12-24 years after treatment. Specifically, we address the following questions:

Q1. How does selective logging affect stem density, basal area, richness and diversity of tree species, and tree community composition when compared with neighbouring unlogged forest?

Q2. Does the trajectory of recovery over time for these metrics differ between selectively logged forests that regenerate naturally compared to those that were actively restored?

We approach these questions for the tree community as a whole and at three distinct stem size classes (saplings 2-5 cm DBH, poles 5-10 cm DBH, and established trees DBH ≥10 cm) to understand how logging and restoration affect successional processes across tree life stages.

2.3.0 Methods

2.3.1 Study site and land-use history

Forest plots were located in unlogged primary forest in the Danum Valley Conservation Area (DVCA) and selectively logged forest in the adjacent Ulu Segama Forest Reserve (USFR). The DVCA comprises 438 km^2 of primary lowland dipterocarp and lower montane rainforest (200-1000 m above sea level), contiguous with a 10,000 km^2 logging concession in East Sabah, Malaysian Borneo (Howlett and Davidson, 2003, Reynolds et al., 2011). Mean daily temperatures range from 22.5 °C to 30.9 °C and mean annual rainfall is ~2700 mm over an average of 220 days with rain (Marsh and Greer, 1992, Walsh and Newbery, 1999).

Over 15,000 plant species (including 511 tree species across 59 families) have been identified in the DVCA, with at least 247 of these able to grow beyond 10 cm diameter at breast height (DBH) (Newbery et al., 1992). The DVCA tree community is characterised by the dominance of the family Dipterocarpaceae, which has especially valuable timber (Newbery et al., 1992). The few early successional tree species within the primary forest flora of DVCA mostly belong to the family Euphorbiaceae (Berry et al., 2008).

Adjacent to the DVCA is a region of selectively logged forest within the USFR, harvested in annual coupes (designated logging areas) between 1981 and 1993 (23-35 years prior to the census used as the basis for this paper) (Foody and Cutler, 2003). The logging coupes were typically ~27 km^2 (Foody and Cutler, 2003) and were harvested using either tractor (for moderate terrain) or high-lead (for steep slopes) logging techniques (Pinard et al., 2000b). In addition, the coupes include a trial of the Reduced

Impact Logging (RIL) technique in 1993, wherein damage to non-targeted vegetation was minimised through directional felling, cutting of climbers before felling, and adjusted harvest and skid-trail planning (Pinard and Putz, 1996, Pinard et al., 2000b). Across all harvest types, each coupe was selectively logged only once, during which all commercially viable trees >60 cm DBH were harvested, resulting in mean timber extraction of 118 m^3 ha^{-1}, although variation within and between coupes was substantial and estimated to range from 42.49 m^3 ha^{-1} to 309.56 m^3 ha^{-1} (Foody and Cutler, 2003).

Active restoration was undertaken for a subset of the forest coupes logged in 1981, 1982, 1983, 1988, and 1989 (Figure 2.1), by silvicultural intervention from 1992 to 2004 (12-24 years prior to census) as part of the Innoprise-FACE Foundation Rainforest Rehabilitation Project (INFAPRO), while other areas were left to regenerate naturally (Moura Costa, 1996, Face the Future, 2011). In actively restored areas, seedlings (~50 cm tall with 10 leaves and grown for 4-8 months in a nursery from locally collected seeds) of 52 species of dipterocarps, five non-dipterocarp canopy species, and 16 non-dipterocarp native fruit tree species (Table S2.1), were planted every 3 m along parallel lines (2 m wide and cut 10 m apart) an average of nine years after logging (Moura

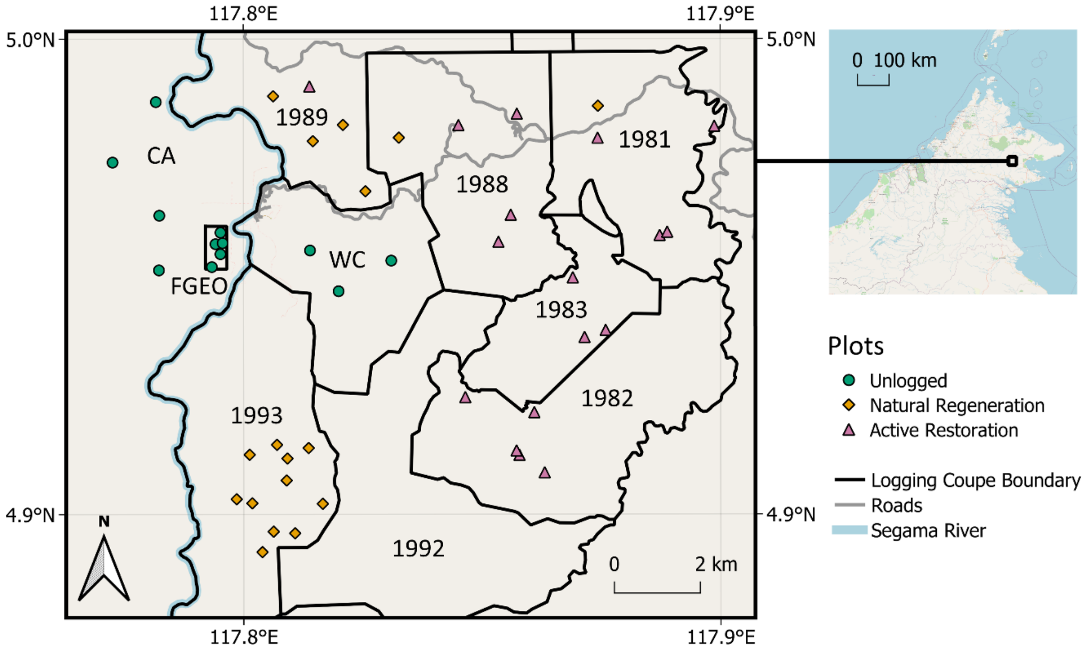


Figure 2.1 *Location of plots used in this study within the INDFORSUS and ForestGEO plot networks in the Danum Valley Conservation Area and Ulu Segama Forest Reserve. Colours indicate logging and regeneration method (consistent throughout this paper). Coupes are labelled by logging year, WC (Water Catchment), CA (Conservation Area), or FGEO (the Forest Global Earth Observatory study area). Access roads, which have been retained since logging, are shown in grey and the Segama River in blue.*

Costa, 1996, Face the Future, 2011). Enrichment plantings were primarily dipterocarps, which made up 90-95% of all planted seedlings (Face the Future, 2011). Additional native fruit trees and three early successional tree species were planted in particularly open sites (Face the Future, 2011). Early successional stems which were already present (i.e. not those which were planted), were girdled to reduce competition for resources (Face the Future, 2011). After the initial line cutting and planting, weeding was carried out every three months for three years (Moura Costa, 1996, Face the Future, 2011).

2.3.2 Forest inventory

In 2016, 46 circular forest plots (radius = 12.61 m, area = 500 m^2) were censused across seven selective logging coupes (34 plots) and unlogged forest (12 plots) as part of the Indicators of Forest Sustainability (INDFORSUS) project network and the Forest Global Earth Observation Network (ForestGEO) (Figure 2.1). Although the INDFORSUS project was established in 1996 (Foody and Cutler, 2003), we use only the 2016 census here due to poor taxonomic resolution of earlier records. Four of these unlogged plots were positioned within the Danum 50 ha ForestGEO (Burslem, et al. unpublished) and were selected by random placement of circular plot centroids within each quarter of the full 50 ha plot. Where tree positions overlapped the perimeter of the 12.61 m radius plot, their inclusion was decided based on the centre point of the tree.

Of the 34 plots in selectively logged forest, 17 were regenerating naturally and 17 were in areas that had been actively restored (Moura Costa, 1996). Plots in naturally regenerating forests had been logged in 1981 (one plot), 1988 (one plot), 1989 (four plots), and 1993 (five plots selectively logged using conventional techniques and six plots using reduced impact techniques). Plots in actively restored forest had been selectively logged in 1981 (four plots), 1982 (four plots), 1983 (four plots), 1988 (four plots), and 1989 (one plot) (see Figure 2.1).

In each plot, all live stems ≥2 cm DBH (at 1.3 m or immediately above buttresses if higher) were recorded and subsequently categorised as saplings (2 cm ≤ DBH < 5 cm), poles (5 cm ≤ DBH < 10 cm) or established trees (DBH ≥ 10 cm). These size classes match previous studies within the same landscape which categorise saplings as <5 cm DBH (Stride et al., 2018) and small trees as <10 cm DBH (Berry et al., 2008). The established tree size class was then further divided into 10-40 cm, 40-60 cm, and ≥60cm

DBH subsets to allow additional exploration of effects amongst the large stems. Each stem was identified using leaf specimens, based on collections available at the Danum Valley Field Centre Herbarium and in collaboration with local botanical experts. Across all size classes, 93.9%, 92.5%, and 72.1% of stems were identified to family, genus, and species levels, respectively. All dipterocarps were identified to genus and 95.2% to species (Table S2.2). Unidentified stems were assigned to distinct morphospecies which were consistent within the 2016 census. From these inventory data we derived plot-level stem density (i.e. the number of stems per 500 m^2 plot) and plot-level basal area (the summed cross-sectional area of the recorded stems).

2.3.3 Data analysis

Total stem basal area was calculated from all DBH measurements in each plot, assuming circular tree cross-sections, and all stems were counted to represent forest structure. Species richness, rarefied richness, and Shannon’s Diversity and Evenness were calculated for each plot using the *vegan* package in *R* version 3.6.1 (R Core Team, 2017, Oksanen, 2019) to represent different dimensions of diversity.

To assess the effect of logging on structural and diversity metrics at each size class, we fitted generalised linear mixed models (GLMMs), comparing unlogged and naturally regenerating logged plots at each size class (Eq. 2.1; presented using *R* syntax for the *lme4* package; Bates et al., 2015). A set of GLMMs were also fitted to explain the same metrics, using data from all selectively logged forest plots at each size class, testing the fixed effects of time since logging and regeneration method (natural vs active restoration) and their interaction (Eq. 2.2). A single combined random effect of site (logging coupe or unlogged forest location; Figure 2.1) and logging method (RIL, tractor, or high-lead) was included in each model (Philipson et al., 2020). Models with and without the interaction term between fixed effects were compared using Akaike Information Criterion (AIC) values, and the model with the lowest AIC (or the fewest terms if AIC differed by less than two) was selected to determine the best models for analysis (Symonds and Moussalli, 2011). GLMMs with Gaussian error distributions were used to analyse all metrics, except for plot-level stem density, which was modelled with a Poisson error distribution for all size classes. Basal area was log transformed prior to model fitting to account for positive skew, then back-transformed for presentation in the results. Each GLMM was validated by visual interpretation of residual diagnostic plots to check for linearity of model-fitted values and residuals, as well as verifying no significant leverage by any data point outside of Cook's distance (Cook, 1977).

Eq. 2.1 *Response_variable ~ Logging + (1|Site:Logging_method))*

Eq. 2.2 *Response_variable ~ scale(Years_since_logging) * Regeneration_method + (1|Site:Logging_method)*

Differences in community composition among plots were analysed by calculating the Bray-Curtis dissimilarity (Bray and Curtis, 1957) of species abundances between plots within each stem size class (Oksanen, 2019). Bray-Curtis dissimilarity was chosen for these analyses as it is robust for both linear and rank correlations of ecological data (Faith et al., 1987). Permutational Analyses of Variance (PERMANOVA) were used to test the significance of differences in Bray-Curtis dissimilarity among tree community compositions in response to logging (unlogged vs naturally regenerating logged plots) and regeneration types (natural regeneration vs active restoration) (Bray and Curtis, 1957). A PERMANOVA was then performed to test the significance of time since logging for logged plot communities, irrespective of regeneration type. All PERMANOVA were performed using the *adonis* function in the *vegan R* package (Oksanen, 2019) because it is less sensitive to differences in data dispersion than other similar functions (Warton et al., 2012).

To explore taxon-specific changes, indicator species were identified for unlogged *vs* logged forest and naturally regenerating *vs* actively restored logged forest by stem abundance within each stem size class, using the *multipatt* function of the *indicspecies* package in *R* (Cáceres and Legendre, 2009). As determined by these analyses, a significant indicator species is able to predict the treatment of the forest in which it is recorded (e.g. unlogged forest) with 95% certainty, versus other known treatments (Cáceres and Legendre, 2009).

Each analysis described above was run for each size class, including subsets of the established tree size class (10-40 cm, 40-60 cm, and ≥60 cm DBH), however these subsets were limited by the low number of stems in the categories ≥40 cm DBH in our plots (total n = 152).

Each analysis was run using the full taxonomic community and then again using only stems from the family Dipterocarpaceae, in order to compare general trends with those of the dominant family of large and commercially important timber trees. Due to potential bias from the greater taxonomic resolution of identification amongst smaller stems within the Danum ForestGEO 50 ha plot, the four plots from that data source were removed during analyses of the sapling and pole size classes where species richness, diversity, and evenness metrics or the community composition were considered. We are able to retain these plots for analyses of plot-level stem density, basal area, and in all analyses of stems ≥10 cm DBH due to the more equitable taxonomic resolution of IDs for established trees. Data from all other plots were collected by the same field-team so, despite non-comprehensive identification of stems, we could be confident that unidentified stems were allocated to consistent morphospecies across the census and that each morphospecies was distinct from the list of resolved taxa.

2.4.0 Results

A total of 5466 stems ≥2 cm DBH was recorded on 46 plots (3831 in selectively logged and 1635 in unlogged forests; Table S2.2), which included 2927 saplings, 1428 poles and 1111 established trees (2-5 cm, 5-10 cm, and ≥10 cm DBH respectively). In total 545 species of trees and shrubs were recorded in 198 genera and 81 families, of which 689 stems of 37 species in five genera were Dipterocarpaceae.

2.4.1 Effects of selective logging history on forest structure

Mean (± SE) basal area of stems per 500 m^2 plot was significantly higher in unlogged than naturally regenerating logged forest (3.828 ± 0.706 m^2 vs 1.597 ± 0.157 m^2; GLMM $p < 0.001$; Figure 2.2; Table S2.3). This was reflected in the higher mean plot-level stem density in unlogged compared to naturally regenerating logged forests for poles (45.73 ± 6.21 vs 29.41 ± 4.05; $p = 0.014$), although stem density was not significantly different in saplings (98.64 ± 11.43 vs 64.47 ± 9.18; $p = 0.065$). Established tree stem density was unaffected by logging when all stems ≥10 cm DBH

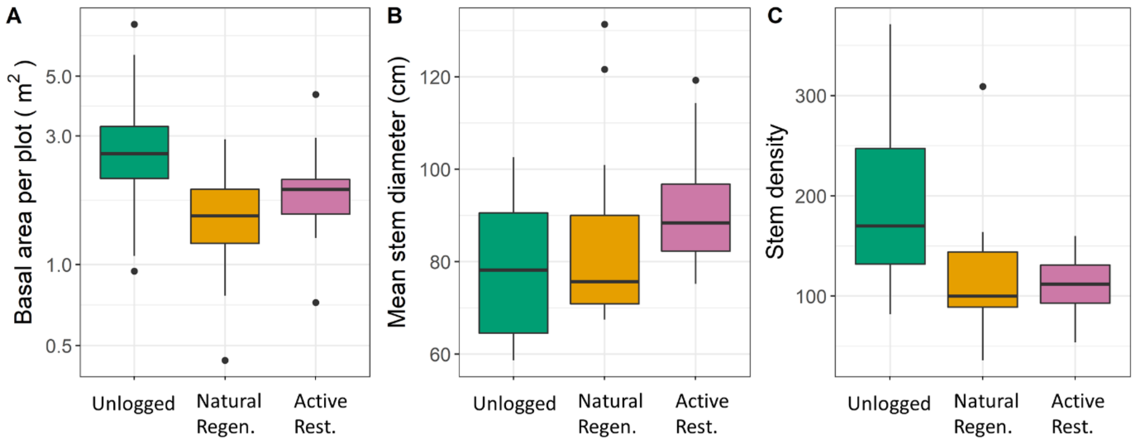


Figure 2.2 *Box plots of structural metrics (per 500 m^2 plot) calculated using all stems ≥2 cm DBH in unlogged (n = 12), naturally regenerating logged (n = 17), and actively restored logged forest (n = 17): A) total stem basal area, B) mean stem DBH, C) stem density (stems per 500 m^2).*

were considered (29.27 ± 4.35 vs 20.82 ± 2.18; p = 0.069, Table S2.4) but a marginally significant negative effect was found for stems 10-40 cm and ≥60 cm DBH (p = 0.045 and 0.046; Table S2.4). Considering dipterocarps alone, the plot-level stem density of poles was higher in unlogged than selectively logged plots (4.27 ± 1.33 vs 3.17 ± 0.58; p = 0.042), but there was no significant difference in the number of dipterocarp saplings or established trees (Table S2.4).

Within the logged forests, and whilst accounting for the effects of time since logging (23-35 years; Figure 2.3, Table S2.5), plot-level stem density was lower in actively restored (12-24 years after treatment & 27-35 years post-logging) than naturally regenerating (23-35 years post-logging) plots for saplings (55.99 ± 4.27 vs 64.47 ± 9.18; $p < 0.001$) and poles (29.18 ± 2.48 vs 29.41 ± 4.05; p = 0.002). Regeneration treatment had no effect on stems of established trees (25.59 ± 1.33 vs 20.82 ± 2.18; p = 0.702; Figure 2.3, Table S2.5) nor total basal area per plot (1.972 ± 0.190 m^2 vs 1.597 ± 0.157 m^2; p = 0.091; Figure 2.2; Table S2.3), although mean DBH was higher in actively restored forest (91.64 ± 3.14 cm vs 84.38 ± 4.62 cm; p = 0.034; Figure 2.2; Table S2.3). Standard errors of mean plot-level stem density were greater in naturally regenerating forest than actively restored forest at all size classes, indicating greater variability across plots. In saplings and poles, the relationship between plot-level stem density and time since logging differed between the naturally regenerating (slopes = -0.018 and -0.005) and actively restored plots (slopes = 0.254 and 0.357), as demonstrated by the significance of the interaction term (p = 0.014 and 0.018). There was no effect of time since logging for density of established tree stems and no change in total basal area over time (slope = -0.102, $p = 0.476$; Table S2.3).

Dipterocarp plot-level stem density was lower in actively restored than naturally regenerating forest for saplings ($p < 0.001$) and varied in relationship to time since logging (natural slope = -0.012, restored slope = 1.076, interaction $p = 0.026$). The effect of time since logging on dipterocarp established tree stem density also differed according to restoration treatment (naturally regenerating slope = -0.469, actively restored slope = 0.740, interaction $p = 0.032$). Dipterocarp pole stem density increased with time since logging ($p = 0.028$) and this relationship was consistent across restoration treatments (interaction term $p = 0.833$; Table S2.5).

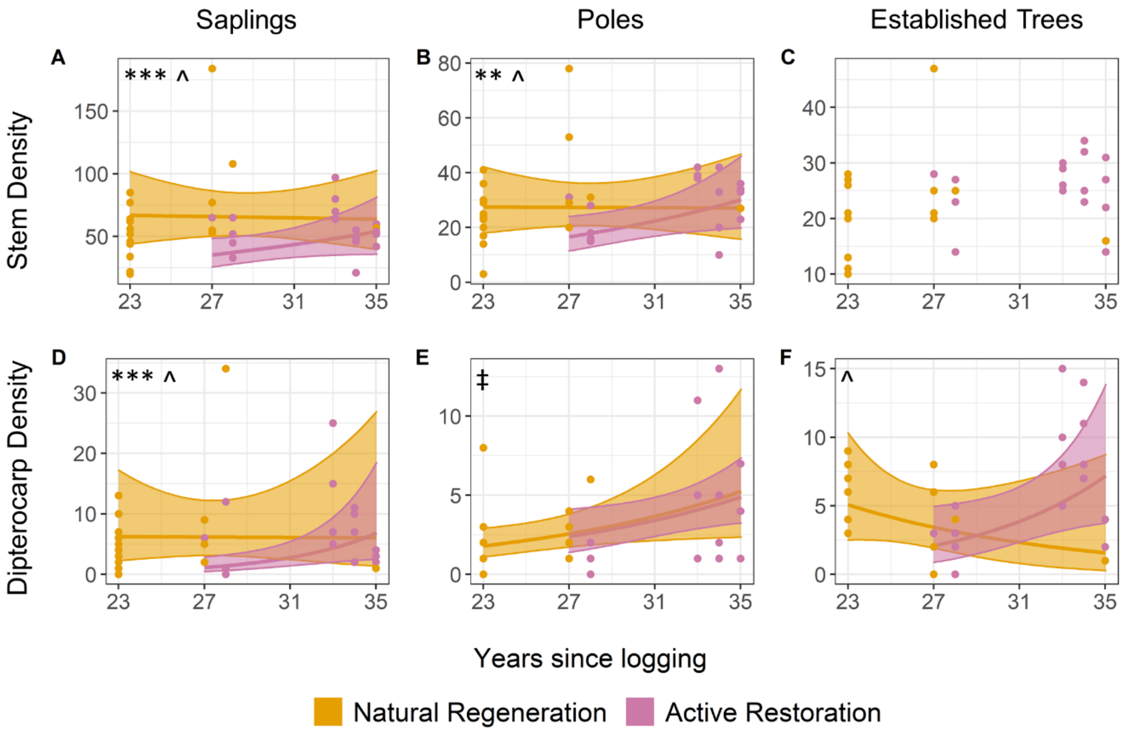


Figure 2.3 *Effects of time since logging on stem density (stems per 500 m^2 plot) of saplings (2-5 cm DBH), poles (5-10 cm DBH), and established trees (≥10 cm DBH) in actively restored and naturally regenerating forest for the full tree community (A, B, and C) and the Dipterocarpaceae (D, E, and F). Models where the effect of active regeneration was significant are marked * ($p < 0.05$), ** ($p < 0.01$), or *** ($p < 0.001$). Models where the effect of time since logging was significant are marked ‡ ($p < 0.05$). GLMMs were fitted with a Poisson error distribution and random effect of coupe and logging method; shading indicates 95% confidence intervals. Best models in panels A, B, D and F include an interaction term between active restoration and time since logging. Models where there is a significant interaction between active restoration and time since logging are marked ^ ($p < 0.05$). Full GLMM summaries are presented in Table S2.5.*

Across all models, exploration of the random effect estimates (a combination of site and logging method [Eq. 2.1 & 2.2]) showed no consistent or substantial variation between RIL plots and other plots logged in the same year.

2.4.2 Effects of selective logging history on tree richness and diversity

Shannon's diversity index of saplings was higher in unlogged than in naturally regenerating logged forest (3.374 ± 0.088 vs 2.852 ± 0.099; $p = 0.043$, Table S2.4). No other measures of species richness, rarefied species richness, diversity, or evenness were significantly affected by logging, within any size class ($p > 0.24$; Table S2.4). In selectively logged forests, species evenness of established trees was higher in naturally regenerating than actively restored plots (0.962 ± 0.005 vs 0.954 ± 0.007; $p < 0.043$, Table S2.5), however there were no other significant effects of time since logging or regeneration treatment on species richness, rarefied species richness, diversity, or evenness in any size class ($p > 0.05$; Table S2.5). In dipterocarps, species richness, diversity, and evenness did not differ in response to implementing active restoration treatments, nor with time since logging, for any size class ($p > 0.19$; Table S2.5).

2.4.3 Effects of logging and active restoration on tree species composition

Community composition was significantly different between naturally regenerating logged forest and unlogged forest for all size classes (PERMANOVA, $p < 0.05$; Table 2.1). Exploring subsets of the established tree size class however, stems in the 40-60 cm and ≥60 cm DBH ranges showed no difference in community composition due to logging ($p > 0.05$; Table S2.6). There was no difference in community composition between naturally regenerating and actively restored logged forest ($p > 0.14$; Table 2.1). Comparisons of pairwise dissimilarity for the established tree community compositions suggest that, while there was high dissimilarity among all plots, unlogged forest exhibited particularly high community dissimilarity among plots (Figure 2.4). By contrast, logged plot communities were on average more similar to one another, for comparisons either within or between areas that were naturally regenerating or had been actively restored (Table 2.1; Figure 2.4). There were no differences in dipterocarp community compositions at any size class in response to logging, implementation of an active restoration treatment, or for time since logging (PERMANOVA, $p > 0.09$; Table 2.1). Although there were significant differences in selectively logged and unlogged forest communities, there was no directional change to community composition between 23 and 35 years post-logging within any size class ($p > 0.05$; Table 2.1), indicating a lack of community recovery in selectively logged forest on the multi-decadal timescale of our study.

Table 2.1 *Results of PERMANOVA tests (10,000 permutations) showing the effect of logging (unlogged vs naturally regenerating logged), restoration treatment (naturally regenerating vs actively restored), and time since logging (logged forest only) on tree community composition within sapling (2-5 cm DBH), pole (5-10 cm DBH), and established tree (≥10 cm DBH) size classes across the full community and repeated to consider only the dipterocarp community.*

	Full Community				**Dipterocarpaceae**			
	R^2	**F**	**df**	**p**	**R^2**	**F**	**df**	**p**
Saplings								
Logging	0.055	1.343	1	0.045*	0.040	0.881	1	0.546
Restoration Type	0.033	1.090	1	0.287	0.052	1.620	1	0.091
Time since logging	0.028	0.929	1	0.633	0.023	0.734	1	0.723
Poles								
Logging	0.059	1.434	1	0.029*	0.048	0.900	1	0.584
Restoration Type	0.036	1.198	1	0.143	0.047	1.338	1	0.167
Time since logging	0.026	0.865	1	0.769	0.037	1.051	1	0.399
Established Trees								
Logging	0.056	1.534	1	0.009*	0.031	0.773	1	0.655
Restoration Type	0.030	0.996	1	0.480	0.034	1.047	1	0.399
Time since logging	0.027	0.893	1	0.699	0.311	0.965	1	0.481

There were 23 significant indicator species (whereby presence of an indicator species predicts logging treatment with 95% certainty) of unlogged forest across all size classes when data were pooled, and 14, 10, and 4 indicator species at the sapling, pole, and established tree size classes respectively (Table 2.2). By contrast, there were no significant indicator species of logged forest at any size class. When the logged forest plots were considered in isolation, there were two indicator species of naturally regenerating areas and three indicator species of actively restored areas (Table 2.3). Notably, *Dryobalanops lanceolata* was an indicator species of actively restored forest across all size classes ($p = 0.008$-0.034) and was one of the species planted during enrichment planting of those sites, as was *Neolamarckia cadamba* ($p = 0.045$ in the established tree size class; Table S2.1; Face the Future, 2011). Indicator species for the

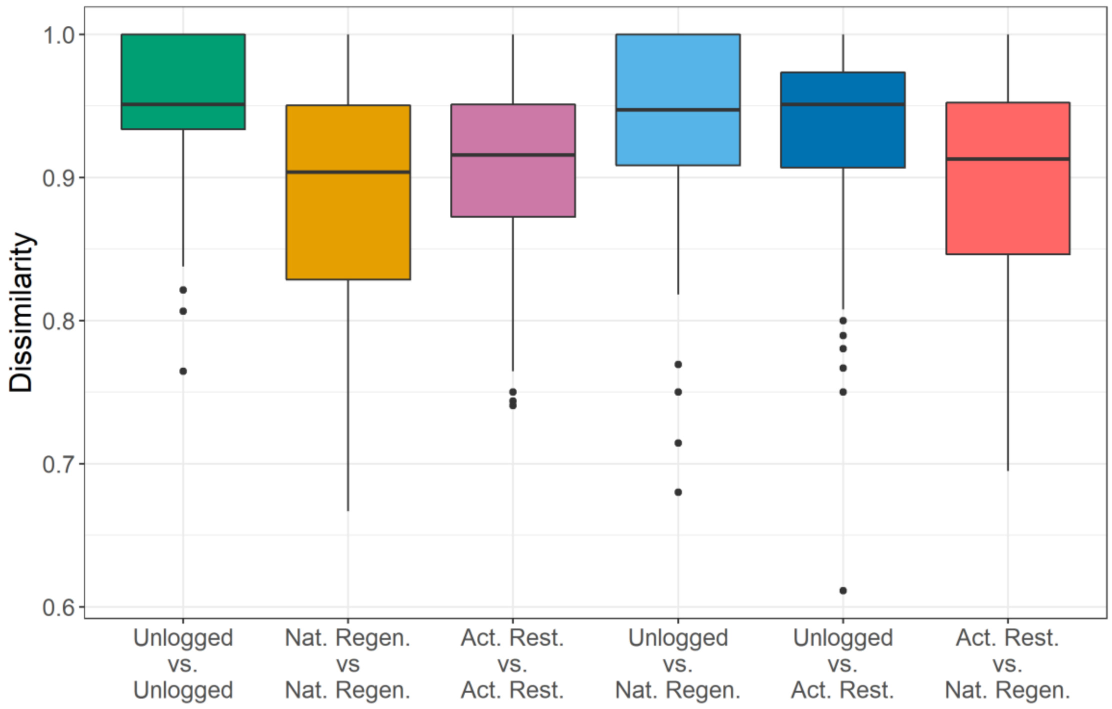


***Figure 2.4** Boxplots of pairwise Bray-Curtis dissimilarity between plots for tree communities within and between logging treatments at the established tree (≥10 cm DBH) size class.*

established tree size class, determined independently for stems 10-40 cm, 40-60 cm, and ≥60 cm DBH revealed a similar pattern, with no indicator species for logged (vs unlogged) or naturally regenerating (vs actively restored) forest (Table S2.7).

2.5.0 Discussion

Our results link the tree communities now present in the DVCA and USFR with historic selective logging and restoration practices. Forest structure and community composition were both evidently affected by selective logging, despite little significant difference in richness or diversity. Total stem basal area and stem density were higher in unlogged forest than in naturally regenerating logged forest, driven by greater stem density in the pole size class. In logged forest, sapling and pole stem density increased with time since logging across the censused chronosequence for actively restored areas. By contrast, in naturally regenerating forest, stem density was greater but did not increase over time. Tree community composition was significantly different between unlogged and naturally regenerating logged forest, with unlogged forest exhibiting more variation

Table 2.2 *Significant indicator species of tree communities with distinct logging histories at each size class. No significant indicator species were found for logged forest when compared with unlogged forest. Unique unidentified morphospecies are labelled as 'sp.' Species planted during restoration efforts are marked '*'. Species or genera which can grow as shrubs are marked '‡' (Slik, 2009, Kew Science, 2021, Encyclopedia of Life, n.d., Flora Malaysiana, n.d.)*

Family	**Indicator species**	**Indicator p-value at size class**		
		Sapling	**Pole**	**Established tree**
Unlogged (vs Logged)				
Achariaceae	*Ryparosa acuminata*	0.002	<0.001	-
Annonaceae	*Polyalthia zanthopetala ‡*	0.033	-	-
Cardiopteridaceae	*Gonocaryum calleryanum ‡*	0.032	-	-
Dilleniaceae	*Dillenia excelsa*	-	0.025	0.040
Dipterocarpaceae	*Shorea symingtonii **	-	0.032	-
Euphorbiaceae	*Mallotus lackeyi ‡*	0.039	-	-
	Mallotus wrayi ‡	-	0.007	-
Fabaceae	*Fordia splendidissima ‡*	0.042	-	-
Lauraceae	*Litsea castanea*	0.033	0.032	-
	Nothaphoebe umbelliflora	-	0.033	-
Malvaceae	*Pentace laxiflora*	-	-	0.005
Melastomataceae	*Memecylon laevigatum*	0.032	-	-
	Memecylon sp. ‡	0.031	-	-
Meliaceae	*Chisocheton sp.*	-	0.018	-
	Reinwardtiodendron humile ‡	-	-	0.009
Myrtaceae	*Syzygium kunstleri ‡*	0.034	-	-
Phyllanthaceae	*Aporosa elmeri*	0.002	0.028	-
	Aporosa grandistipulata	0.002	-	-
	Aporosa sp. ‡	-	0.012	-
	Baccaurea tetrandra ‡	0.041	-	-
	Cleistanthus hirsutulus	-	0.005	-
Rubiaceae	*Urophyllum sp. ‡*	0.027	-	-
Rutaceae	*Melicope sp. ‡*	0.033	-	0.002
Logged (vs Unlogged)				
	No significant indicator species identified	-	-	-
Natural Regeneration (vs Active Restoration)				
Dipterocarpaceae	*Shorea faguetiana **	0.040	-	-
Ebenaceae	*Diospyros sp. ‡*	-	0.044	-
Active Restoration (vs Natural Regeneration)				
Dipterocarpaceae	*Dryobalanops lanceolata**	0.018	0.008	0.034
Euphorbiaceae	*Mallotus penangensis ‡*	0.048	-	-
Rubiaceae	*Neolamarckia cadamba**	-	-	0.045

among plots and having more indicator species than other treatments. In logged forest, there was no effect of active restoration (conducted 12-24 years pre-census) or time since logging on the overall community composition, however several individual species were indicators of the active restoration treatment. Together, our results suggest that the effects of selective logging on tree communities can still be observed 23-35 years after harvesting regardless of active restoration efforts.

2.5.1 Forest structure

Logged forest had lower stem basal area per plot and fewer pole stems per unit area than adjacent unlogged forest. However, stem density in actively restored plots was shown to increase with time since logging (27-35 years) in saplings and poles. In these size classes, stem density in actively restored forest approached or exceeded values for naturally regenerating forest by 35 years after logging. This adds nuance to findings from a meta-analysis of previous studies, which concluded natural regeneration results in greater stem density than active restoration, as well as in greater structural heterogeneity of vegetation (Crouzeilles et al., 2017), showing that, despite time lags, the structure of actively restored forests is able to recover to the same extent as forests left to regenerate naturally. Our results also complement findings from the neotropics which suggest that, despite successful regrowth, actively restored forests do not have sufficiently increased productivity to justify the costs of treatment at current harvesting intervals (Gräfe and Köhl, 2020).

Although we find that established tree stem density remains distinct in logged forest and has not recovered over time, other Bornean forests, allowed to regenerate naturally, report similar stem density of trees >10 cm DBH in logged and unlogged forest by 5-15 years (Slik et al., 2002) and 22 years (Hector et al., 2011) after logging. This may be a result of varying logging intensities or remnant forest structure between studies.

We show that total basal area does not vary between naturally regenerating and actively restored forests, nor with time since logging, when considered across all size classes (Table S2.3). However, greater light availability, weeding, and climber cutting treatments at 10 m intervals may have allowed trees in the smaller size classes to grow more rapidly in actively restored sites, resulting in greater mean DBH and basal area per stem (Table S2.3). This suggests that restoration practices in Sabah are likely to be successful at increasing overall above ground biomass, relative to natural regeneration, given that trees with larger diameters are likely to have greater volumes due to taller stems. This supports previous findings of accelerated carbon recovery from active restoration in this landscape (Philipson et al., 2020), as well as elsewhere in Borneo (Ruslandi et al., 2017), in Uganda (Wheeler et al., 2016) and Costa Rica (Holl and Zahawi, 2014).

The overall lower plot-level stem density we found in the selectively logged forest plots in USFR than in adjacent unlogged forest may reflect inhibition of tree seed production and seedling recruitment and survival by localised intense disturbances, such as log landings and skid trails (Nussbaum et al., 1995, Guariguata and Dupuy, 1997), and liana colonisation of logged forests (Nabe-Nielsen et al., 2009). Lianas limit light availability in the understory, compete with trees for below-ground soil resources, including nutrients and water, and mechanically restrict tree growth (Schnitzer and Bongers, 2002), as found previously in this landscape (Magrach et al., 2016) and elsewhere (Schnitzer et al., 2000, Hall et al., 2003, van der Heijden and Phillips, 2009). Competition for soil resources may be amplified by export of nutrients in the harvested timber as well as soil compaction, leading to pervasive nutrient limitation in logged forests that may be further exacerbated through time as forests recover (Swinfield et al., 2020).

Recruitment may also be limited by the low fecundity of adult trees arising from pollination limitation or low genetic diversity among progeny, especially in late successional stems (Kettle, 2010, Nutt et al., 2016). Dipterocarp seedlings with lower genetic diversity (heterozygosity) have a reduced survival probability under field conditions, exacerbating recruitment limitation to larger size classes (Nutt et al., 2016, Tito de Morais et al., 2020). This might explain our finding that established tree dipterocarp density increases over time in actively restored forest, where additional genetic diversity has been added to the community through planting, while they decrease over time in forests allowed to regenerate naturally after logging (Figure 2.3, Panel F). These differences in recruitment through size classes may affect trajectories of change in tree community composition and represent an important component of future monitoring.

2.5.2 Effects of selective logging on tree community composition

Taxonomic diversity of tree communities differed solely amongst saplings, between unlogged and naturally regenerating logged forest, and at no size class for species richness, 23-35 years after logging. However, species composition did differ in response to logging. Results from multiple studies, including several from Sabah (Berry et al., 2008, Hector et al., 2011, Lussetti et al., 2016), provide strong evidence of high retention of tree species richness and rapid recovery of species diversity in the first two decades following selective logging of tropical forests (Slik et al., 2002, Laing et al., 2019). In French Guiana, richness and diversity of tree communities was actually higher ten years after logging than unlogged reference sites (Molino and Sabatier, 2001), reflecting initially greater recruitment of disturbance-dependent species at the landscape scale. This supports the view that selectively logged forest habitats are likely to be of reasonably high ecosystem service value (Gibson et al., 2011, Putz et al., 2012).

Although we find no difference in pole and established tree species richness and diversity of unlogged and logged forests sampled in 500 m^2 plots, there may be differences in these metrics at larger spatial scales (Berry et al., 2008, Imai et al., 2012). For example, negative effects of selective logging on richness and diversity may occur at landscape scales, where logging creates a heterogeneous disturbance mosaic (Marsh and Greer, 1992, Imai et al., 2019). Fully capturing these patterns of localised community variation therefore requires sampling across a wide range of spatial scales (Imai et al., 2012). This may also help to explain why we see lower Shannon diversity amongst saplings in logged forest, which vary more locally than larger, more dispersed, stems within the landscape. However, we found that mean community dissimilarity was greater in unlogged plots, despite the much greater number and spatial dispersion of plots in logged forest (Figure 2.1). This suggests our sampling effort was sufficient to avoid bias from highly localised, high diversity patches embedded within more degraded logged forest, even within the larger size classes.

The species composition of tree communities varied between selectively logged and unlogged forest plots for all size classes in this study, although there was no difference in the dipterocarp community composition when this family was analysed in isolation. Similar shifts in taxonomic community composition have been seen in tropical forests in Borneo (Verburg and van Eijk-Bos, 2003, Hector et al., 2011, Both et al., 2019), elsewhere in Southeast Asia (Okuda et al., 2003), and in other tropical forest regions (Baraloto et al., 2012, de Avila et al., 2015, Osazuwa-Peters et al., 2015). Furthermore, unlogged forest communities had high inter-plot dissimilarity by comparison with logged forest (Figure 2.4), indicating greater spatial variation in species composition. This reflects a previous finding from Sabah, that beta diversity was higher in unlogged than selectively logged forest plots (Imai et al., 2013). Indicator species analysis shows that this difference was manifest through the presence of 23 species that were relatively common in unlogged forest but either rare or absent from logged forest, rather than addition of new species to logged areas (Table 2.2).

Although several indicator species of unlogged forest were capable of reaching the canopy once established (*e.g. Shorea symingtonii*), they generally comprised shade-tolerant seedlings that require understorey conditions for successful establishment and survival. This matches findings from elsewhere in Southeast Asia (Okuda et al., 2003) and the wider tropics (Baraloto et al., 2012), suggesting that changes in community composition may be attributed to decreased relative abundance of mid to late successional species and an inability of some shade tolerant species to propagate and recruit into selectively logged forest. This may be due to altered canopy structure and light availability that persist for several decades after logging. While more indicator species were identified in the sapling size class than the pole or established tree size classes (14, 10, and 4, respectively; Table 2.2), this does not necessarily suggest that understory species were disproportionately affected, because the same trend could be seen in the overall number of species recorded for each size class across all plots (409, 312, and 280; Table S2.2). Shifts in community composition may also be due to differing species-specific abilities to cope with increased prevalence of lianas post-logging (Schnitzer and Bongers, 2002, Magrach et al., 2016). Slow-growing species, like dipterocarps, have been shown to be affected less than fast-growing species by liana infestation, possibly explaining why we see no significant difference in dipterocarp community composition between regeneration treatments (Visser et al., 2018).

2.5.3 Effects of time since logging and restoration on tree community composition

Species richness, diversity, and community composition were unaffected by time since logging or restoration treatment, for any tree size class. This supports findings from previous studies in Borneo (Verburg and van Eijk-Bos, 2003) and Hainan Island, China (Xu et al., 2015), which found established tree communities in logged forest remained distinct from unlogged forest 20 and 50 years post-logging, respectively. By contrast, a Brazilian study finds that the community composition of stems >10 cm DBH was significantly different between naturally regenerating and actively restored forest 30 years after intervention, despite unaffected diversity across treatments (de Avila et al., 2015). Community composition in the initial 20 years post-logging tends to be dictated by variation in pre-logging conditions such as elevation, water availability, and soil type, as well as widespread recruitment of early successional stems which are able to take advantage of the open and disturbed habitats created by logging (Verburg and van Eijk-Bos, 2003, Xu et al., 2015). We investigated a chronosequence covering 23-35 years post-logging, which is insufficient to capture complete convergence of community composition with that of an unlogged reference forest.

Frequently the aim of active restoration in logged forest is to improve regeneration of valuable timber species but at the potential cost of reduced biodiversity (Face the Future, 2011). This has led to increasing concerns surrounding the negative effects of active restoration on tree community composition and particularly the recruitment of native tree species (Hector et al., 2011, Holl and Brancalion, 2020). We found no difference in tree community composition between naturally regenerating and restored forests, which suggests there was no negative effect due to restoration. However, we found several significant indicator species for restoration treatment. Naturally regenerating forest had two indicator species (*Shorea faguetiana* and an unidentified *Diospyros* species) but neither of these were significant indicators within the established tree size class, suggesting that recruitment through to stem sizes ≥10 cm DBH is not, at this time, common for either species under either restoration treatment. By contrast, both *Dryobalanops lanceolata* and *Neolamarckia cadamba* were indicator species in actively restored forests at the established tree size class. These native species were planted as part of the active restoration process (Face the Future, 2011; Table S2.1). Although these are only two of 76 planted species to be reported as indicators, their presence in the established community suggests there have been some ecological benefits of active restoration at USFR. It is therefore important to select carefully, and subsequently monitor, the species planted as part of active restoration projects.

Overall, we found little evidence that the restoration techniques employed (liana cutting and enrichment planting) had substantially altered the recovery trajectory of tree community composition in these forests. This indicates that their positive impacts on carbon recovery in this landscape (Philipson et al., 2020) were not to the detriment of ecological conditions, as has been proposed elsewhere (Hector et al., 2011, Holl and Brancalion, 2020). Although we found no change in community composition over time, this was limited by the relatively short interval since restoration began (12-24 years prior to the census) compared to time-scales of successional change, and it remains possible that restoration would have an impact over longer timescales. It is therefore important to maintain ongoing long-term monitoring to reveal any emerging trajectories of community recovery. Our results contribute to the emerging consensus that the extent to which active restoration techniques promote recovery of tree communities in logged forest is determined by site-specific factors, such as logging intensity, soil disturbance, and connectivity to old growth forest. While the effect of active restoration on community composition is currently somewhat unpredictable as a generalised trend across tropical forests (Curran et al., 2014, Meli et al., 2017), pooling evidence will hopefully help to identify predictive relationships.

While there is currently limited evidence that active restoration of selectively logged forest in Sabah accelerates the recovery of tree community composition, there is increasing evidence for a positive impact on other taxonomic groups. Insectivorous bird (Edwards et al., 2009) and invertebrate communities (Edwards et al., 2012), for example, have been shown to recover rapidly after disturbance in actively restored Bornean forests. Active restoration may therefore have an important role to play in targeting the conservation of threatened functional groups, providing that the costs and benefits of utilised techniques are thoroughly considered and interventions are tailored to each site and species assemblage (Aerts and Honnay, 2011). A range of silvicultural techniques aimed at regeneration can be selected and combined to maximise ecological co-benefits to restoration at a landscape scale. For example, active restoration could be targeted towards threatened species or particularly degraded locations that are less likely to recover unassisted, while other areas are left to regenerate naturally (Holl and Aide, 2011, Cerullo and Edwards, 2019).

2.6.0 Conclusions

Our results indicate a clear difference in community composition and forest structure between unlogged and naturally regenerating logged forest across tree size classes ≥2 cm DBH. While richness and diversity are shown to be approximately equivalent to pre-logging values within 35 years post-logging, community composition remains distinct from nearby unlogged forest with no detectable directional shifts at the decadal time-scale. As a result, it is unlikely that selective logging cycles of 40-60 years (as intended for the region; Sist et al., 2003) will be successful in balancing economic management of Sabah's forests with long-term tree species conservation. Furthermore, we find that, although active restoration efforts in Danum Valley may have had positive impacts on mean stem size and therefore aboveground biomass, they did not have a negative effect on tree community composition, richness, or diversity by comparison with naturally regenerating plots for plots censused 12-24 years after the start of the intervention. We recommend that future active restoration strategies for climate change mitigation should be designed and implemented with biodiversity co-benefits specifically in mind, targeting the barriers to recruitment which are most likely to be faced by vulnerable shade-tolerant species if left to regenerate naturally.

2.7.0 Acknowledgements

We are grateful to the Sabah Biodiversity Centre for granting us permission to undertake this research and to our research assistants, who provided vital help in the field and identifying specimens. This research was supported by a UKRI Natural Environment Research Council PhD studentship (R.M.H.) and an Ashton Award from the Arnold Arboretum (R.M.H.). Collection of field data was funded by the Carnegie Trust for the Universities of Scotland (ref. 50076 to M.E.J.C. and D.F.R.P.B.) and the DfID and NERC Programme "Understanding the impact of the current El Nino event" (NE/P004806/1 to M.E.J.C. and D.F.R.P.B.). L.F.B and D.F.R.P.B were further funded by NERC Global Partnerships Seedcorn Fund (FOR-RESTOR; NE/T005092/1). We thank two anonymous reviewers for their input which has helped to improve the ideas in this paper.

2.8.0 Supplementary materials

Table S2.1 *Species planted in actively restored logged plots within the INFAPRO network (Face the Future, 2011)*

Dipterocarps	**Non-Dipterocarp Hardwoods**	**Fruit Trees**	**Other Trees**
Dipterocarpus applanatus *Dipterocarpus caudiferus* *Dipterocarpus acutangulus* *Dipterocarpus confertus* *Dipterocarpus conformis* *Dipterocarpus gracilis* *Dipterocarpus lowii* *Dryobalanops beccarii* *Dryobalanops keithii* *Dryobalanops lanceolata* *Hopea beccariana* *Hopea dryobalanoides* *Hopea ferruginea* *Hopea nervosa* *Hopea nutans* *Hopea pentanervia* *Hopea sangal* *Hopea spp.* *Parashorea malaanonan* *Parashorea smythiesii* *Parashorea tomentella* *Shorea acuminatissima* *Shorea agami* *Shorea argentifolia* *Shorea beccariana* *Shorea faguetiana* *Shorea falciferoides* *Shorea fallax* *Shorea flaviflora* *Shorea gibbosa* *Shorea guiso* *Shorea johorensis* *Shorea laevis* *Shorea leprosula* *Shorea leptoderma* *Shorea macroptera* *Shorea macrophylla* *Shorea mecistopteryx* *Shorea ovalis* *Shorea parvifolia* *Shorea parvistipulata* *Shorea pauciflora* *Shorea pilosa* *Shorea pinanga* *Shorea seminis* *Shorea smithiana* *Shorea superba* *Shorea symingtonii* *Vatica albiramis* *Vatica dulitensis*	*Azadirachta excelsa* *Eusideroxylon zwageri* *Intsia palembanica*	*Aglaia squamulosa* *Alangium javanicum* *Allophylus cobbe* *Artocarpus integer* *Baccaurea angulata* *Baccaurea latifolia* *Dimocarpus longan* *Diospyros spp.* *Durio spp.* *Garcinia parvifolia* *Lansium domesticum* *Nephelium lappaceum* *Nephelium mutabile* *Parartocarpus spp.* *Walsura pinnata*	*Agathis borneensis* *Aquilaria sinensis* *Duabanga moluccana* *Koompassia excelsa* *Neolamarckia cadamba* *Octomelis sumatrana* *Palaquium spp.* *Scaphium macropodum*

Table S2.2 *A summary of the number, community density, taxonomic resolution of identification, richness, diversity, and evenness of stems in the 2016 census. Statistics are divided by logging treatment and stem size class (saplings 2-5 cm DBH, poles 5-10 cm DBH, and established trees >10 cm DBH). Statistics for the whole tree community are presented, as well as for the subset of stems within the family Dipterocarpaceae.*

[redacted]	[redacted]	[redacted]	**Stems**	**Stem Density (m^{-1})**	**Identified to Family (%)**	**Identified to Genus (%)**	**Identified to Species (%)**	**Family Richness**	**Genus Richness**	**Species Richness**	**Shannon's Diversity Index**	**Species Evenness**
Unlogged	**Saplings**	**Community**	881	0.220	94.78	94.78	77.64	41	95	188	4.612	0.881
		Dipterocarps	66	0.019	-	100	96.97	-	4	14	2.384	0.881
	Poles	**Community**	432	0.108	95.14	95.14	81.25	30	65	114	4.153	0877
		Dipterocarps	47	0.013	-	100	97.87	-	4	12	2.200	0.858
	Established Trees	**Community**	332	0.059	93.48	93.48	82.30	33	69	129	4.560	0.938
		Dipterocarps	67	0.013	-	100	95.52	-	3	15	2.277	0.821
	Total	**Community**	1635	0.273	94.62	94.62	79.51	46	120	265	4.810	0.862
		Dipterocarps	180	0.033	-	100	96.67	-	5	21	2.533	0.819
Logged	**Saplings**	**Community**	2046	0.120	93.9	92.1	68.9	58	158	354	5.073	0.859
		Dipterocarps	222	0.014	-	100	98.2	-	5	26	2.832	0.859
	Poles	**Community**	996	0.059	94.6	92.7	69.7	47	125	275	4.998	0.885
		Dipterocarps	108	0.007	-	100	94.4	-	5	25	2.607	0.800
	Established Trees	**Community**	789	0.046	92.0	89.9	68.3	46	119	223	4.875	0.896
		Dipterocarps	183	0.011	-	97.8	88.5	-	6	29	2.848	0.837
	Total	**Community**	3831	0.226	93.7	91.8	67.0	62	191	491	5.293	0.850
		Dipterocarps	513	0.030	-	99.2	94.0	-	6	36	2.986	0.827
Total	**Saplings**	**Community**	2927	0.140	93.99	92.72	71.40	74	167	409	5.150	0.852
		Dipterocarps	288	0.149	-	100	97.92	-	5	30	2.924	0.851
	Poles	**Community**	1428	0.068	94.75	93.42	73.18	57	133	312	5.015	0.869
		Dipterocarps	155	0.009	-	100	95.48	-	5	27	2.710	0.813
	Established Trees	**Community**	1111	0.049	92.35	90.82	72.28	58	133	280	5.092	0.899
		Dipterocarps	246	0.012	-	100	91.87	-	5	28	2.802	0.932
	Total	**Community**	5466	0.238	93.85	92.52	72.05	81	198	545	5.342	0.844
		Dipterocarps	689	0.031	-	100	95.21	-	5	37	2.996	0.824

Table S2.3 *GLMM model summaries for stem basal area and mean stem DBH in the 2016 census. In Model 1, unlogged plots are modelled against naturally regenerating logged plots. Site variance is the variance explained by the combined random effect of plot location and logging method.*

	Estimate	**Error**	**df**	**t**	**p-value**	**Site variance**
Basal Area$_{\text{Log10}}$ Model 1						0.000
(Intercept)	1.298	0.173	22	7.500	<0.001***	
Logged	-0.918	0.206	22	-4.462	<0.001***	
Basal Area$_{\text{Log10}}$ Model 2						0.048
(Intercept)	0.281	0.152	13.81	1.846	0.086	
Recovery Time	-0.102	0.137	8.48	-0.746	0.476	
Restoration Treatment	0.389	0.224	30.29	1.740	0.091	
Mean DBH$_{\text{Log10}}$ Model 1						0.000
(Intercept)	4.499	0.070	22	64.000	<0.001***	
Logged	-0.085	0.084	22	-1.015	0.321	
Mean DBH$_{\text{Log10}}$ Model 2						0.000
(Intercept)	4.361	0.054	31	80.879	<0.001***	
Recovery Time	-0.070	0.046	31	-1.529	0.136	
Restoration Treatment	0.201	0.091	31	2.214	0.034*	

Table S2.4 *GLMM model summaries for logging, with natural regeneration, as a predictor of community metrics in the 2016 census. Site variance is the variance explained by the combined random effect of plot location and logging method. Rarefied richness is not presented for dipterocarps because a majority of plots rarefy to zero.*

	Full Community						**Dipterocarpaceae**					
	Estimate	**Error**	**df**	**t**	**p-value**	**Site variance**	**Estimate**	**Error**	**df**	**t**	**p-value**	**Site variance**
Saplings												
Stem Density						0.070						0.677
(Intercept)	4.568	0.1565		29.194	<0.001***		1.702	0.493		3.448	<0.001***	
Logging	-0.358	0.194		-1.846	0.065		-0.011	0.616		-0.018	0.985	
Species Richness						36.64						0.000
(Intercept)	34.139	5.130	2.049	6.654	0.021		2.625	0.627	23.000	4.186	<0.001***	
Logging	-6.060	6.118	2.245	-0.991	0.416		0.199	0.760	23.000	0.261	0.796	
Rarefied Richness						2.293						-
(Intercept)	24.049	2.020	3.065	11.907	0.001**		-	-	-	-	-	
Logging	-2.748	2.445	3.205	-1.124	0.338		-	-	-	-	-	
Diversity						0.000						0.000
(Intercept)	3.184	0.128	23.000	24.933	<0.001***		0.790	0.204	23.000	3.878	<0.001***	
Logging	-0.332	0.155	23.000	-2.144	0.043*		-0.033	0.247	23.000	-0.134	0.895	
Evenness						0.000						0.000
(Intercept)	0.904	0.015	23.000	61.415	<0.001***		0.741	0.107	19.000	6.899	<0.001***	
Logging	-0.018	0.018	23.000	-0.984	0.336		0.060	0.137	19.000	0.437	0.667	
Poles												
Stem Density						0.058						0.070
(Intercept)	3.816	0.146		26.151	<0.001***		1.413	0.216		6.547	<0.001***	
Logging	-0.457	0.185		-2.471	0.014*		-0.603	0.297		-2.030	0.042*	
Species Richness						2.349						0.199
(Intercept)	20.495	2.648	2.081	7.739	0.015*		2.279	0.530	0.283	4.303	0.467	
Logging	-4.602	3.210	2.136	-1.434	0.281		-0.863	0.640	0.301	-1.348	0.630	
Rarefied Richness						0.569						-
(Intercept)	18.132	2.124	1.586	8.536	0.026*		-	-	-	-	-	
Logging	-2.717	2.576	1.595	-1.055	0.425		-	-	-	-	-	
Diversity						0.022						0.129
(Intercept)	2.670	0.212	1.807	12.607	0.009**		0.757	0.291	2.206	2.604	0.110	

Logging	-0.255	0.257	1.882	-0.993	0.431		-0.443	0.345	2.407	-1.286	0.308	
Evenness						0.000						0.007
(Intercept)	0.896	0.021	23.000	41.940	<0.001***		0.794	0.159	1.440	4.988	0.071	
Logging	0.023	0.026	23.000	0.881	0.387		-0.301	0.218	1.577	-1.379	0.331	
Established Trees												
Stem Density						0.038						0.346
(Intercept)	3.355	0.127		26.510	<0.001***		1.604	0.371		4.328	<0.001***	
Logging	-0.295	0.162		-1.819	0.069		-0.345	0.474		-0.727	0.467	
Species Richness						0.365						0.000
(Intercept)	15.816	1.441	3.850	10.973	<0.001***		2.546	0.546	26.000	4.664	<0.001***	
Logging	-2.604	1.853	3.496	-1.406	0.242		0.631	0.701	26.000	0.901	0.376	
Rarefied Richness						0.503						-
(Intercept)	15.726	1.454	3.885	10.817	<0.001		-	-	-	-	-	
Logging	-2.503	1.870	3.563	-1.338	0.260		-	-	-	-	-	
Diversity						0.014						0.000
(Intercept)	2.591	0.131	4.460	19.833	<0.001***		0.679	0.187	26.000	3.631	0.001**	
Logging	-0.159	0.168	4.448	-0.947	0.392		0.306	0.240	26.000	1.273	0.214	
Evenness						<0.001						0.095
(Intercept)	0.950	0.0153	6.333	62.011	<0.001***		0.793	0.195	4.418	4.071	0.012*	
Logging	0.012	0.020	6.661	0.614	0.560		0.006	0.247	4.439	0.022	0.983	
10-40 cm												
Stem Density						0.031						0.350
(Intercept)	3.217	0.118		27.174	<0.001***		1.110	0.394		2.821	0.005**	
Logging	-0.308	0.154		-2.006	0.045*		-0.076	0.491		-0.156	0.876	
Species Richness						2.069						0.314
(Intercept)	13.924	1.798	2.373	7.743	0.009**		2.077	0.631	2.692	3.292	0.054	
Logging	-2.084	2.176	2.501	-0.958	0.421		0.402	0.762	2.868	0.528	0.636	
Rarefied Richness						0.359						-
(Intercept)	7.212	0.550	2.289	13.104	<0.003**		-	-	-	-	-	
Logging	0.194	0.660	2.498	0.294	0.791		-	-	-	-	-	
Diversity						0.042						0.059
(Intercept)	2.444	0.196	2.546	12.504	<0.002**		0.495	0.244	2.425	2.027	0.157	
Logging	-0.133	0.235	2.767	-0.566	0.614		0.289	0.294	2.621	0.984	0.407	
Evenness						0.000						0.121

(Intercept)	0.937	0.014	23.000	65.359	<0.001***		0.726	0.263	3.844	2.758	0.053	
Logging	0.027	0.017	23.000	1.544	0.136		0.073	0.313	3.886	0.233	0.828	
40-60 cm												
Stem Density						0.001						0.000
(Intercept)	0.747	0.231		3.240	0.001**		-0.811	0.500		-1.622	0.105	
Logging	-0.054	0.293		-0.184	0.854		0.236	0.601		0.392	0.695	
Species Richness						0.000						0.000
(Intercept)	1.667	0.355	20.000	4.701	<0.001***		0.500	0.403	20.000	1.242	0.228	
Logging	-0.042	0.416	20.000	-0.100	0.921		0.063	0.472	20.000	0.132	0.896	
Rarefied Richness						0.000						-
(Intercept)	1.667	0.355	20.000	4.701	<0.001***		-	-	-	-	-	
Logging	-0.042	0.416	20.000	-0.100	0.921		-	-	-	-	-	
Diversity						0.000						0.000
(Intercept)	0.405	0.191	20.000	2.123	0.046*		0.183	0.144	20.000	1.270	0.219	
Logging	-0.041	0.224	20.000	-0.183	0.856		-0.071	0.169	20.000	-0.421	0.678	
Evenness						0.000						0.000
(Intercept)	0.973	0.038	8.000	25.481	<0.001***		0.167	0.161	16.000	1.033	0.317	
Logging	0.000	0.046	8.000	0.006	0.995		-0.000	0.198	16.000	0.000	1.000	
>60 cm												
Stem Density						0.000						0.000
(Intercept)	1.022	0.200		5.108	<0.001***		0.847	0.218		3.883	<0.001***	
Logging	-0.616	0.309		-1.993	0.046*		-1.030	0.384		-2.680	0.007**	
Species Richness						0.000						0.017
(Intercept)	1.667	0.289	19.000	5.774	<0.001***		1.336	0.254	4.328	5.258	0.005**	
Logging	-0.417	0.382	19.000	-1.091	0.289		-0.604	0.337	3.806	-1.790	0.152	
Rarefied Richness						0.000						-
(Intercept)	1.667	0.289	19.000	5.774	<0.001***		-	-	-	-	-	
Logging	-0.417	0.382	19.000	-1.091	0.289		-	-	-	-	-	
Diversity						0.000						0.000
(Intercept)	0.382	0.144	19.000	2.660	0.016*		0.217	0.105	19.000	2.065	0.053	
Logging	-0.122	0.190	19.000	-0.640	0.530		-0.048	0.139	19.000	-0.346	0.733	
Evenness						0.000						0.000
(Intercept)	0.966	0.201	8.000	4.797	0.001**		0.937	0.253	10.000	3.703	0.004**	
Logging	-0.313	0.260	8.000	-1.205	0.263		-0.613	0.292	10.000	-2.098	0.062	

Table S2.5 *GLMM model summary for the effects of restoration treatment (naturally regenerating/ actively restored) and time since logging as predictors of Dipterocarpaceae and total community metrics in the 2016 census. Site variance is the variance explained by the combined random effect of plot location and logging method. Models were selected to include or exclude an interaction effect between Recovery Time and Restoration Treatment, based on which model had the lowest Akaike Information Criterion value. Rarefied richness is not presented for dipterocarps because a majority of plots rarefy to zero*

	Full Community						**Dipterocarpaceae**					
	Estimate	**Error**	**df**	**t**	**p-value**	**Site variance**	**Estimate**	**Error**	**df**	**t**	**p-value**	**Site variance**
Saplings												
Stem Density						0.132						0.701
(Intercept)	4.182	0.129		32.457	<0.001***		1.815	0.357		5.084	<0.001***	
Recovery Time	-0.018	0.145		-0.126	0.900		-0.012	0.415		-0.028	0.977	
Restoration Treatment	-0.536	0.084		-6.363	<0.001***		-1.347	0.263		-5.121	<0.001***	
Interaction	0.272	0.111		2.458	0.014*		1.088	0.488		2.229	0.026*	
Species Richness						42.610						0.000
(Intercept)	28.867	4.018	17.551	7.185	<0.001***		2.506	0.644	31.000	3.891	<0.001***	
Recovery Time	3.430	4.348	12.910	0.789	0.444		-0.421	0.550	31.000	-0.766	0.450	
Restoration Treatment	-2.446	5.230	29.716	-0.468	0.643		0.930	1.083	31.000	0.858	0.397	
Interaction	-2.964	5.957	26.864	-0.498	0.623		-	-	-	-	-	
Rarefied Richness						3.216						-
(Intercept)	21.945	2.294	17.411	9.568	<0.001***		-	-	-	-	-	
Recovery Time	1.163	2.352	9.242	0.495	0.632		-	-	-	-	-	
Restoration Treatment	1.596	3.258	27.904	0.490	0.628		-	-	-	-	-	
Interaction	-1.579	3.438	12.200	-0.459	0.654		-	-	-	-	-	
Diversity						0.015						0.014
(Intercept)	2.881	0.142	10.000	20.248	<0.001***		0.650	0.203	15.302	3.210	0.006**	
Recovery Time	0.052	0.124	6.216	0.424	0.686		-0.129	0.174	10.959	-0.737	0.476	
Restoration Treatment	0.071	0.229	30.621	0.309	0.760		0.317	0.334	30.329	0.951	0.349	
Interaction	-	-	-	-	-		-	-	-	-	-	
Evenness						0.000						0.005
(Intercept)	0.883	0.015	31.000	60.773	<0.001***		0.848	0.126	21.232	6.712	<0.001***	
Recovery Time	-0.004	0.012	31.000	-0.338	0.738		0.059	0.112	19.545	0.525	0.606	
Restoration Treatment	0.031	0.024	31.000	1.266	0.215		-0.047	0.217	21.573	-0.215	0.832	
Interaction	-	-	-	-	-		-	-	-	-	-	
Poles												
Stem Density						0.128						0.067

(Intercept)	3.307	0.141		23.375	<0.001***		1.080	0.215		5.014	<0.001***	
Recovery Time	-0.005	0.158		-0.033	0.973		0.428	0.195		2.193	0.028*	
Restoration Treatment	-0.383	0.123		-3.104	0.002**		-0.071	0.339		-0.210	0.833	
Interaction	0.362	0.153		2.370	0.018*		-	-	-	-	-	
Species Richness						27.74						0.164
(Intercept)	15.438	2.886	16.598	5.350	<0.001***		1.712	0.574	15.813	2.981	0.009**	
Recovery Time	0.628	3.156	13.239	0.199	0.845		0.483	0.496	11.245	0.974	0.351	
Restoration Treatment	-1.516	3.611	29.166	-0.420	0.678		0.232	0.938	30.579	0.247	0.806	
Interaction	3.110	4.176	29.169	0.745	0.462		-	-	-	-	-	
Rarefied Richness						22.17						-
(Intercept)	15.060	2.745	16.421	5.486	<0.001***		-	-	-	-	-	
Recovery Time	0.664	2.985	12.368	0.222	0.828		-	-	-	-	-	
Restoration Treatment	-0.670	3.514	29.445	-0.191	0.850		-	-	-	-	-	
Interaction	2.668	4.031	27.897	0.662	0.514		-	-	-	-	-	
Diversity						0.240						0.002
(Intercept)	2.355	0.221	11.551	10.657	<0.001***		0.313	0.198	16.221	1.583	0.133	
Recovery Time	0.085	0.216	7.620	0.393	0.705		0.043	0.169	12.259	0.257	0.801	
Restoration Treatment	0.019	0.254	25.997	0.076	0.940		0.229	0.332	29.878	0.689	0.496	
Interaction	-	-	-	-	-		-	-	-	-	-	
Evenness						0.000						0.012
(Intercept)	0.916	0.015	31.000	60.869	<0.001***		0.757	0.244	11.007	3.101	0.010*	
Recovery Time	-0.004	0.013	31.000	-0.274	0.786		0.260	0.191	13.394	1.359	0.197	
Restoration Treatment	0.016	0.025	31.000	0.615	0.543		-0.077	0.376	14.997	-0.206	0.839	
Interaction	-	-	-	-	-		-	-	-	-	-	
Established Trees												
Stem Density						0.015						0.252
(Intercept)	3.108	0.083		37.389	<0.001***		1.081	0.368		2.935	0.003**	
Recovery Time	0.100	0.075		1.326	0.185		-0.469	0.418		-1.122	0.262	
Restoration Treatment	0.046	0.119		0.383	0.702		-0.108	0.384		-0.281	0.779	
Interaction	-	-	-	-	-		1.209	0.563		2.148	0.032*	
Species Richness						0.807						1.544
(Intercept)	14.488	1.393	13.974	10.401	<0.001***		2.866	0.7686	20.633	3.728	0.001**	
Recovery Time	1.764	1.201	9.696	1.469	0.173		-0.389	0.831	16.186	-0.468	0.656	
Restoration Treatment	1.343	2.286	30.327	0.588	0.561		-0.574	1.002	29.828	-0.572	0.571	

Interaction	-	-	-	-	-		2.005	1.140	27.819	1.758	0.090	
Rarefied Richness						0.807						-
(Intercept)	14.488	1.393	13.974	10.401	<0.001***		-	-	-	-	-	
Recovery Time	1.764	1.201	9.696	1.469	0.173		-	-	-	-	-	
Restoration Treatment	1.343	2.286	30.327	0.588	0.561		-	-	-	-	-	
Interaction	-	-	-	-	-		-	-	-	-	-	
Diversity						0.004						0.132
(Intercept)	2.538	0.097	13.221	26.121	<0.001***		0.812	0.231	20.863	3.512	0.002**	
Recovery Time	0.159	0.084	9.049	1.895	0.091		-0.239	0.249	16.166	-0.959	0.352	
Restoration Treatment	0.030	0.159	30.264	0.186	0.854		-0.168	0.304	29.885	-0.553	0.584	
Interaction	-	-	-	-	-		0.750	0.344	27.358	2.178	0.038*	
Evenness						0.000						0.174
(Intercept)	0.972	0.008	31.000	122.565	<0.001***		0.770	0.135	8.223	5.721	<0.001***	
Recovery Time	0.014	0.007	31.000	2.021	0.052		0.101	0.148	8.084	0.679	0.516	
Restoration Treatment	-0.028	0.013	31.000	-2.106	0.043*		-0.030	0.033	19.076	-0.921	0.368	
Interaction	-	-	-	-	-		-	-	-	-	-	
10-40 cm												
Stem Density						0.012						0.290
(Intercept)	2.972	0.084		35.232	<0.001***		1.256	0.279		4.506	<0.001***	
Recovery Time	0.119	0.075		1.581	0.114		0.158	0.257		0.615	0.539	
Restoration Treatment	0.029	0.126		0.234	0.815		0.007	0.349		0.020	0.984	
Interaction	-	-	-	-	-		-	-	-	-	-	
Species Richness						0.000						1.085
(Intercept)	12.993	1.263	31.000	10.283	<0.001***		2.316	0.620	19.297	3.735	0.001**	
Recovery Time	1.705	1.079	31.000	1.581	0.124		-0.281	0.673	15.106	-0.417	0.683	
Restoration Treatment	1.133	2.126	31.000	0.533	0.598		-0.156	0.799	29.687	-0.195	0.847	
Interaction	-	-	-	-	-		1.540	0.914	28.184	1.684	0.103	
Rarefied Richness						0.000						-
(Intercept)	7.639	0.248	31.000	30.860	<0.001***		-	-	-	-	-	
Recovery Time	0.247	0.211	31.000	1.170	0.251		-	-	-	-	-	
Restoration Treatment	-0.007	0.416	31.000	-0.017	0.986		-	-	-	-	-	
Interaction	-	-	-	-	-		-	-	-	-	-	
Diversity						0.012						0.124
(Intercept)	2.400	0.109	12.112	21.922	<0.001***		0.842	0.202	14.492	4.176	<0.001***	

Recovery Time	0.146	0.096	7.622	1.526	0.167		0.079	0.187	9.097	0.420	0.684	
Restoration Treatment	0.081	0.173	30.955	0.465	0.645		0.054	0.276	29.090	0.195	0.847	
Interaction	-	-	-	-	-		-	-	-	-	-	
Evenness						0.000						0.175
(Intercept)	0.970	0.008	31.000	120.103	<0.001***		0.778	0.136	8.292	5.726	<0.001***	
Recovery Time	0.008	0.007	31.000	1.203	0.238		0.102	0.149	8.110	0.686	0.512	
Restoration Treatment	-0.017	0.014	31.000	-1.224	0.230		-0.031	0.038	19.099	-0.832	0.416	
Interaction	-	-	-	-	-		-	-	-	-	-	
40-60 cm												
Stem Density						0.000						0.000
(Intercept)	0.715	0.217		3.289	0.001**		-0.386	0.374		-1.030	0.303	
Recovery Time	0.032	0.186		0.171	0.865		0.309	0.328		0.945	0.345	
Restoration Treatment	0.258	0.366		0.705	0.481		-0.117	0.646		-0.182	0.856	
Interaction	-	-	-	-	-		-	-	-	-	-	
Species Richness						0.000						0.000
(Intercept)	1.816	0.366	27.000	4.964	<0.001***		0.690	0.290	27.000	2.380	0.025*	
Recovery Time	0.275	0.326	27.000	0.843	0.407		0.183	0.258	27.000	0.709	0.484	
Restoration Treatment	0.252	0.642	27.000	0.392	0.698		-0.121	0.509	27.000	-0.237	0.814	
Interaction	-	-	-	-	-		-	-	-	-	-	
Rarefied Richness						0.000						-
(Intercept)	1.816	0.366	27.000	4.964	<0.001***		-	-	-	-	-	
Recovery Time	0.275	0.326	27.000	0.843	0.407		-	-	-	-	-	
Restoration Treatment	0.252	0.642	27.000	0.392	0.698		-	-	-	-	-	
Interaction	-	-	-	-	-		-	-	-	-	-	
Diversity						0.000						0.020
(Intercept)	0.475	0.172	27.000	2.765	0.010*		0.144	0.112	16.799	1.286	0.216	
Recovery Time	0.161	0.153	27.000	1.050	0.303		0.039	0.103	12.788	0.380	0.710	
Restoration Treatment	0.032	0.302	27.000	0.108	0.915		-0.051	0.180	26.907	-0.282	0.780	
Interaction	-	-	-	-	-		-	-	-	-	-	
Evenness						0.000						0.017
(Intercept)	0.962	0.028	12.000	34.516	<0.001***		0.231	0.156	11.193	1.484	0.165	
Recovery Time	-0.019	0.031	12.000	-0.596	0.563		0.091	0.136	9.488	0.671	0.518	
Restoration Treatment	0.040	0.057	12.000	0.693	0.501		-0.103	0.261	17.346	-0.393	0.699	
Interaction	-	-	-	-	-		-	-	-	-	-	

>60 cm

Stem Density						0.000						0.861
(Intercept)	0.397	0.357		1.111	0.267		-0.726	0.983		-0.739	0.460	
Recovery Time	-0.010	0.331		-0.031	0.975		-0.103	0.881		-0.117	0.907	
Restoration Treatment	0.159	0.650		0.244	0.807		-0.073	1.667		-0.044	0.965	
Interaction	-	-	-	-	-		-	-	-	-	-	
Species Richness						0.000						0.524
(Intercept)	0.489	0.536	19.000	0.912	0.373		0.608	0.479	14.728	1.269	0.224	
Recovery Time	-0.938	0.604	19.000	-1.552	0.137		-0.009	0.469	12.675	-0.020	0.985	
Restoration Treatment	0.980	0.672	19.000	1.459	0.161		0.023	0.766	19.981	0.030	0.976	
Interaction	1.230	0.713	19.000	1.724	0.101		-	-	-	-	-	
Rarefied Richness						0.000						-
(Intercept)	0.489	0.536	19.000	0.912	0.373		-	-	-	-	-	
Recovery Time	-0.938	0.604	19.000	-1.552	0.137		-	-	-	-	-	
Restoration Treatment	0.980	0.672	19.000	1.459	0.161		-	-	-	-	-	
Interaction	1.230	0.713	19.000	1.724	0.101		-	-	-	-	-	
Diversity						0.024						0.039
(Intercept)	0.265	0.193	14.085	1.373	0.191		0.151	0.175	15.168	0.862	0.402	
Recovery Time	0.022	0.184	12.983	0.119	0.907		0.002	0.168	13.530	0.011	0.992	
Restoration Treatment	0.164	0.345	19.276	0.474	0.641		0.030	0.300	19.770	0.101	0.920	
Interaction	-	-	-	-	-		-	-	-	-	-	
Evenness						0.017						0.139
(Intercept)	0.401	0.264	2.901	1.519	0.229		0.269	0.242	13.096	1.112	0.286	
Recovery Time	-0.277	0.251	2.908	-1.102	0.353		-0.040	0.239	11.827	-0.165	0.872	
Restoration Treatment	0.875	0.512	3.906	1.709	0.164		0.023	0.377	14.379	0.062	0.951	
Interaction	-	-	-	-	-		-	-	-	-	-	

Table S2.6 *Results of PERMANOVA tests (10,000 permutations) showing the effect of logging (unlogged vs naturally regenerating logged), restoration treatment (naturally regenerating vs actively restored), and time since logging (logged forest only) on tree community composition within subsets of the established tree size class (>10 cm DBH) across the full community and repeated to consider only the dipterocarp community.*

	Full Community				**Dipterocarpaceae**			
	R^2	**F**	**df**	**p**	**R^2**	**F**	**df**	**p**
10-40 cm								
Logging	0.036	1.485	1	0.012*	0.029	1.112	1	0.341
Restoration Type	0.030	0.991	1	0.481	0.031	0.953	1	0.489
Time since logging	0.031	1.011	1	0.453	0.038	1.182	1	0.313
40-60 cm								
Logging	0.032	1.134	1	0.225	0.090	1.185	1	0.496
Restoration Type	0.043	1.246	1	0.138	0.071	0.811	1	0.613
Time since logging	0.034	1.003	1	0.470	0.048	0.542	1	0.831
>60 cm								
Logging	0.033	0.941	1	0.494	0.033	0.605	1	0.781
Restoration Type	0.057	1.149	1	0.269	0.166	1.754	1	0.118
Time since logging	0.053	1.081	1	0.358	0.080	0.843	1	0.600

Table S2.7 *Significant indicator species of tree communities with distinct logging histories at size-class subsets within established trees (>10 cm DBH). No significant indicator species were found for logged forest when compared with unlogged forest. Unique unidentified morphospecies are labelled as ‘sp.’ Species planted during restoration efforts are marked ‘*’. Species or genera which can grow as shrubs are marked ‘‡’*

Family	**Indicator species**	**Indicator p-value at size class**		
		10-40 cm DBH	**40-60 cm DBH**	**>60 cm DBH**
Unlogged (vs Logged)				
Achariaceae	*Hydnocarpus sp.*	0.033	-	-
Annonaceae	*Polyalthia sumatrana ‡*	0.324	-	-
Euphorbiaceae	*Mallotus wrayi ‡*	0.004	-	-
Malvaceae	*Pentace laxiflora*	0.014	-	-
Myristicaceae	*Knema laurina ‡*	0.033	-	-
Phyllanthaceae	*Aporosa elmeri*	0.033	-	-
	Cleistanthus hirsutulus	0.034	-	-
Primulaceae	*Ardisia sp. ‡*	0.032	-	-
Logged (vs Unlogged)				
	No significant indicator species identified	-	-	-
Natural Regeneration (vs Active Restoration)				
	No significant indicator species identified	-	-	-
Active Restoration (vs Natural Regeneration)				
Dipterocarpaceae	*Dryobalanops lanceolata**	0.025		
Rubiaceae	*Neolamarckia cadamba**	-	0.036	

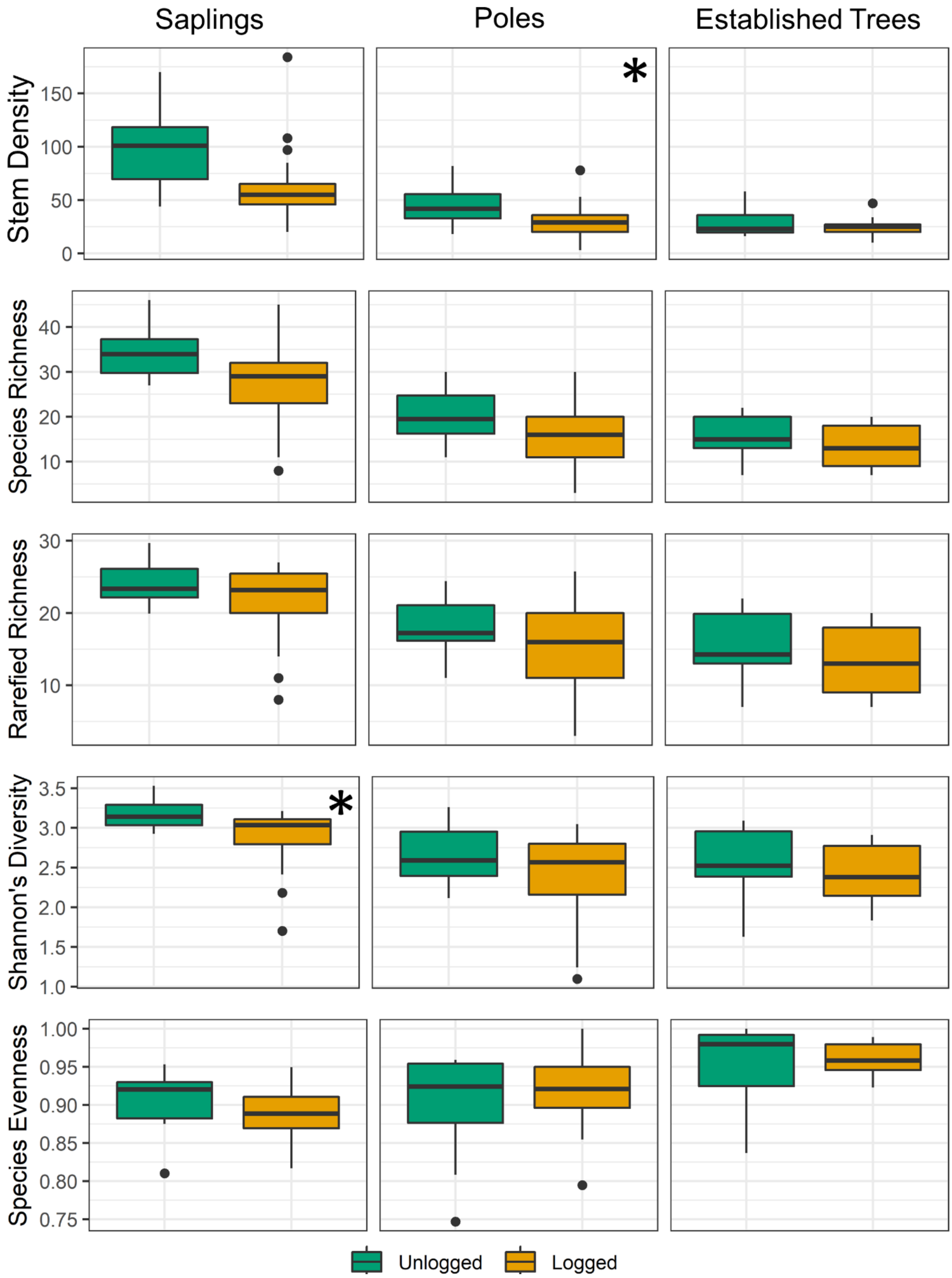


Figure S2.1 *Comparisons of full community stem density (per 500 m*^{2} *plot), species richness, Shannon's diversity and evenness at each size class in unlogged and naturally regenerating logged forest. Significant differences are marked **

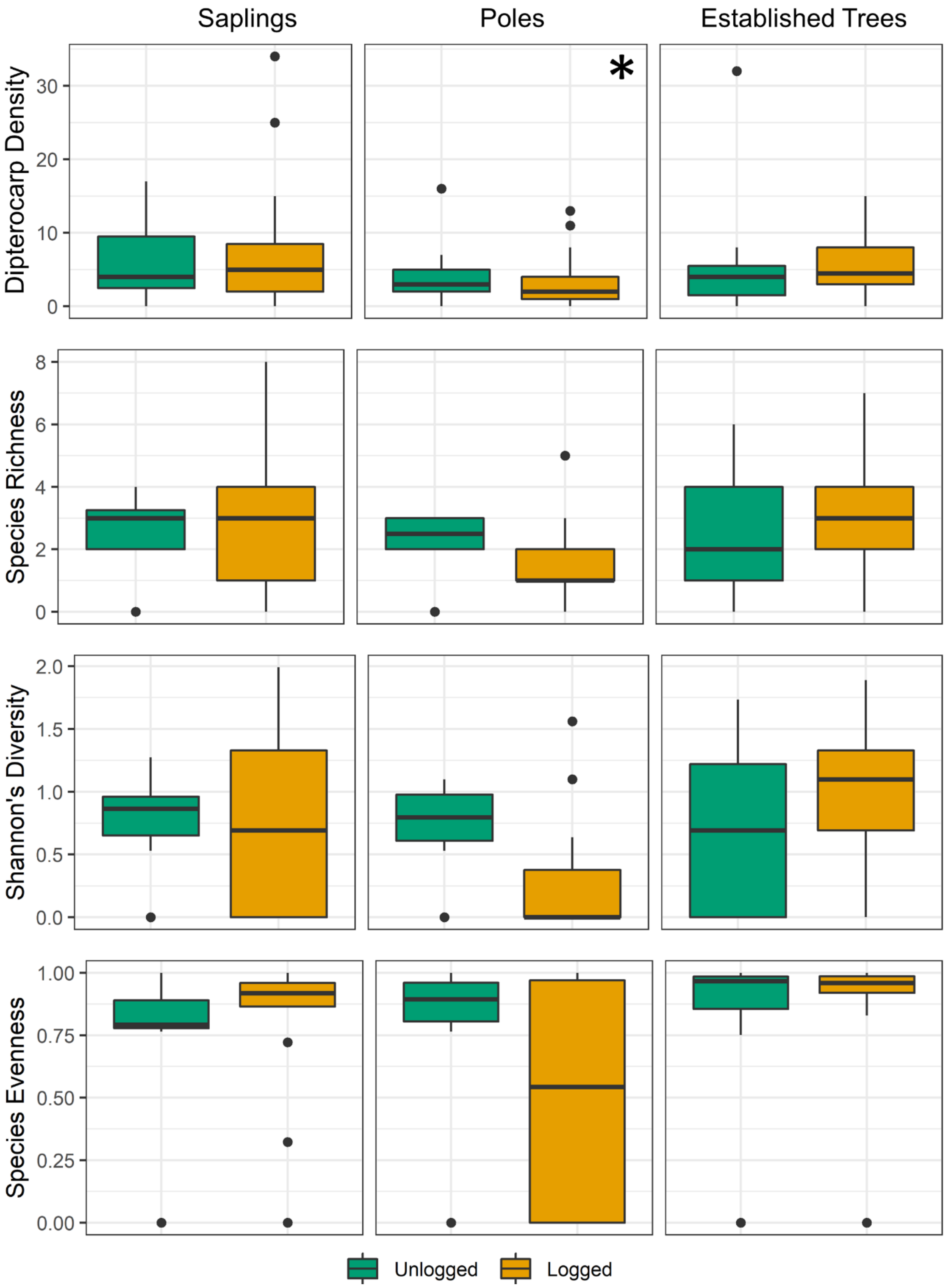


***Figure S2.2** Comparisons of dipterocarp community stem density (per 500 m^2 plot), species richness, Shannon's diversity and evenness at each size class in unlogged and naturally regenerating logged forest plots. Significant differences are marked **

Chapter 3: Recruitment and survival of seedlings following a mast fruiting event in Borneo’s old-growth and disturbed forests

Photo: masted seedlings in old-growth forest at Danum
[credit: Christian Ziegler]

Chapter collaborators: Robin Hayward, Lindsay Banin, David Burslem, Daniel Chapman, Christopher Philipson, Mark Cutler, Glen Reynolds, and Daisy Dent.

Research ideas were formulated by RH and DD. Seedling plots were established by RH and seedling data were collected by the South East Asia Rainforest Research Partnership (SEARRP) team at Danum. Established tree data were collected by CP, MC, DB, GR, and SEARRP. Canopy data were collected by RH. RH collated and analysed data with advice from DD, LB, DC, and DB. RH led the writing of the text and DD, LB, DC, and DB commented on a draft version of this chapter.

3.1.0 Abstract

Selective logging has affected more than half of the world's tropical forests. There is increasing interest in the potential for logged forests to recover structural complexity and biodiversity, and the role that active restoration can play in accelerating recovery. To understand the impact of logging and subsequent restoration on seedling recruitment and survival we tracked seedlings that germinated immediately after a mast fruiting in North Borneo in 2019. We followed 5119 seedlings from germination for ~1.5 years, across a mixed landscape of unlogged forest and forest regenerating 26-38 years after logging, which included areas that had been actively restored 15-27 years prior to the masting event. We found that unlogged and actively restored forests had higher initial seedling densities than naturally regenerating forest, but seedling survival in actively restored forests was lower than in unlogged or naturally regenerating forest in the six months post mast, resulting in lower seedling densities in actively restored forest 1.5 years after the mast event (0.85% survival in actively restored forest, versus 7.30% in naturally regenerating and 5.37% in unlogged forests). Community composition of seedlings differed among forest types. Although restoration increases recovery of carbon storage in logged forest, it does not seem to increase recruitment of seedlings from late-successional species. This finding has implications for the longer-term recovery of logged forests, and further research is needed to understand the mechanisms driving increased seedling mortality in restored forest systems.

3.2.0 Introduction

Over half of all tropical forests have been selectively logged (Asner et al., 2009), and forests in the Asia-Pacific region have been especially impacted (Laurance and Edwards, 2014). Logged forests are able to retain relatively high species diversity and provide habitat for many animal species (Edwards et al., 2011, Wearn et al., 2017, Yano et al., 2021). However, the long-term effects of selective logging on forest tree communities remain poorly understood (Brown and Gurevitch, 2004, Baraloto et al., 2012, Cazzolla Gatti et al., 2015, Ewers et al., 2015, Shima et al., 2018).

Short-term recovery of forest communities is largely driven by seedlings and saplings that survive and grow into the canopy after logging (Brokaw and Busing, 2000, Meijaard, 2005, Putz et al., 2008), however longer-term recovery from large-scale disturbances relies on recruitment from future generations of seedlings (Chazdon, 2003, Bagchi et al., 2011). The seed-to-seedling transition is a critical point in plant lifecycles for maintenance of diverse tree communities (Grubb, 1977, Wright, 2002, Poulsen et al., 2012) and if conditions are not suitable for seedling germination and survival, limited seedling recruitment may preclude complete forest recovery (Pillay et al., 2018). Despite the importance of seedling recruitment, little is known about the long-term impacts of selective logging on seedling communities, due the rarity of in-situ monitoring studies and because studies mostly examine forests for relatively short periods after logging (within 12 years; Curran et al., 1999, Bagchi et al., 2011). In Southeast Asia where most seeds are produced in mast fruiting events, the logistical challenges of predicting mast occurrence and the complexities of rapid seedling data collection at a landscape scale make seedling studies even more rare. In these forests previous studies of masted seedlings have focussed on seedlings from only a few accessible parent trees (Itoh et al., 1995, Oshima et al., 2015).

Selectively logged forests retain higher conservation value than other degraded and disturbed forest systems (Edwards et al., 2011, Putz et al., 2012, Bicknell et al., 2015, Wearn et al., 2017), since selective logging practices aim to remove just 4-15 commercially valuable stems per hectare, leaving a viable forest ecosystem post-harvest (Pinard and Putz, 1996, Edwards et al., 2014b). In theory, remnant stems should be able to grow to recolonise the gaps from which larger, valuable timber trees (≥40-60 cm diameter at breast height; DBH) were removed (Sist et al., 2003, Edwards et al., 2014b). However, it has been suggested that by disproportionately removing reproductive stems of slow-growing timber species and altering forest structure and environment, selective logging alters seedling recruitment with long-term implications for forest composition (Johns and Burley, 1997, Pillay et al., 2018).

The community composition of adult trees in selectively logged forests is often distinct from that of adjacent unlogged forest (Verburg and van Eijk-Bos, 2003, Baraloto et al., 2012, Osazuwa-Peters et al., 2015, Both et al., 2019, Hayward et al., 2021), with lower relative abundance of mid to late successional species than unlogged forests (Hector et al., 2011, Both et al., 2019, Hayward et al., 2021). Therefore, seed rain in logged forests may contain a disproportionate number of early successional species, reflecting the species' relative abundances in the forest canopy (Souza et al., 2020, Huanca Nuñez et al., 2021). The abundance of seeds in logged forest may also be constrained due to reduced density of adult trees and altered fecundity (Ghazoul et al., 1998, Curran and Webb, 2000). At one site in Kalimantan, masted seed rain in logged forest was ~23% of the number of propagules produced in unlogged forest (Curran and Webb, 2000). This may be due to the reduced density and increased isolation of reproductive trees in logged forests and the inability of some dipterocarp species to self-pollinate (Ghazoul et al., 1998).

Logged forests may also experience higher rates of seed predation and reduced seed viability compared to unlogged forests (Curran and Webb, 2000, Granados et al., 2017). Seed limitation may be compounded in Southeast Asian forests as the majority of canopy trees reproduce primarily during mast fruiting events (every 3-9 years; Curran and Leighton, 2000). This recruitment strategy results in the establishment of discrete seedling cohorts that experience within-cohort competition for resources immediately post-mast (Paine et al., 2008, Oshima et al., 2015). The predator satiation hypothesis suggests that masting is successful within functioning forest ecosystems because seed predators are unable to consume all propagules (Janzen, 1971, Silvertown, 2008). However, earlier and more intensive seed predation in logged forest, as by bearded pigs in Kalimantan, coupled with reduced seed rain, might diminish this satiation effect (Curran and Webb, 2000). Ungulate seed predator populations may be larger and more likely to travel in groups in logged than unlogged forests creating greater seed predator pressure (Brodie et al., 2015, Davison et al., 2019).

Selective logging not only changes the composition of the tree community but also impacts abiotic and biotic components of the forest environment. For example, logged forests can be less buffered from extreme climatic events than unlogged forests, and experience much greater extremes in microclimatic conditions (Blonder et al., 2018), although after two decades of post-logging recovery these effects are likely reduced (Senior et al., 2017a). Selective logging also reduces canopy cover that can result in increased light availability in the forest understory as well as increased temperatures and airflow. In combination, these factors drive higher variation in forest microclimates (Fetcher et al., 1985, Fauset et al., 2017, Senior et al., 2017b, Blonder et al., 2018), which can cause increased seedling mortality in logged forest and select for ruderal traits, arresting trajectories of forest succession (Stride et al., 2018, Qie et al., 2019). This may especially disfavour the Dipterocarpaceae (dipterocarps) – a family of shade-tolerant canopy trees that characterise old growth forests across Southeast Asia (Appanah et al., 1998) – leading to diverging community compositions of seedling cohorts between forest types, due to higher rates of early mortality amongst sensitive taxa.

Active restoration techniques are often used to hasten the recovery of forest biomass and abundance of stems from species targeted during selective logging (Gourlet-Fleury et al., 2013, Mills et al., 2019, Osuri et al., 2019, Philipson et al., 2020). Techniques commonly include enrichment planting of trees and liberation cutting of early successional stems and lianas to reduce competition (Finegan, 2014). In the selectively logged dipterocarp forests of Southeast Asia, trees planted through enrichment programs are commonly of high value, both in terms of timber and carbon sequestration, and represent a relatively small subset of natively occurring species (Moura Costa, 1996, Sovu et al., 2010, Widiyatno et al., 2020). Restoration strategies have been shown to increase carbon recovery in logged forests relative to naturally regenerating forest (Gourlet-Fleury et al., 2013, Mills et al., 2019, Osuri et al., 2019, Philipson et al., 2020). However, the impacts of restoration practices on tree community composition are unclear and may even drive shifts in composition further from an unlogged reference community (de Avila et al., 2015, Hayward et al., 2021). We know of no previous studies that consider how restoration practices affect natural seed production and seedling recruitment in logged tropical forests.

Here we study seedling recruitment and survival immediately post-mast in unlogged, logged, and restored forest plots, where overstorey composition has previously been characterised (Hayward et al., 2021). We analyse the effects of selective logging and subsequent restoration on the survival of seedlings from a masting event over the first 1.5 years post-germination. We compare seedling communities in unlogged forest with those from forests logged 26-38 years ago; logged forests have either regenerated naturally or have been actively restored through a combination of enrichment planting and liberation cutting 15-27 years ago (Face the Future, 2011). Specifically, we address the following hypotheses:

Q1. *Are germinated seedling numbers higher in unlogged than logged forests due to the greater size, density, and fecundity of reproductive adults?*

Q2. Does community composition of newly germinated seedlings differ among unlogged, logged and restored forests due to differences in the adult community?

Q3. Does seedling community composition change over time, post germination, and is this affected by logging, restoration treatment, and the established tree community?

3.3.0 Methods

3.3.1 Study sites

This study was conducted in the Danum Valley Conservation Area (DVCA) and adjacent Ulu Segama Forest Reserve (USFR), where a mast fruiting event occurred from July to August 2019, enabling comparison of seedling community responses in unlogged (DVCA) and selectively logged (USFR) forests.

The DVCA and USFR both contain lowland dipterocarp forests and are within a 10,000 km^2 concession in East Sabah, Malaysian Borneo that is currently designated for conservation (Reynolds et al., 2011). DVCA (438 km^2) has remained unlogged while the USFR (1268 km^2) was divided into logging coupes (~27 km^2) that were harvested annually between 1981 and 1993 (figure 3.1) (Reynolds et al., 2011, Sabah Forestry Department, 2019). Harvesting was carried out once per coupe by a mixture of tractor and high-lead logging with a mean timber extraction rate of 118 m^3 ha^{-1} (42.5-128.2 m^3 ha^{-1}), where all commercially viable stems >60 cm DBH were removed (Pinard et al., 2000a, Foody and Cutler, 2003).

Active restoration strategies were applied to a subset of the logged coupes (logged 1981-1989; figure 3.1) between 1992 and 2004 (15-27 years pre-mast and an average of 9 years post-logging) as part of the Innoprise-FACE Foundation Rainforest Rehabilitation Project (INFAPRO) (Moura Costa, 1996, Face the Future, 2011). Strategies comprised a mixture of liberation cutting, girdling of early successional tree species, and planting of seedlings every 3 m along parallel lines (cut 2 m wide and 10 m apart) throughout the targeted areas (Moura Costa, 1996, Face the Future, 2011). Seedlings were grown in nurseries to a height of ~50 cm and with 10 leaves (4-8 months growth), before being planted in logged forest, and were a mix of 52 dipterocarp species, five non-dipterocarp canopy species, and 16 non-dipterocarp native fruit tree species (Table S3.1) (Moura Costa, 1996, Face the Future, 2011). In particularly open sites, three early successional tree species and a range of native fruit trees were planted in addition to those listed in Table S3.1 (Face the Future, 2011). After the initial restoration effort, actively restored sites were then weeded every three months for three years (Moura Costa, 1996, Face the Future, 2011).

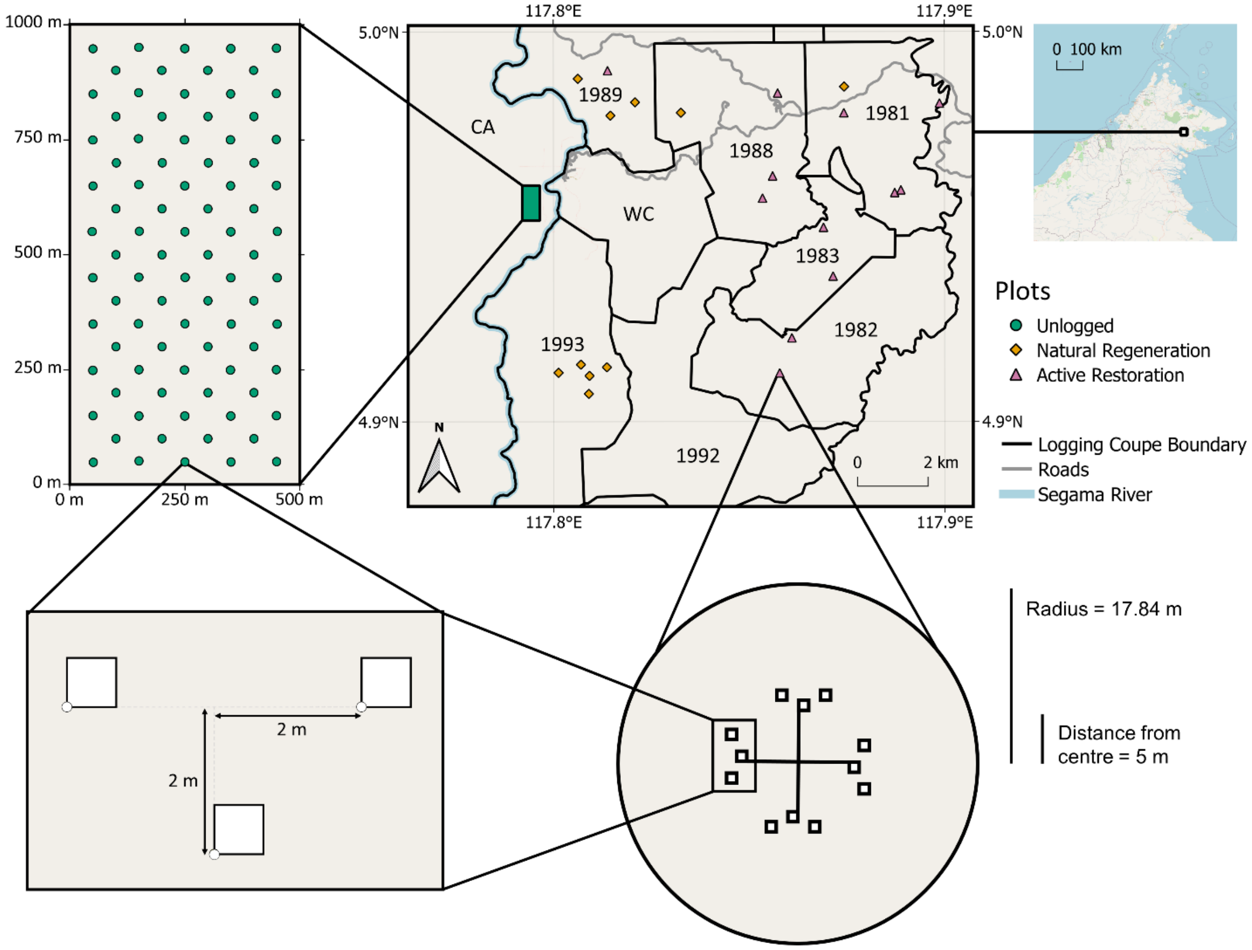


Figure 3.1 *Location of seedling plots in the Danum Valley Conservation Area and Ulu Segama Forest Reserve. Colours indicate logging and regeneration method (consistent throughout this paper). Coupes are labelled by logging year, WC (Water Catchment), or CA (Conservation Area). Access roads, which have been retained since logging, are shown in grey and the Segama River in blue. Locations of unlogged seedling stations are shown within the Forest Global Earth Observatory (ForestGEO) study area (rectangular inset). Arrangement of seedling stations, clustered in groups of four at logged forest plots, is shown within the radius of the mature tree census area (circular inset).*

3.3.2 Seedling censuses

Following the end of mast fruiting in August 2019, seedling communities were censused four times between September 2019 and March 2021 (census 1 at 1-2 months, census 2 at 3-4 months, census 3 at 5-6 months, and census 4 at 18-19 months post-mast). Censuses were carried out across 174 stations (86 unlogged, 40 naturally regenerating, and 48 actively restored; figure 3.1). Each station consisted of three 1x1 m quadrats, located 2 m from a central point in a T-shaped configuration (figure 3.1). At each census, all recently germinated seedlings were counted and identified with reference to collections held at the Danum Valley Herbarium, seedling mortality was assessed and census date was recorded. Where seedlings could not be identified to species, they were assigned to genera or to distinct morphospecies which were kept consistent between plots and censuses. At census 1, 75.9% of seedlings were identified to species and 88.4% to genus. In logged forest, stations were clustered in groups of four to maximise census efficiency.

3.3.3 Established tree census

Established trees (>20 cm DBH) were censused in plots surrounding each seedling station centroid (radius = 17.26 m, area = 1000 m^2) in 2016, as part of the Forest Global Earth Observatory (ForestGEO; Anderson-Teixeira et al., 2015) 50 ha plot and Indicators of Forest Sustainability (INDFORSUS; Foody and Cutler, 2003) projects. For each tree, stem diameter was measured and the precise location recorded. Stems were identified by collection of specimens, where possible, and with reference to collections held at the Danum Valley Field Centre Herbarium and the Forest Research Centre Herbarium, in Sepilok. Stems that remained unidentified were assigned to distinct morphospecies, which were consistent within the ForestGEO and INDFORSUS projects.

3.3.4 Canopy cover survey

To quantify exposure of seedlings to sunlight, canopy gap fractions immediately above each seedling station subplot (figure 3.1) were recorded between July and November 2018 by upwards-facing hemispherical photography. A Nikon D-7000 DSLR, equipped with a Jintu 180° fish-eye lens (8 mm, F 3.0), was used for all canopy photography and was held manually at a height of 1.3 m when recording (Origo et al., 2017). To ensure fidelity, the lens was kept clean and demisted immediately prior to each photograph. Photographs were taken during intervals without rain or direct sunlight, whenever possible, to avoid distortion or sunbursts in images. Where distortion or sunbursts were unavoidable and the seedling station was too remote to revisit within the field season, canopy data were not collected for that subplot. Canopy photos from each station subplot were processed to determine percentage gap fractions using Can-Eye version 6.495 (INRA, 2017) then averaged to give a mean canopy gap fraction for each seedling station.

3.3.5 Data analysis of seedling density

Seedling density (per 3 m^2 station) at census 1 was compared among unlogged (UL), naturally regenerating (NR), and actively restored (AR) logged forest by Mann-Whitney U test. The full seedling community, the dipterocarp seedling community, and the non-dipterocarp seedling community were analysed separately to explore the effects of logging and restoration on dipterocarps in comparison with non-dipterocarp tree species. This distinction was made because dipterocarps were targeted both for removal during logging and for planting during active restoration (Face the Future, 2011).

Trends in seedling density up to 1.5 years post-mast were explored by generalised linear mixed models (GLMMs) for plots where one or more seedlings were observed at any census. Models used generalised Poisson residuals to account for under-dispersion and a log link function (Consul and Famoye, 1992). Maximal models (equation 3.1; presented using syntax for the *glmmTMB* package in *R* (Brooks et al., 2017b)) were constructed to test for the effect of census date, restoration/logging treatment (UL vs NR vs AR), established community basal area (m^2; stems >20 cm DBH), and canopy gap fraction (%) (as fixed effects) on seedling density. Further maximal models for logged forest only (equation 3.2) were created with the addition of logging intensity (m^3 ha^{-1}) and time since logging as explanatory variables to explore effects of active restoration.

Eq. 3.1 *Seedling stem count ~ Census date * **(**Forest type + log(Canopy gap fraction) + sqrt(Established tree basal area)**)** + (1|Location/Station)*

Eq. 3.2 *Seedling stem count ~ Census date * **(**Forest type + log(Canopy gap fraction) + sqrt(Established tree basal area) + Logging intensity + Time since logging**)** + (1|Location/Station)*

Census date was measured in days since the start of census 1 and was log$_{10}$ transformed where AIC comparison of models with and without transformation suggested this would have a better fit. Interactions between date and all other variables were included in the maximal models to test which variables affected rates of seedling mortality post-mast across different treatments. Canopy gap fraction and established community basal area were transformed (log$_{10}$ and square root, respectively) to normal distributions and all continuous numeric variables were centred and scaled to zero mean and unit variance prior to modelling. Nested random effects of location and seedling station were included in the model to account for clustering of stations within the logged forest plots. Best models were then selected by using the *MuMin::dredge* function (Barton, 2009) to find the model with the lowest AIC or the fewest terms if AIC differed by less than two. Residual diagnostics and zero inflation were checked within the *DHARMa* package (Hartig and Hartig, 2017).

Due to low seedling numbers at census 4 and the long interval between censuses 3 and 4, exploration of community subsets (dipterocarp vs non-dipterocarp) could not be modelled over the full study period without introducing substantial uncertainty around the gradient of seedling density over time. We therefore present a model of full community seedling density only over 1.5 years (census 1-4; equation 3.1) as well as models of the full community, dipterocarps, and non-dipterocarps separately over the first six months post-mast, wherein the majority of seedling mortality is expected to occur (census 1-3; equations 3.1 & 3.2) (Itoh et al., 1995, Oshima et al., 2015).

Station-level seedling densities were plotted by census for species with over 100 individuals, and for significant indicator species (as derived below) with over 25 individuals, to visualise rates of survival and mortality between different logging and restoration treatments.

3.3.6 Data analysis of seedling community composition

Differences in community composition of seedlings between forest types (UL, NR, and AR) over the first six months post-mast (censuses 1-3) were analysed by permutational analysis of variance (PERMANOVA; 10,000 permutations) accounting for effects of date, time since logging, and logging intensity. Interactions were modelled between date and all other variables to test for differing trajectories of community change over time. Bray-Curtis dissimilarity was used as the metric for these analyses (Bray and Curtis, 1957) and all PERMANOVA were performed in the *vegan R* package (Oksanen, 2019).

Non-metric multidimensional scaling (NMDS) was used to explore Bray-Curtis dissimilarity of seedling station communities in more detail, as well as to compare visually those dissimilarities at census 1 and census 3. Census 4 had too few surviving stems for meaningful ordination of community dissimilarities. For use in NMDS, seedling communities were standardised by dividing species' seedling counts at each plot by the total count for that species across all plots, using the *decostand* function in *vegan* (Oksanen, 2019).

Indicator species analysis was performed for seedlings at each census to determine whether certain species were driving community differences between logging and restoration treatments. Indicator species were defined using the *multipatt* function of the *indicspecies* package in *R* (Cáceres and Legendre, 2009), whereby a significant indicator species is able to predict with 95% certainty the treatment in which it is located (Cáceres and Legendre, 2009). Where indicator species predict multiple treatments (e.g. unlogged and naturally regenerating forest), they predict with 95% certainty their absence in other treatments (e.g. actively restored forest) (Cáceres and Legendre, 2009).

3.4.0 Results

At census 1, a total of 5119 germinated seedlings were recorded across forest types (2847 in 86 unlogged plots (UL), 274 in 40 naturally regenerating plots (NR), and 1998 in 48 actively restored forest plots (AR)). Of these, 78.9% were dipterocarp seedlings (88.0% UL, 50.9% NR, and 79.2% AR). At census 3 (approximately six months post-mast), the total number of seedlings had declined to 1296 (25.3% of the original cohort, 964 = 33.9% UL, 114 = 41.6% NR, and 215 = 10.8% AR). Whilst the proportion of dipterocarps had stayed roughly the same across the whole dataset (80.9%), it had increased in UL forest (89.6%), and decreased in NR (36.8%) and AR (65.6%) forest. By census 4 (1.5 years post-mast), 190 seedlings remained (3.71% of the original cohort, 153 = 5.37% UL, 20 = 7.30% NR, and 17 = 0.85% AR) and the proportion of dipterocarps remained similar to census 3 (83.2% full dataset, 90.8% UL, 35.0% NR, and 70.6% AR). Total seedling morpho-species richness across all censuses was 63 (32 UL, 29 NR, and 31 AR), from 32 genera (17 UL, 18 NR, and 15 AR) and 16 families (10 UL, 11 NR, and 8 AR). Basal area of established trees (>20 cm DBH) and canopy density varied among forest types. Established trees had a median basal area of 12.51 m^2 ha^{-1} (238 dipterocarps, 87 non-dipterocarps total; median stem DBH = 39.5 cm) in UL, 3.34 m^2 ha^{-1} (80 dipterocarps, 8 non-dipterocarps; median DBH = 31.5 cm) in NR, and 5.84 m^2 ha^{-1} (156 dipterocarps, 16 non-dipterocarps; median DBH = 33.2 cm) in AR. Median canopy gap fraction was 3.03% (interquartile range = 2.00-4.94%) in UL, 3.76% (IQR = 2.31-7.20%) in NR, and 2.71% (IQR = 1.62-3.51%) in AR.

3.4.1 Effects of logging and restoration on seedling density

At census 1, median germinated seedling density (m^{-2}) was significantly higher in UL (median = 9.66, Mann-Whitney U = 3218, $p < 0.001$; figure 3.2, figure S3.1, & table S3.2) and AR forests (median = 8.33, U = 479, $p < 0.001$) than in NR forest (median = 1.33). Likewise, for dipterocarp seedlings, density was higher in UL (median = 8.33, U = 3319, $p < 0.001$) and AR (median = 4.33, U = 422, $p < 0.001$) than in NR forest (median = 0.33). There was no difference among forest types in density of non-dipterocarp seedlings (all medians ≤ 0.33, $p > 0.05$) and there was no difference between UL and AR forests in the seedling densities of dipterocarps, non-dipterocarps, or the full seedling community ($p > 0.05$).

For plots that contained at least one seedling in any census, GLMM predictions (figure 3.2, table 3.1) showed that, for most of the first 1.5 years post-logging, both naturally regenerating and actively restored logged forest had fewer seedlings present than unlogged forest. Seedling density in actively restored logged forest declined at a faster rate than in unlogged forest (see Date: Act. Rest. interaction term, $p < 0.001$; Table 3.1), such that restored forests had lower average seedling density than other forest types by census 4, despite having the highest density of germinated seedlings immediately post-mast (figure 3.2). In contrast, seedling densities in unlogged and naturally regenerating forests declined at similar rates (see Table 3.1, Date: Nat. Regen. interaction term, p = 0.454).

Table 3.1 *GLMM model summary for the effects of logging and restoration treatment (naturally regenerating/actively restored) and time since masting as predictors of seedling density following the 2019 masting event at Danum Valley. All numeric independent variables are centred and scaled. The best model was selected using the R MuMIn dredge function (Barton, 2009). Where variables were not selected as part of the best model, they are still listed but value columns are filled by '-'. Station variance (a nested random effect of different seedling stations at each plot location) was 0.344 and model* R^2 *values were 0.900 (conditional) and 0.707 (marginal).*

	Estimate	**Error**	**Z-value**	**P-value**
Seedling density (m^{-2})				
(intercept)	2.548	0.079	32.26	<0.001***
Nat. Regen.	-0.898	0.177	-5.07	<0.001***
Act. Rest	-0.405	0.151	-2.68	0.007**
Log(Census date)	-0.754	0.027	-27.59	<0.001***
Log(Canopy gap fraction)	-0.079	0.059	-1.33	0.183
Sqrt(Established tree basal area)	0.047	0.063	0.75	0.453
Date:Nat.Regen.	0.076	0.101	0.75	0.454
Date:Act.Rest.	-1.148	0.082	-13.96	<0.001***
Date:log(Canopy gap fraction)	-	-	-	-
Date:sqrt(Est. tree basal)	-	-	-	-

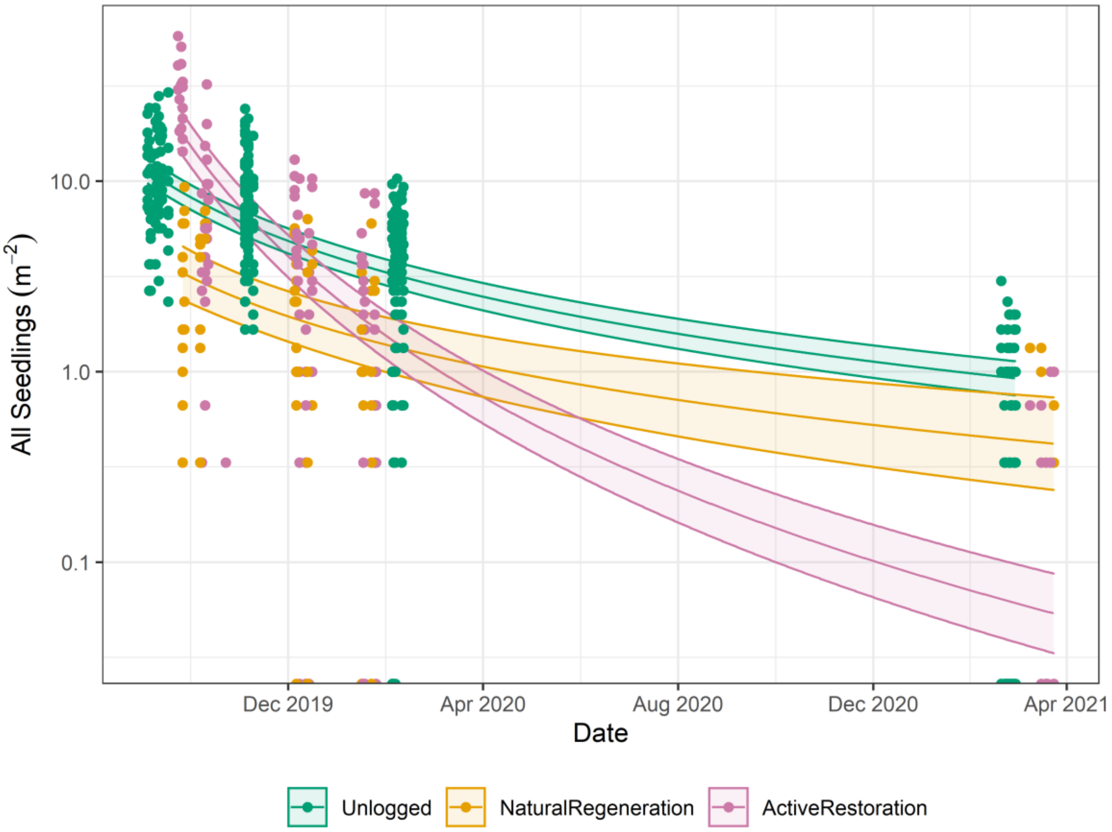


Figure 3.2 *GLMM predictions and standard errors for density of all seedlings per m^2 at censuses 1-4, taking into account all variables retained within the best model (table 3.1). The model compares seedling density over time in unlogged, naturally regenerating, and actively restored logged forest plots where at least one seedling was present in any census. Zero values occur as a result of complete mortality, or first germination of seedlings in later censuses.*

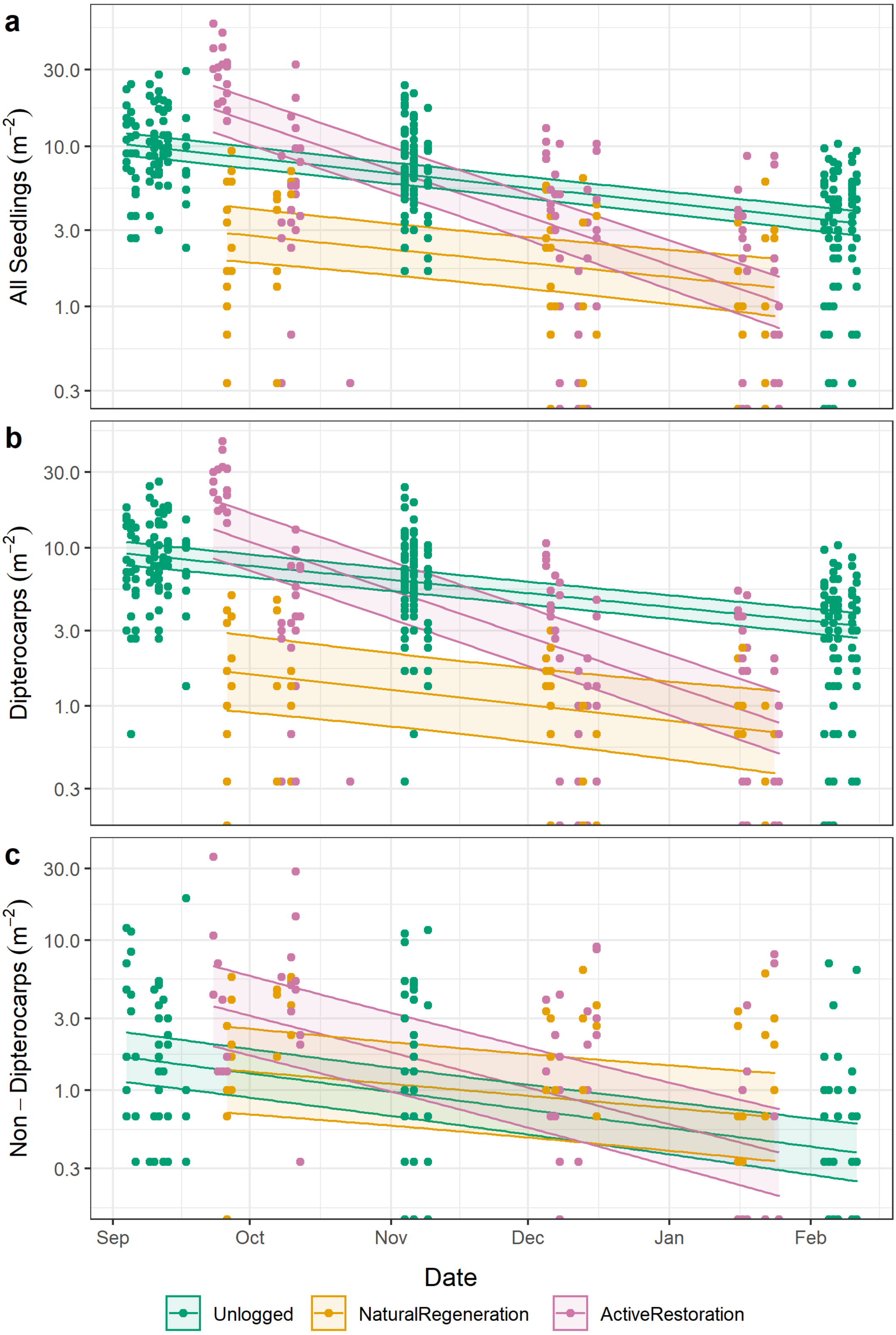


Figure 3.3 *Seedling densities of a) all seedlings, b) dipterocarp seedlings, and c) non-dipterocarp seedlings per m^2 at censuses 1-3. Lines indicate GLMM predictions and standard errors, using average values for covariates retained within best models (table S3.3). Models compare seedling density over time in unlogged, naturally regenerating, and actively restored logged forest plots where at least one seedling was present in any census. Zero values occur as a result of complete mortality, or first germination of seedlings in later censuses.*

More targeted GLMMs to assess changes in seedling density over the first six months post-mast (censuses 1, 2, and 3) indicate that differences in seedling density and mortality among forest types were evident soon after germination (figure 3.3 & table S3.3). Seedling density was, on average, greater in UL than in NR ($p < 0.001$) but was not significantly different from AR forest ($p = 0.094$; figure 3.3 & table S3.3). However, seedling density declined more rapidly in AR than in UL (interaction term $p < 0.001$; figure 3.3 & table S3.3), resulting in seedling densities in AR that were higher than UL immediately post mast, but lower than UL after six months. Despite significantly lower seedling densities in NR than UL across censuses, the rate at which seedlings in these forest types declined could not be statistically distinguished ($p = 0.681$; figure 3.3 & table S3.3). Both NR and AR forest had fewer dipterocarp seedlings than UL forest on average ($p < 0.001$ and $p = 0.020$), and the density of dipterocarp seedlings in AR plots declined faster than in UL forest (negative interaction term $p < 0.001$) so that by census 4 dipterocarp density was similar in NR and AR forests, while NR declined at the same rate as in UL forest (interaction term $p = 0.698$, figure 3.3 & table S3.3). This rapid decline of seedlings in the AR forest appears to be largely driven by the disproportionately high percentage mortality of the two most common species between censuses 1 & 2: *Shorea parvifolia* (UL = 27% of seedlings at census 1 died by census 2, NR = 33%, AR = 84%) and *Shorea johorensis* (UL = 18%, NR = 100%, AR = 86%) (figure 3.4). Non-dipterocarp seedling density was, on average, not significantly different across forest types ($p > 0.05$) but declined more quickly in AR than UL forest or NR forest (interaction terms $p < 0.001$), while rates of decline in UL and NR seedling density did not differ (interaction term $p = 0.122$; Figure 3.3 & Table S3.3).

3.4.2 Effects of biotic & environmental variables on seedling density in logged forest

In logged forest, GLMMs showed that seedling density was sensitive to the basal area of established stems (>20 cm DBH) of species present in the seedling community. More dipterocarp seedlings were found in plots with higher basal areas of established dipterocarps (estimate = 0.193, $p = 0.009$; Table S3.3), while fewer non-dipterocarp seedlings were found in plots with higher basal area of established non-dipterocarp trees (estimate = -0.324, $p = 0.015$; Table S3.3). Greater canopy gap fraction was associated

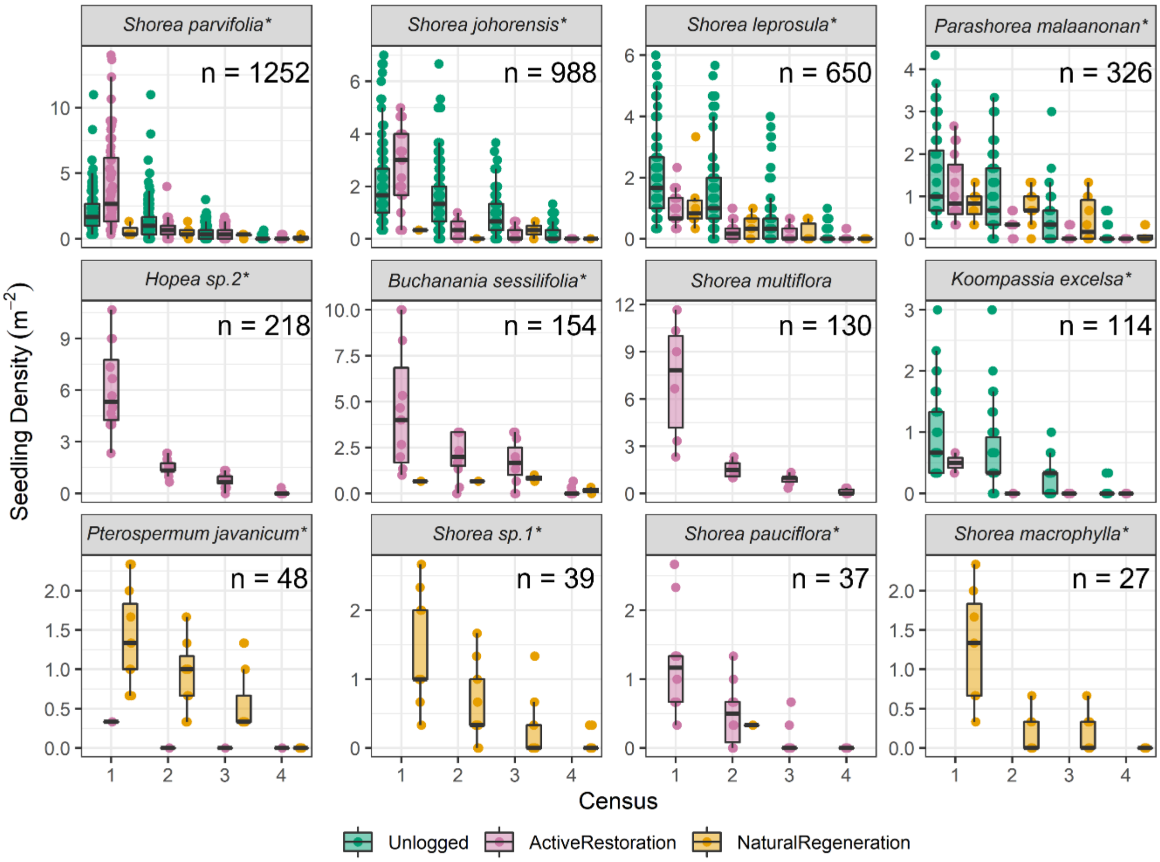


Figure 3.4 *Seedling stem counts of species from plots where n > 1 for that species across all censuses. Panels show identified indicator species with > 25 stems in a single census (marked *) and all species with > 100 stems in a single census. Species are presented in descending order of abundance at the census in which they are most common (n).*

with greater decline of seedlings over time (interaction term estimate = -0.091, p = 0.037; table S3.3 & figure S3.2). Non-dipterocarp seedlings showed greater declines in forests with greater time since logging (p = 0.027), however there were no significant effects of time since logging for dipterocarps or the full seedling community. Logging intensity (m^3 ha^{-1} timber harvest) was not retained in any best model.

3.4.3 Effects of logging and restoration on seedling community composition

Across censuses, seedling community composition differed significantly among forest types (PERMANOVA; p < 0.001; table 3.2). Community composition also changed over time across all treatments (p < 0.001). In comparisons of seedling communities between forest types, there was significant interaction between date and forest type (p = 0.043, 0.040, and 0.003, for UL vs NR, UL vs AR, and NR vs AR respectively), indicating that the similarity of these communities changed over time due to processes that occurred post-germination. In actively restored and naturally regenerating forests, PERMANOVA showed significant effects of logging year (time since logging, $p < 0.001$) and logging intensity ($p < 0.001$) on seedling community composition. These variables had no interaction with date ($p = 0.284$ and 0.286 respectively) and therefore had no effect on seedling community trajectory after germination.

Table 3.2 *Results of PERMANOVA tests (10,000 permutations) showing the effect of forest type (unlogged forest, naturally regenerating logged forest, or actively restored logged forest), and date of census on seedling community composition over the first six months post-mast.*

	R^2	**F**	**df**	**p**
Unlogged vs Natural Regeneration				
Date	0.018	6.635	1	<0.001***
Forest Type	0.084	30.369	1	<0.001***
Date : Forest Type	0.005	1.845	1	0.043*
Unlogged vs Active Restoration				
Date	0.026	9.945	1	<0.001***
Forest Type	0.051	19.548	1	<0.001***
Date : Forest Type	0.005	1.903	1	0.040*
Natural Regeneration vs Active Restoration				
Date	0.016	3.188	1	<0.001***
Forest Type	0.050	10.034	1	<0.001***
Logging Year	0.034	6.855	1	<0.001***
Logging Intensity	0.028	5.566	1	<0.001***
Date : Forest Type	0.010	2.056	1	0.003**
Date : Logging Year	0.006	1.138	1	0.284
Date : Logging Intensity	0.006	1.133	1	0.286

Community differences between censuses 1 and 3 are illustrated in the NMDS (figure 3.5, figure S3.3), which also highlights retention of relatively high plot-level species richness within unlogged plots (median richnesses at census 1 & census 3 were 3 & 2 in UL, 1 & 1 in NR, and 2.5 & 1 in AR). At census 1, the majority of unlogged plots contained relatively similar seedling communities that were distinct from those in logged forests. Seedling communities in actively restored forest appeared to show high inter-plot dissimilarity and had limited overlap with other forest types. By census 3, however, reduced seedling numbers and species richness in actively restored forest (figure 3.3 & table S3.3), caused greater community overlap with naturally regenerating plots and reduced similarity with unlogged seedling communities (figure 3.5).

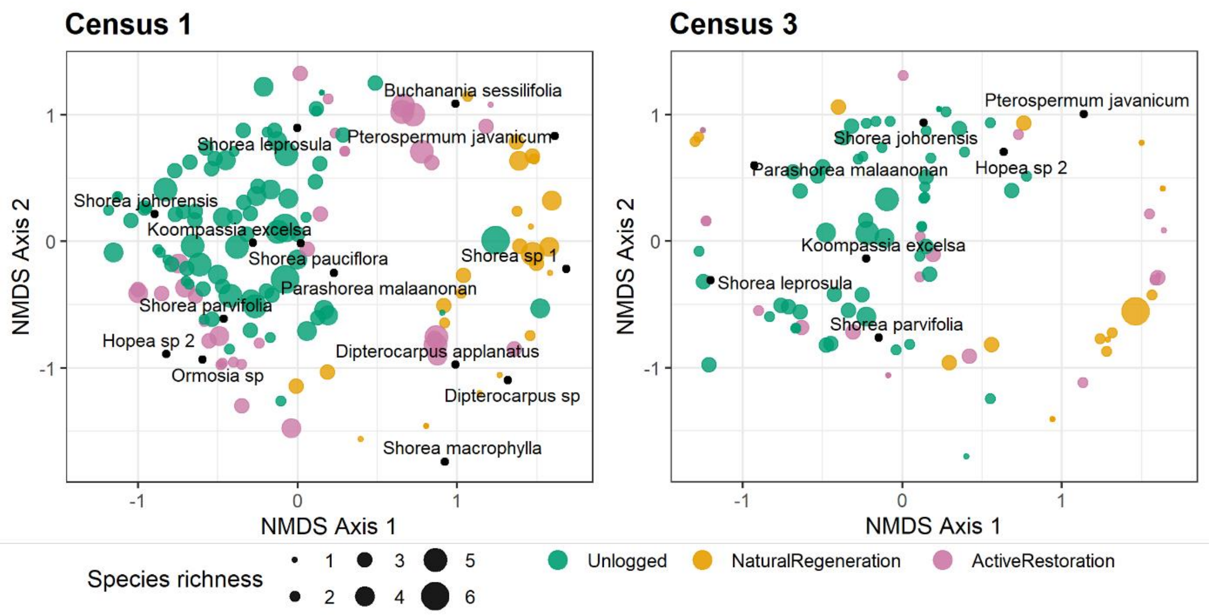


Figure 3.5 *NMDS for seedling communities in unlogged, naturally regenerating logged, and actively restored logged forest at census 1 and census 3. For each census, significant indicator species (table 3.2) have been plotted. Plots are scaled by species richness and coloured by logging and restoration history.*

Differences between initial seedling community compositions and those recorded after six months reflected patterns of variation in indicator species abundances (Table 3.3). Across censuses, there was some overlap between indicator species of unlogged and actively restored forest, but no mutual indicators of naturally regenerating logged forest with actively restored forest. At census 3, *Parashorea malaanonan* was mutually indicative of unlogged and naturally regenerating forest (p = 0.039), however, by census 4 it was indicative solely of unlogged forest (p = 0.043). Of the mutual indicators of unlogged and actively restored forest (*P. malaanonan*, *S. johorensis*, *S. leprosula*, and *S. parvifolia*; table 3.3), only *S. parvifolia* was retained as an indicator of both forest types past census 1 (p < 0.001), despite exhibiting high mortality in actively restored forest (figure 3.5). In census 2 and census 3, *S. johorensis* and *S. leprosula* were indicators for unlogged forest only (p < 0.001). Across censuses 1-3, *Koompassia excelsa* was a significant indicator species of unlogged forest, *Buchanania sessilifolia* was a significant indicator species of actively restored forest, and *Pterospermum javanicum* was a significant indicator of naturally regenerating forest (table 3.3).

Table 3.3 *Significant indicator species (Cáceres and Legendre, 2009) of seedling communities in unlogged forest, naturally regenerating logged forest, and actively restored logged forest. Unique unidentified morphospecies are labelled as 'sp.' with a numeric suffix where there are multiple unresolved species within a genus. Species are marked '✓' which may be harvested for timber (Mark et al., 2014) or which were planted as part of the active restoration treatment (Face the Future, 2011).*

Treatment	**Family**	**Indicator species**	**Timber species**	**Planted species**	**Indicator p-value at census**			
					Census 1	**Census 2**	**Census 3**	**Census 4**
Unlogged								
	Dipterocarpaceae	*Shorea johorensis*	✓	✓	-	<0.001***	<0.001***	<0.001***
		Shorea leprosula	✓	✓	-	<0.001***	<0.001***	-
		Parashorea malaanonan	✓	✓	-	-	-	0.043*
	Fabaceae	*Koompassia excelsa*	✓	✓	<0.001***	<0.001***	<0.001***	-
Natural Regeneration								
	Dipterocarpaceae	*Shorea macrophylla*	-	✓	0.012*	-	-	-
		Shorea sp.1	-	-	<0.001***	<0.001***	-	-
	Malvaceae	*Pterospermum javanicum*	✓	-	0.004**	0.003**	0.003**	-
	Sapindaceae	*Dimocarpus dentatus*	-	-	-	0.049*	-	-
Active Restoration								
	Anacardiaceae	*Buchanania sessilifolia*	-	-	0.014*	0.011*	0.030*	-
	Dipterocarpaceae	*Dipterocarpus applanatus*	-	✓	0.032*	-	-	-
		Hopea sp.2	-	-	0.008**	0.008**	0.008**	-
		Shorea pauciflora	✓	✓	<0.001***	0.016*	-	-
	Fabaceae	*Ormosia sp.*	-	-	0.031*	-	-	-
		Intsia palembanica	✓	✓	-	0.034*	-	-
Unlogged or Natural Regeneration								
	Dipterocarpaceae	*Parashorea malaanonan*	✓	✓	-	-	0.039*	-
Unlogged or Active Restoration								
	Dipterocarpaceae	*Parashorea malaanonan*	✓	✓	0.028*	-	-	-
		Shorea johorensis	✓	✓	<0.001***	-	-	-
		Shorea leprosula	✓	✓	<0.001***	-	-	-
		Shorea parvifolia	✓	✓	<0.001***	<0.001***	<0.001***	-
Natural Regeneration or Active Restoration								
	No indicators at any census		-	-	-	-	-	-

3.5.0 Discussion

Our results reveal differences in seedling density over time across unlogged, naturally regenerating, and actively restored forest types in the 1.5 years following a mast fruiting event. More seedlings germinated in unlogged and actively restored logged forest than in naturally regenerating logged forest. However subsequent seedling mortality was significantly higher in actively restored forest than in the other two forest types, and overall seedling survival at 1.5 years was just 3.7% of the initial cohort. As a result, seedling density in actively restored forest was lower than in other forest types by 1.5 years post-mast. The negative association between logging, restoration and seedling survival was greater for dipterocarp seedlings than non-dipterocarp seedlings, and in logged forest dipterocarp seedling survival was lower under more open canopies, compared with non-dipterocarps, which were not affected. Seedling community composition varied between all forest types and changed over time.

3.5.1 Initial seedling density and community composition

At census 1, shortly post-mast, an order of magnitude more seedlings were found in unlogged forest than in naturally regenerating logged forest. This matches findings from Indonesia, where unlogged forest had four times more dipterocarp seedlings than logged forest following a mast fruiting (Curran and Webb, 2000). We found that actively restored forest had a similar number of seedlings as unlogged forest, indicating that active restoration strategies may successfully increase seed production in these forests, potentially by replacing parent trees or restoring the conditions required for remnant trees to successfully mast. Community composition of seedlings at census 1 likewise differed among forests, although unlogged forest had greater similarity to actively restored than naturally regenerating forest (figure 3.5). Differences in initial seedling density and community composition are likely products of variations in seed production, seed predation, and seed germination.

Higher densities of parent trees result in greater seed production in unlogged than selectively logged Bornean forests (Curran and Webb, 2000, Bagchi et al., 2011). Within the Danum Valley landscape, stem density and basal area of established trees (>20 cm DBH) were greatest in unlogged forest and lowest in naturally regenerating logged forest (Hayward et al., 2021), supporting the concept that seed production is related to biomass and density of parent trees. Dipterocarps comprised 79% of seedlings at census 1, across all forest types. This is likely due to the high proportion of dipterocarps within the established tree community (Hayward et al., 2021) and the prevalence of mast fruiting as a reproductive strategy within Dipterocarpaceae, compared to other families (Curran et al., 1999).

Seed predation may further influence initial differences in seedling density between forest types, if logging and active restoration practices affect predator distributions or activity. Previous studies from Borneo suggest that ungulate seed predators in logged forests may be more sensitive to mast than those in unlogged forest, responding earlier, more intensively, and in larger groups to the availability of food (Curran and Webb, 2000, Brodie et al., 2015, Davison et al., 2019). Where some vertebrate seed predators – particularly birds – may be less abundant in logged forest (Burivalova et al., 2015), a recent experiment in Danum Valley suggests this may be compensated for by increased seed mortality from insects and fungi, resulting in no net difference across forest types (Williams et al., 2021). Thus absolute seed predation may be unlikely to drive local variation in initial seedling density but predation relative to the fruited population size may vary if the mast event is unable to satiate predators at a landscape scale (Curran and Webb, 2000).

Germination rates for unpredated seeds are high in Southeast Asian rain forests (Curran and Webb, 2000, McConkey, 2005). Dipterocarps especially have large seeds that germinate rapidly and are less affected by site specific resource limitation than smaller seeded species (Foster, 1986, Brown et al., 1992, Pinard et al., 1996). Thus the effects on germination of differing resource availabilities across forest types, such as increased light availability through canopy gaps in logged forest, may potentially be species dependent, with larger impacts on germination rates of smaller-seeded, non-dipterocarp species (Bebber et al., 2002b, O'Brien et al., 2013).

Differences in seedling community composition at census 1 were primarily driven by the dipterocarp seedling community, and particularly the four most common species: *S. parvifolia*, *S. johorensis*, *S. leprosula*, and *P. malaanonan*. These species were all significant indicator species for unlogged and actively restored forest and were planted in active restoration (Face the Future, 2011) suggesting that enrichment planting can lead to continued recruitment of target species in subsequent generations. Not all species planted during active restoration were successful in producing offspring during the mast however, as evidenced by *K. excelsa*, which was an indicator of only unlogged forest despite being planted during active restoration efforts. This pattern might be because slow growing species planted during restoration, such as *K. excelsa*, have not yet attained reproductive maturity or because some planted species have failed to successfully recruit due to local environmental conditions (Charles et al., 2018, Kardiman et al., 2019, Minh Quang et al., 2020).

Unlike dipterocarps, non-dipterocarp seedling densities did not vary with forest type. This suggests that any reduction in densities of non-dipterocarp adult trees that took place when the forests were logged has been compensated by recruitment of a new tree community – although not necessarily from the same non-dipterocarp species – that is now supplying seeds in equivalent numbers during a masting event.

3.5.2 Trajectories of seedling survival and community composition

Seedling densities initially declined rapidly across all forest types. Two previous studies from Malaysian Borneo reported high dipterocarp mortality (60-90% and 25-70% per species) in the seven months immediately post mast (Itoh et al., 1995, Oshima et al., 2015). This is consistent with our finding of 66.1% mortality over the first six months post-mast in unlogged forest and covers approximately the same period for which dipterocarp seedlings remain reliant on cotyledons for photosynthesis (Itoh et al., 1995).

Actively restored logged forest had a significantly greater rate of seedling loss than unlogged or naturally regenerating logged forest. Thus, despite having higher seedling densities in census 1, actively restored forest had similar numbers of seedlings to naturally regenerating forest by census 3 and the fewest seedlings of all forest types by census 4. In contrast, seedling declines did not differ between unlogged and naturally regenerating forest, which has been reported elsewhere in Borneo (Curran and Webb, 2000). These results suggest that the elevated seedling declines in actively restored forest are unique to this forest type and not due to logging. While dipterocarps and non-dipterocarps both declined more rapidly in actively restored logged forest than in either other forest type, this difference was more pronounced amongst dipterocarp stems (figure 3.2) and was exemplified by the three most abundant species, which accounted for >40% of seedlings at census 1: *S. johorensis*, *S. leprosula*, and *P. malaanonan*.

These species were all planted as part of active restoration strategies (Face the Future, 2011) and, at census 1, were indicators of both unlogged and actively restored forest, suggesting that restoration techniques had successfully resulted in their masting and germination. However, by census 4, *S. johorensis* and *P. malaanonan* were solely indicators of unlogged forest, suggesting that those germinated seedlings were unable to successfully recruit in actively restored logged forest. Higher rates of decline in seedling density in restored forest may be due to increased seedling predation rates, low genetic diversity of seedlings, and/or shifts in local environmental conditions.

Intense seed and seedling predation immediately after mast fruiting drives early mass mortality of seedlings (Curran and Webb, 2000). However, the high seedling densities observed in unlogged forest in this study and previously at Danum, should ensure predator satiation thus reducing seedling mortality (Janzen, 1971, Still, 1993, Curran and Webb, 2000). Despite greater seed production and germination in actively restored forest than either unlogged or naturally regenerating forest however, the steep decline in seedling density suggests that predator satiation may not have occurred in this forest. Restored forests tend to be embedded in larger areas of naturally regenerating logged forest, which produce few seeds. This high predation of seedlings in restored areas may be driven by mobile seed predators being particularly attracted to areas of high seedling density (Hautier et al., 2010). Seed predators may choose to remain in restored areas, which retain higher food availability than the surrounding naturally regenerating forest, instead of moving on to new areas as would typically be the case in unlogged forest (Curran and Leighton, 2000). As such, actively restored forests may potentially be victims of their own successfully increased fecundity.

High seedling mortality in actively restored forest could be further exacerbated by low genetic diversity amongst parent trees (Nutt et al., 2016, Tito de Morais et al., 2020). Seedlings planted during active restoration are often collected from a small number of parent trees (Nef et al., 2021). In Danum, planted stems were grown in nurseries from seeds and cuttings, likely collected from a relatively small and accessible group of parent trees (Face the Future, 2011). Assuming some of those stems have since matured sufficiently to produce seeds (as seems likely, based on the high initial density of masted seedlings in restored forest), this suggests that masted seedlings in actively restored forest could have low genetic diversity. Previous studies from Sabah show that low genetic diversity can reduce seedling survival, possibly due to shared vulnerability of closely related seedlings to pathogens (Nutt et al., 2016, Tito de Morais et al., 2020). Dipterocarp seedlings especially would be expected to have low diversity due to their short pollination ranges leading to high rates of inbreeding amongst planted parent trees (Kettle et al., 2011).

Logged forests exhibit hotter and more variable microclimates than unlogged forests (Hardwick et al., 2015, Fauset et al., 2017, Blonder et al., 2018), and indeed we recorded the greatest canopy gap fractions at Danum in naturally regenerating forest, making seedlings more vulnerable to droughts such as the one that both preceded and overlapped our recorded mast period in 2019 (Woods, 1989, Qie et al., 2019). As a result, germinated seedlings face additional thermal and hydraulic stress and may require greater availability of resources (or increased competitiveness to acquire resources) to invest in the production of non-structural carbohydrates for maintenance of high stem water potentials and hydraulic functioning (O’Brien et al., 2014, Adams et al., 2017). In the case of actively restored forests, drought has been shown previously in Borneo to temporarily reduce the effects of liberation cutting, from which logged forest seedlings would typically be expected to benefit (O'Brien et al., 2019). Dipterocarp seedling declines may be particularly related to drought conditions as water stress puts them at higher risk of mortality after damage from herbivores (Curran and Webb, 2000). Previous studies from Borneo show that dipterocarp seedlings are more likely to die after root or leaf damage from invertebrate attacks during drought than after rain (Bebber et al., 2002a, Bebber et al., 2004). Thus, shifting climates may interact with other factors such as canopy openness, herbivory, and initial seedling community composition to limit seedling recruitment in logged forests.

3.6.0 Summary

We find evidence that active restoration of a selectively logged forest in Sabah, Borneo, has enabled greater seed production and germination than naturally regenerating logged forest and a similar mast intensity to unlogged forest. However, we show that, subsequent to germination, actively restored forest seedling populations exhibit high mortality compared to unlogged forest. This could risk recruitment failure in actively restored logged forests, especially amongst dipterocarps, despite an initially successful mast. As a result, seedling community compositions diverge between forest types after germination. We suggest that the mechanisms limiting seedling survival in actively restored forest could be a combination of high seed predator pressure, low genetic diversity, and increased susceptibility to drought and microclimatic stress. Further research is needed to understand the mechanisms that drive increased seedling mortality in restored forest systems to support restoration practitioners with the long-term management of selectively logged forests.

3.7.0 Acknowledgements

We are grateful to the Sabah Biodiversity Centre and the Danum Valley Management Committee for permitting us to complete this research; to Tambi Karolus and the SEARRP 50 ha team for their hard work conducting rapid seedling censuses at short notice over a wide landscape; and to Mikey O’Brien for his assistance coordinating these efforts. This research was supported by an Iapetus DTP studentship (R.M.H.) and urgency grant (NE/T006552/1 to D.F.R.P.B., L.F.B., D.H.D, and Dr Lucy Rowland) from the UKRI Natural Environment Research Council as well as the Arnold Arboretum Ashton Award (R.M.H.).

3.8.0 Supplementary materials

Table S3.1 *Species planted in actively restored logged plots within the INFAPRO network (Face the Future, 2011)*

Dipterocarps	**Non-Dipterocarp Hardwoods**	**Fruit Trees**	**Other Trees**
Dipterocarpus applanatus *Dipterocarpus caudiferus* *Dipterocarpus acutangulus* *Dipterocarpus confertus* *Dipterocarpus conformis* *Dipterocarpus gracilis* *Dipterocarpus lowii* *Dryobalanops beccarii* *Dryobalanops keithii* *Dryobalanops lanceolata* *Hopea beccariana* *Hopea dryobalanoides* *Hopea ferruginea* *Hopea nervosa* *Hopea nutans* *Hopea pentanervia* *Hopea sangal* *Hopea spp.* *Parashorea malaanonan* *Parashorea smythiesii* *Parashorea tomentella* *Shorea acuminatissima* *Shorea agami* *Shorea argentifolia* *Shorea beccariana* *Shorea faguetiana* *Shorea falciferoides* *Shorea fallax* *Shorea flaviflora* *Shorea gibbosa* *Shorea guiso* *Shorea johorensis* *Shorea laevis* *Shorea leprosula* *Shorea leptoderma* *Shorea macroptera* *Shorea macrophylla* *Shorea mecistopteryx* *Shorea ovalis* *Shorea parvifolia* *Shorea parvistipulata* *Shorea pauciflora* *Shorea pilosa* *Shorea pinanga* *Shorea seminis* *Shorea smithiana* *Shorea superba* *Shorea symingtonii* *Vatica albiramis* *Vatica dulitensis*	*Azadirachta excelsa* *Eusideroxylon zwageri* *Intsia palembanica*	*Aglaia squamulosa* *Alangium javanicum* *Allophylus cobbe* *Artocarpus integer* *Baccaurea angulata* *Baccaurea latifolia* *Dimocarpus longan* *Diospyros spp.* *Durio spp.* *Garcinia parvifolia* *Lansium domesticum* *Nephelium lappaceum* *Nephelium mutabile* *Parartocarpus spp.* *Walsura pinnata*	*Agathis borneensis* *Aquilaria sinensis* *Duabanga moluccana* *Koompassia excelsa* *Neolamarckia cadamba* *Octomelis sumatrana* *Palaquium spp.* *Scaphium macropodum*

Table S3.2 *Mann-Whitney U tests of seedling frequency in comparison across unlogged forest, naturally regenerating logged forest, and actively restored logged forest at first census after germination. Tests were performed across the full seedling community, for dipterocarp seedlings only, and for non-dipterocarp seedlings only. Results where p < 0.001 are labelled '***'.*

	All Seedlings		**Dipterocarps**		**Non-Dipterocarps**	
Comparison	U	P	U	P	U	P
Unlogged *vs* Nat. Regen.	3218	<0.001***	3319	<0.001***	1733	0.856
Unlogged *vs* Act. Rest.	2235	0.363	2415	0.079	2043	0.992
Nat. Regen. *vs* Act. Rest	479	<0.001***	422	<0.001***	928	0.770

Table S3.3 *GLMM model summaries for the effects of logging and restoration treatment (naturally regenerating/ actively restored) and time since masting as predictors of Dipterocarpaceae and total community stem densities in the 2019 masting event at Danum Valley. All numeric independent variables are centred and scaled. Site variance is the variance explained by the random effect of plot location and station variance is a nested random effect of different seedling stations at each plot location. Best models were selected using the R MuMIn dredge function (Barton, 2009). Where variables were not selected as part of the minimum adequate model, they are still listed but value columns are filled by '-'. Models 1 and 2 use data from censuses 1-3 in equations 3.1 and 3.2 respectively. Model 3 uses data from censuses 1-4 in equation 3.1.*

	Estimate	**Error**	**Z-value**	**P-value**	**Site Variance**	**Nested Variance**
Model 1 (Unlogged vs. Natural Regeneration vs. Active Restoration)						
All Seedlings					0.131	0.233
(intercept)	2.892	0.076	38.11	<0.001***		
Logged (Nat. Regen.)	-1.084	0.204	-5.32	<0.001***		
Logged (Act. Rest)	-0.304	0.182	-1.67	0.094		
Date	-0.379	0.021	- 18.02	<0.001***		
Log(mean_gap_fraction)	-0.108	0.063	-1.70	0.089		
Sqrt(mature basal area)	-	-	-	-		
Date:Nat.Regen.	0.033	0.079	0.41	0.681		
Date:Act.Rest.	-0.852	0.053	-15.97	<0.001***		
Date:log(gap_fraction)	-0.042	0.020	-2.08	0.037*		
Date:sqrt(mat. basal)	-	-	-	-		
Dipterocarp Seedlings					0.274	0.140
(intercept)	2.676	0.084	31.89	<0.001***		
Logged (Nat. Regen.)	-1.618	0.278	-5.82	<0.001***		
Logged (Act. Rest)	-0.516	0.222	-2.33	0.020*		
Date	-0.364	0.021	-17.75	<0.001***		
Log(mean_gap_fraction)	-0.011	0.066	-0.16	0.870		
Sqrt(mature basal area)	0.193	0.074	2.61	0.009**		
Date:Nat.Regen.	-0.044	0.114	-0.39	0.698		
Date:Act.Rest.	-0.903	0.054	-16.61	<0.001***		
Date:log(gap_fraction)	-	-	-	-		
Date:sqrt(mat. basal)	-	-	-	-		
Non-Dipterocarp Seedlings					0.193	0.590
(intercept)	1.145	0.174	6.58	<0.001***		
Logged (Nat. Regen.)	0.191	0.339	0.56	0.574		
Logged (Act. Rest)	0.401	0.324	1.24	0.215		
Date	-0.505	0.059	-8.50	<0.001***		
Log(mean_gap_fraction)	-0.102	0.125	-0.81	0.416		
Sqrt(mature basal area)	-0.324	0.134	-2.43	0.015*		

Date:Nat.Regen.	0.169	0.110	1.55	0.122		
Date:Act.Rest.	-0.497	0.107	-4.63	<0.001***		
Date:log(gap_fraction)	-	-	-	-		
Date:sqrt(mat. basal)	-	-	-	-		
Model 2 (Natural Regeneration vs. Active Restoration)						
All Seedlings					0.301	0.236
(intercept)	1.867	0.257	7.25	<0.001***		
Act. Rest.	0.467	0.349	1.34	0.181		
Date	-0.258	0.072	-3.61	<0.001***		
Log(mean_gap_fraction)	-0.308	0.126	-2.45	0.014		
Sqrt(mat. Basal area)	-	-	-	-		
Logging intensity	-	-	-	-		
Years since logging	-	-	-	-		
Date:Act.Rest	-0.781	0.094	-8.29	<0.001***		
Date:log(gap fraction)	-0.094	0.041	-2.32	0.021*		
Date:sqrt(basal)	-	-	-	-		
Date:logging_intensity	-	-	-	-		
Date:years_since_logging	-	-	-	-		
Dipterocarp Seedlings					0.410	0.149
(intercept)	1.348	0.407	3.31	<0.001***		
Act. Rest.	0.330	0.579	0.57	0.569		
Date	-0.268	0.100	-2.68	0.007**		
Log(mean_gap_fraction)	-0.020	0.130	-0.16	0.877		
Sqrt(mat. Basal area)	0.600	0.212	2.83	0.005**		
Logging intensity	-	-	-	-		
Years since logging	0.279	0.274	1.02	0.310		
Date:Act.Rest	-0.817	0.121	-6.77	<0.001***		
Date:log(gap fraction)	-0.091	0.044	-2.09	0.037*		
Date:sqrt(basal)	-	-	-	-		
Date:logging_intensity	-	-	-	-		
Date:years_since_logging	-	-	-	-		
Non-Dipterocarp Seedlings					0.177	0.483
(intercept)	1.676	0.287	5.84	<0.001***		
Act. Rest.	-0.406	0.451	-0.90	0.368		
Date	-0.231	0.086	-2.69	0.007**		
Log(mean_gap_fraction)	-0.208	0.191	-1.09	0.278		
Sqrt(mat. Basal area)	-	-	-	-		
Logging intensity	-	-	-	-		
Years since logging	0.298	0.237	1.26	0.208		
Date:Act.Rest	-0.680	0.130	-5.24	<0.001***		
Date:log(gap fraction)	-	-	-	-		
Date:sqrt(basal)	-	-	-	-		
Date:logging_intensity	-	-	-	-		
Date:years_since_logging	0.148	0.067	2.21	0.027*		
Model 3 (Unlogged vs. Natural Regeneration vs. Active Restoration; including Census 4)						
All Seedlings					-	0.344
(intercept)	2.548	0.079	32.26	<0.001***		
Logged (Nat. Regen.)	-0.898	0.177	-5.07	<0.001***		
Logged (Act. Rest)	-0.405	0.151	-2.68	0.007**		
Log(Date)	-0.754	0.027	-27.59	<0.001***		
Log(mean_gap_fraction)	-0.079	0.059	-1.33	0.183		
Sqrt(mature basal area)	0.047	0.063	0.75	0.453		
Log(Date):Nat.Regen.	0.076	0.101	0.75	0.454		
Log(Date):Act.Rest.	-1.148	0.082	-13.96	<0.001***		
Log(Date):log(gap_fraction)	-	-	-	-		
Log(Date):sqrt(mat. basal)	-	-	-	-		

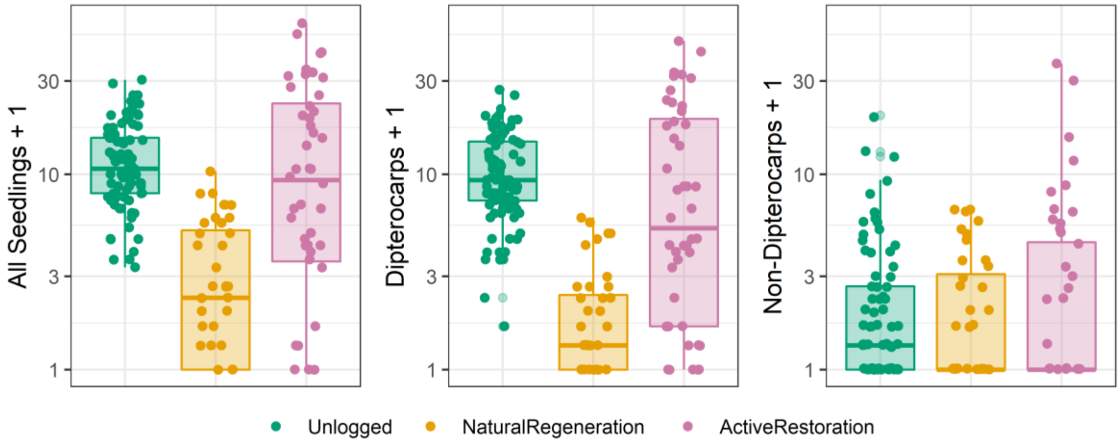


Figure S3.1 *Box plots of seedling density (all seedlings, dipterocarp seedlings, and non-dipterocarp seedlings m^{-2}) at first census after germination in unlogged, naturally regenerating, and actively restored logged forest. Seedling density + 1 is presented to enable representation of zero values on a log scale.*

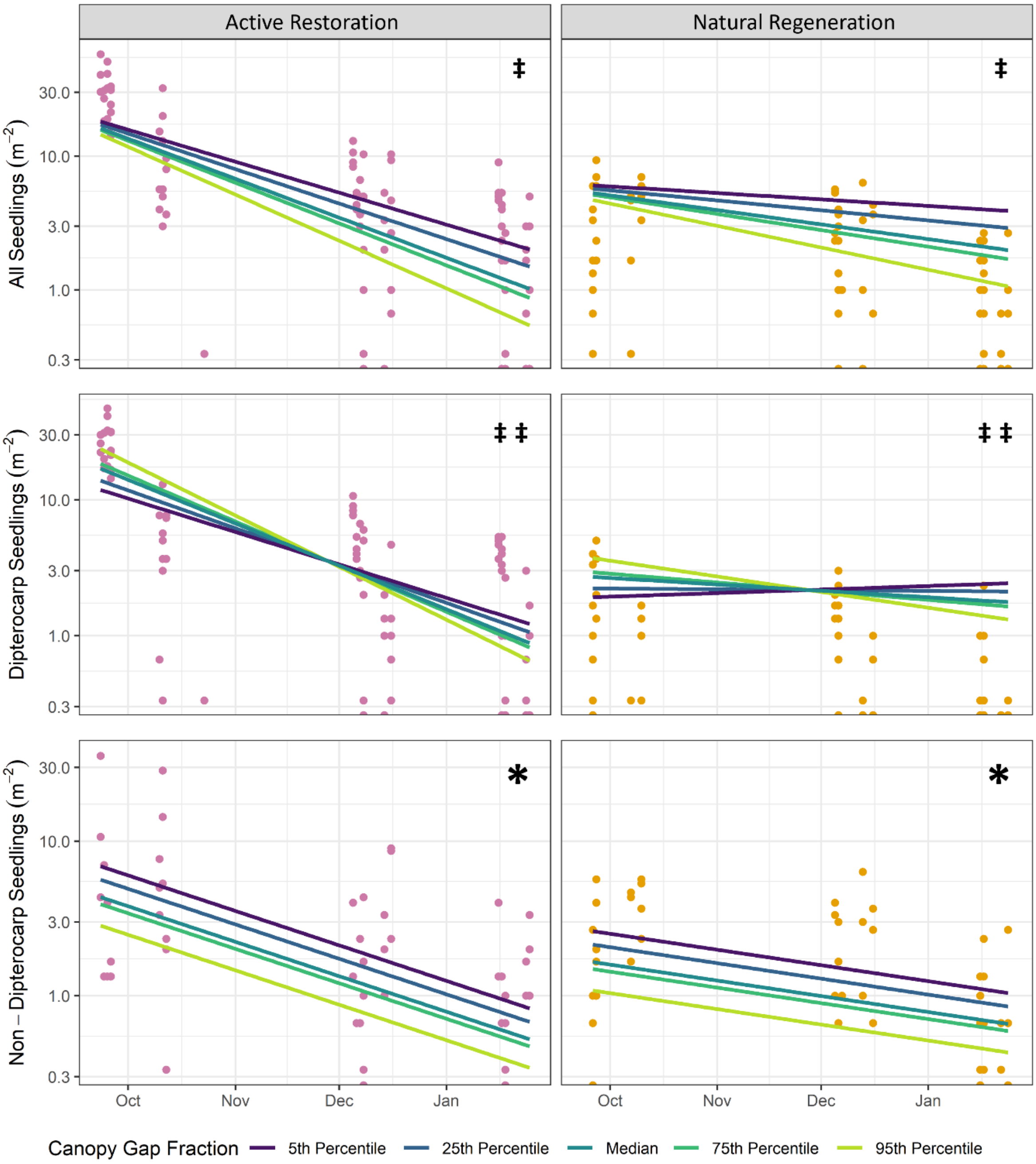


Figure S3.2 *GLMMs for seedling survival in logged forest (equation 3.2, table S3.3). Lines predict seedling abundance for the 5^th^ percentile (1.06 %), 25th percentile (1.72 %), median (3.22 %), 75^th^ percentile (4.15 %), and 95^th^ percentile (8.99 %) values of canopy gap fractions recorded in logged forest. Plots in which seedling abundance is predicted by the interaction between canopy gap percentage and census date are marked '‡' ($p < 0.05$).*

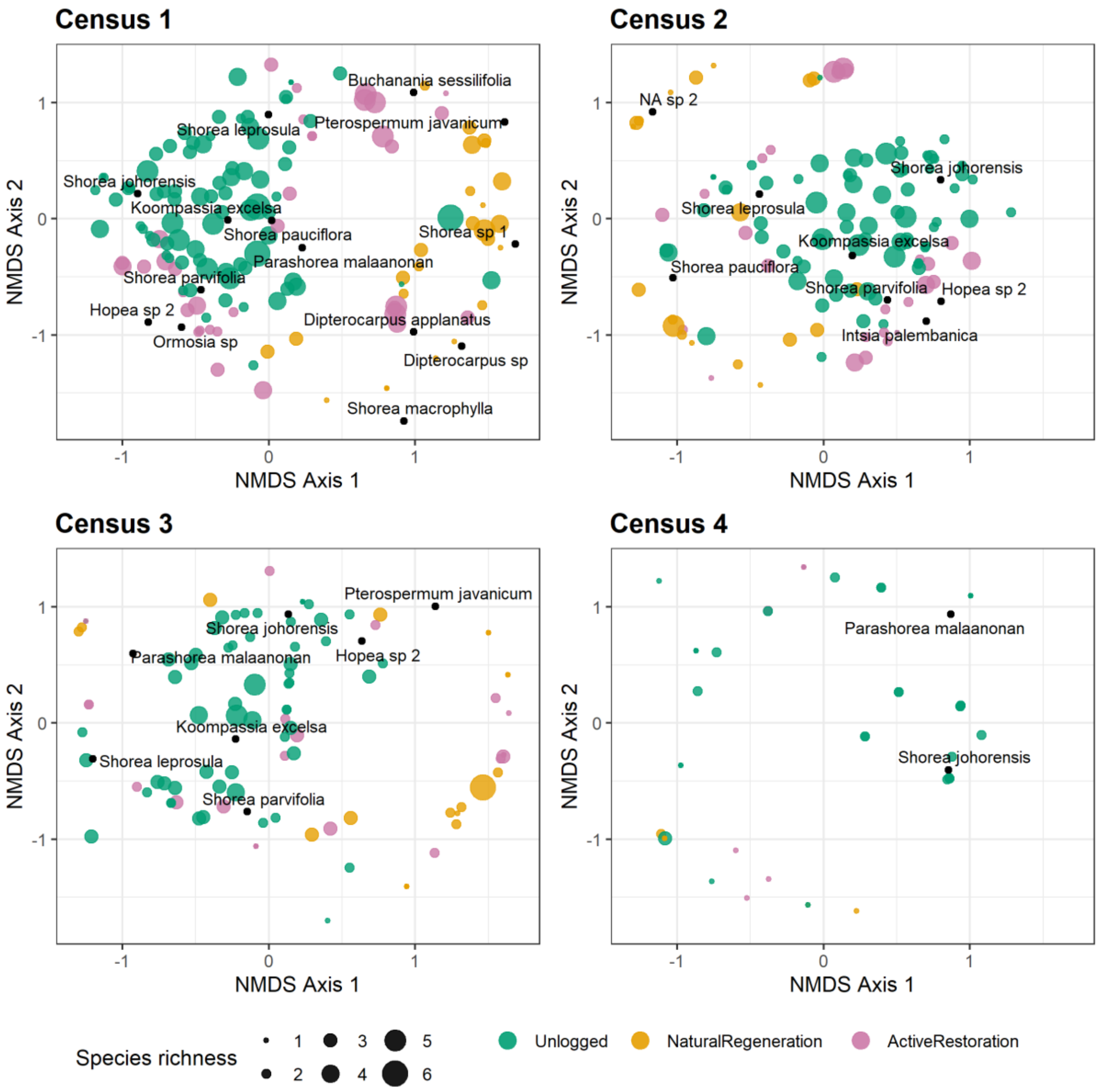


Figure S3.3 *NMDS for seedling communities in unlogged, naturally regenerating logged, and actively restored logged forest at censuses 1-4. For each census, significant indicator species (table 3.3) have been plotted. Plots are scaled by species richness and coloured by logging and restoration history.*

Chapter 4: Seedling dynamics in response to logging and restoration of a lowland tropical wet forest in Borneo

Photo: tagged seedlings in Danum Valley
[credit: Robin Hayward]

Chapter collaborators: Robin Hayward, Lindsay Banin, David Burslem, Daniel Chapman, and Daisy Dent.

Research ideas were formulated by RH and DD. Data were collected by RH and the South East Asia Rainforest Research Partnership team at Danum. RH collated and analysed data with advice from DD, LB, DC, and DB. RH led the writing of the text and all authors commented on a draft version of this chapter.

4.1.0 Abstract

Selective logging is one of the most common forms of forest degradation in the tropics, and there is increasing interest in how selectively logged forests recover and how restoration techniques can accelerate recovery. The recruitment and survival of tree seedlings is key to forest recovery post-logging as it dictates the future forest community composition and possible extinction debts, however the dynamics of seedling communities remain poorly understood. We tracked the survival and relative growth rates of 1506 woody seedlings (≥20 cm tall and <1 cm DBH) for 27.3 - 31.5 months across a Bornean landscape of unlogged forest (UL) and selectively logged forest that had either regenerated naturally (NR) or had been actively restored (AR). Logging was carried out 25-37 years pre-census, and active restoration (enrichment planting and climber cutting) 14-26 years pre-census. To explore responses among functional groups, seedlings were classified as ectomycorrhizal (EcM) trees, non-EcM trees, or lianas. At the first census, seedling density of EcM trees was lower in AR forest than in UL forest (as was true for masted seedlings by the end of the study presented in chapter 3), but did not differ between other forest types or for other functional groups. Over the following 2.5 years, survival was lowest in AR forest for all functional groups (67.4% UL, 63.8% NR, and 51.1% AR). For EcM trees, survival was greatest in NR forest and equal to that of non-EcM trees in NR forest. In UL forest EcM trees had lower survival than other functional groups, and survival of non-EcM trees and lianas was greatest in UL compared to other forest types. By contrast, EcM tree growth was lower in NR forest than UL or AR forest. Differences among forest types were less distinct for non-EcM trees and lianas in terms of both survival and growth. Seedling growth was greater in locations with greater canopy gap fractions. There were consistent trade-offs between survival and growth across forest types and functional groups. Overall, our results suggest that dynamics of EcM tree seedling communities are especially sensitive to environmental conditions created by previous selective logging and active restoration. However, increased growth rates amongst EcM seedlings in actively restored forest may allow for long-term recovery of this group at larger size-classes despite low survival.

4.2.0 Introduction

Selective logging is pervasive throughout the tropics, resulting in the widespread degradation of targeted forests (Asner et al., 2009, Laurance et al., 2014). Over 4,000,000 km^2 of tropical land is currently designated as logging concessions, of which ~320,000 km^2 are located on the island of Borneo (Asner et al., 2009). As such, there is substantial interest in the extent to which forests are affected by selective logging, particularly within Malaysia and Indonesia (Poudyal et al., 2018). Logged forests have high value to multiple stakeholders; as a resource for repeated timber harvest, for regulating ecosystem services such as carbon sequestration and water cycling (Sheil, 2018, Boul Lefeuvre et al., 2022), for the provisioning of food and fuel to local human populations, and as refugia for plant and animal populations (Berry et al., 2010, Putz et al., 2012). Land managers may therefore choose to invest in silvicultural treatments to promote recovery of biomass, biodiversity or specific timber species (Putz and Ruslandi, 2015). The extent to which these strategies are successful, necessary, or economically efficient, however, is an area of ongoing scientific debate (Zahawi et al., 2014, Latawiec et al., 2016, Crouzeilles et al., 2017, Crouzeilles et al., 2020). Furthermore, regeneration success is dependent on the ability of seedlings to survive long-term and become adult trees, which remains poorly studied.

Selective logging differs from clear-fell logging in that only the largest and most valuable stems (4-15 ha^{-1}) are harvested (Pinard et al., 1996, Edwards et al., 2014b). With sufficiently long regeneration periods, this is expected to give the remaining stems and their progeny the opportunity to recover both ecosystem functionality and timber value ahead of future logging rotations (Edwards et al., 2014b). In theory, this makes selectively logged timber an ecologically sustainable resource although, in practice, inconsistent impacts across species and landscapes, paired with short logging intervals, may limit or redirect trajectories of recovery (Howlett and Davidson, 2003, Berry et al., 2008, Reynolds et al., 2011).

Following timber extraction, selectively logged forests experience immediate reductions in tree density, loss of large trees, and above ground biomass that may take many decades to recover to their pre-logged state (Pinard et al., 2000a, Jeyakumar et al., 2017, Philipson et al., 2020). While tree density may recover within the first 15 years post logging at the landscape scale (Slik et al., 2002), localised densities along logging tracks remain lower in tropical Asian forests 20 years post-logging (Pinard et al., 2000a, Jeyakumar et al., 2017). Approximately 30 years post-logging, total basal area of stems >30 cm DBH and biomass of stems >10 cm DBH remained lower in naturally regenerating forests in India and French Guiana respectively (Jeyakumar et al., 2017, Yguel et al., 2019), and in Sabah, Malaysia, above ground carbon in woody stems >1 cm DBH was also reduced compared to unlogged forest (Philipson et al., 2020). Lianas (woody vines) are also sensitive to logging, typically increasing in abundance and species richness in the short-term, after disturbance increases canopy openness (Schnitzer et al., 2004, Magrach et al., 2016, Cleary, 2017). However, 19 years post-logging in Malaysia, lianas were shown to decline in abundance and species richness relative to old growth (Addo-Fordjour et al., 2012), possibly reflecting reduced light availability under canopy closure while preferred host tree species remained sparse (Magrach et al., 2016).

It is now widely acknowledged that current logging rotations are often insufficient to allow sustainable timber harvesting (Putz et al., 2012). For example, in Borneo prescribed logging rotations are 60 years but in practice rotation times are often <20 years (Reynolds et al., 2011). The minimum sustainable interval to allow full regeneration of timber is estimated to be between 50 and 100 years (Kammesheidt et al., 2001, Brienen and Zuidema, 2007). However, active restoration through tree planting and removal of early-successional species or climbers has been shown to accelerate recovery of stem density and biomass in some tropical forest landscapes (Gourlet-Fleury et al., 2013, Mills et al., 2019, Osuri et al., 2019, Philipson et al., 2020).

Tree community composition typically takes much longer than biomass or stem density to recover naturally after selective logging, with projected minimum recovery times ranging from 80 to 200 years depending on the logging techniques used (Appanah et al., 1990, Huth and Ditzer, 2001). Community composition was significantly different between unlogged and naturally regenerating forests after 23-35 years in Malaysia (Hayward et al., 2021), 20 years in French Guiana (Baraloto et al., 2012), and 45 years in Uganda (Osazuwa-Peters et al., 2015). However, we understand relatively little about how active restoration can affect rates of community recovery in selectively logged forests, as relatively few restored sites have data available over long timescales and compositional responses to logging and active restoration efforts vary across study sites. In the Western Ghats, India, 7-15 years post-restoration and >80 years post-logging, tree community composition was more similar to an unlogged baseline in restored than naturally regenerating forest (Osuri et al., 2019); in Sabah, Malaysia, 12-24 years post-restoration and 23-35 years post-logging, community composition did not differ substantially between naturally regenerating and actively restored forest but both remained distinct from unlogged forest (Hayward et al., 2021); and in Pará, Brazil, 18-19 years post-restoration and 30 years post-logging, community composition differed among unlogged, naturally regenerating, and actively restored logged forest (de Avila et al., 2015). In the latter, Brazilian study, community composition was closer to unlogged forest in naturally regenerating than in actively restored forest and, while naturally regenerating forest showed a trend of recovery over time, actively restored forest did not (de Avila et al., 2015). Variation in responses amongst study sites could result from differences in biogeography, baseline degradation, or the modes and intensities of restoration efforts. Further research is required to understand how active restoration may alter community recovery trajectories and how treatments can be optimised for specific landscapes and community assemblages.

Dynamics of survival and growth at the seedling life-stage may hold the key to understanding why differences in plant community composition persist several decades after logging and restoration (Pillay et al., 2018). If naturally seeded generations are unable to survive and grow to become canopy trees within logged forests then we may see shifts in the tree community as mature stems are not replaced by their offspring. Selective logging primarily limits the long-term recruitment of seedlings through reduced seed production per unit area, with logged forests at Sungai Matan in Kalimantan producing only 23% of the dipterocarp seeds produced in unlogged forests during a mast fruiting in 1991 (Curran and Webb, 2000) and *Dryobalanops lanceolata* trees in logged forests at two sites in Sabah producing 37.4% of the seeds produced by these conspecific trees in unlogged forest during a mast fruiting in 2014 (Pillay et al., 2018). Reproduction in the wet lowland dipterocarp forests of Southeast Asia occurs primarily through mast fruiting events, which take place every 3-9 years and result in distinct cohorts of seedlings developing in the forest understorey (Curran and Leighton, 2000). Logged forests tend to experience increased seed predation during mast fruiting events (Curran and Webb, 2000), followed by high growth and mortality of seedlings in the first 6-7 months post-germination (see chapter 3; Itoh et al., 1995, Oshima et al., 2015). These high rates of mortality can be exacerbated in actively restored forest patches, which may produce more seeds than surrounding naturally regenerating forest, concentrating usually mobile seed predator groups (Hautier et al., 2010) and, due to enrichment planting of parent trees with low genetic diversity potentially increasing susceptibility to pathogens (Nutt et al., 2016, Tito de Morais et al., 2020, Nef et al., 2021; chapter 3).

After an initial period of rapid growth and establishment, seedlings may then persist in the understory through alternating periods of growth and suppression for over a decade before recruiting to the canopy (Delissio et al., 2002). By reducing growth, seedlings are able to invest more in defence from biotic (e.g., seed predators) and abiotic (e.g., drought) threats (Daisuke et al., 2013, Inman-Narahari et al., 2014, Philipson et al., 2014, O'Brien et al., 2017). This trade-off has been well documented and the reverse may be equally necessary for recruitment at the community scale, where low survival is acceptable, providing a minority of seedlings can gain competitive advantage through fast growth to recruit into the canopy (Brown et al., 1992). Although growth is slower in periods of suppression, the growth that does occur may be important for structuring hierarchies in seedling height that affect competition among seedlings at later stages of development (Whitmore and Brown, 1996).

Establishment of seedlings in logged forests can be limited by decreased resilience to extreme climatic events, which are likely to become more common under climate change. Logged forests are typically hotter and have more variable microclimates than unlogged forests (Hardwick et al., 2015, Fauset et al., 2017, Blonder et al., 2018), as well as high irradiance and vapour pressure deficit at coarser scales (Senior et al., 2017a), reducing the growth and survival of early successional and low wood density seedlings (Slik, 2004, O'Brien et al., 2017). Compaction of the soil under heavy machinery during harvest (Jusoff and Majid, 1992, Pinard et al., 2000a, Asner et al., 2004a) – and leaching of soil nutrients (Nussbaum et al., 1995) may also limit establishment, growth, and survival of seedlings in logged forest. Ectomycorrhizal (EcM) tree seedlings may be particularly vulnerable to damage to forest soils, since this may damage the EcM hyphal networks that contribute to EcM seedling mineral nutrition in primary forest (Onguene and Kuyper, 2002, McGuire, 2007, Segnitz et al., 2020). However, in high diversity forests, this effect may be ameliorated by lower host specificity of fungi (Brearley et al., 2016). EcM fungal communities have been shown to differ in abundance and community composition between unlogged and logged forest in Malaysia 5-50 years after logging (Kerfahi et al., 2014, McGuire et al., 2015). Seedlings of trees from the family Dipterocarpaceae, which tend to be valuable timber species, may be particularly vulnerable to shifts in the EcM fungal community due to their obligate EcM associations, whilst non-dipterocarp EcM associations are rare in Southeast Asia (Brearley, 2012).

To explore the effects of logging and active restoration on seedling recruitment, we focus on a study site in the Malaysian state of Sabah, a global forest degradation hotspot where only ~30% of forested land remains intact (Bryan et al., 2013). At this site, active restoration of logged forest has accelerated above ground carbon recovery (Philipson et al., 2020). However, tree species richness and diversity were not affected by active restoration, and tree community composition in naturally regenerating and actively restored forests differed similarly from unlogged forest communities 23-35 years post-logging (Hayward et al., 2021). Using repeat censuses of tree seedling communities over a 31 month period, we examined seedling growth and survival in unlogged, naturally regenerating, and actively restored tropical wet forest.

Specifically, we seek to answer the following questions:

Q1. Do seedling densities, survival, and relative growth rates differ amongst unlogged, naturally regenerating, and actively restored logged forest?

Q2. How are seedling growth and survival related and are these relationships consistent across functional groups (EcM trees, non-EcM trees, and lianas)?

4.3.0 Methods

4.3.1 Study site

The Danum Valley Conservation Area (DVCA) and Ulu Segama Forest Reserve (USFR) form a landscape of contiguous forest in East Sabah, Malaysian Borneo (figure 4.1). While both exist as part of a 10,000 km^2 logging concession, only the USFR has been historically logged (Reynolds et al., 2011). Logging was carried out selectively between 1981 and 1993, in annually determined ~27 km^2 regions, commonly referred to as coupes (figure 4.1), using a combination of tractor and high-lead techniques (Pinard et al., 2000a, Foody and Cutler, 2003, Sabah Forestry Department, 2019). All commercially viable stems, mostly Dipterocarpaceae, >60 cm DBH were harvested, resulting in an average of 118 m^3 ha^{-1} (42.5-128.2 m^3 ha^{-1}) of timber being removed across coupes (Foody and Cutler, 2003). Both DVCA and USFR have since been set aside for conservation (Reynolds et al., 2011).

Within the USFR, a subset of logged forest (figure 4.1) was silviculturally treated between 1992 and 2004 to aid recovery of timber stocks and the tree community, an average of nine years post-logging (Moura Costa, 1996, Face the Future, 2011). Through the Innoprise-FACE Foundation Rainforest Rehabilitation Project (INFAPRO), seedlings were planted in parallel lines (every 3 m, cut 10 m apart) using a mixture of 52 dipterocarp species and 21 non-dipterocarp species, including 16 native fruit tree species (table S4.1). Prior to planting, seedlings were grown for 4-8 months in nurseries, until they reached a height of ~50 cm, with ≥10 leaves. After planting, actively restored sites were maintained for a period of three years by weeding every three months to prevent competition from early successional stems. Liberation cutting and girdling of early successional stems was also part of the initial active restoration treatment. Logged forest has since been monitored by identification and measurement of trees >2 cm DBH within the INDFORSUS plot network, established in 1996 (figure 4.1; Foody and Cutler, 2003). Within the unlogged forest in the DVCA, west of the Segama River, the Forest Global Earth Observatory (ForestGEO) 50 ha plot was established in 2010 as part of a global research effort to monitor forest dynamics by measurement and identification of all tree stems >1 cm DBH across multiple sites (Anderson-Teixeira et al., 2015).

4.3.2 Seedling censuses

All woody seedlings >20 cm tall and <1 cm diameter at breast height (DBH at 1.3 m) were recorded across a network of 174 (86 unlogged, 40 naturally regenerating, 48 actively restored) 3 m^2 stations, each comprising three 1 m x 1 m subplots, within the Danum Valley forest between July and November 2018 (figure 4.1). Seedling stations in unlogged forest were located on a grid at 35 m intervals throughout the ForestGEO 50 ha plot, while seedling stations in logged forests were nested within the established INDFORSUS project plots (figure 4.1). Each seedling was individually tagged using flexible plastic rings to leave room for growth. Seedling height was then measured

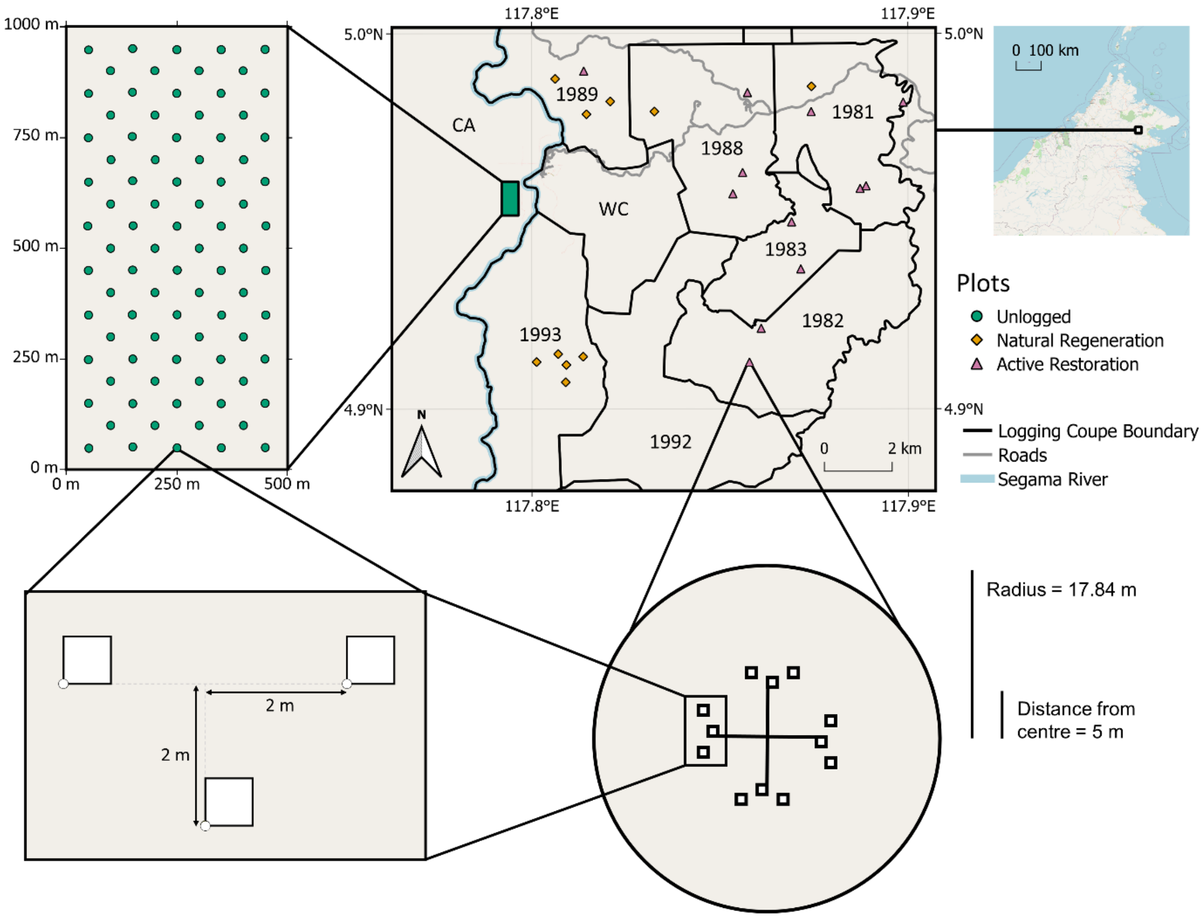


Figure 4.1 *Location of seedling plots in the Danum Valley Conservation Area and Ulu Segama Forest Reserve. Colours indicate logging and regeneration method (consistent throughout this paper). Coupes are labelled by logging year, or as WC (Water Catchment) or CA (Conservation Area). Access roads, which have been retained since logging, are shown in grey and the Segama River in blue. Locations of unlogged seedling stations are shown within the Forest Global Earth Observatory (ForestGEO) study area (rectangular inset). Arrangement of seedling stations, clustered in groups of four at logged forest plots, is shown within the radius of the mature tree census area (circular inset).*

along the length of the stem. Where individual seedlings had multiple or branching stems, the longest distance from base to tip was recorded. Each seedling was identified by comparing them to the botanical collections present at the Danum Valley Field Centre Herbarium and the Royal Botanic Gardens Edinburgh. To avoid destructive sampling of seedlings within the plot network, the majority of individuals were identified by comparing field photographs with reference specimens. Where key features were not sufficiently well captured by photography in the field, specimens were collected from individuals of the same taxon located outside the plots, and were compared with specimens in the Danum Valley Field Centre Herbarium. 81.1% of seedlings were identified to family and genus and 59.1% to species. Once identified, seedlings were classified into three functional groups: EcM trees (trees with ectomycorrhizal associations), non-EcM trees, and lianas (table S4.2). Although EcM trees in the region are overwhelmingly from the family Dipterocarpaceae (Brearley, 2012), these groupings highlight the presence of *Lithocarpus* seedlings within our plots (table S4.2), which may also be influenced by EcM associations during seedling establishment and growth and should therefore be considered similarly within analyses. Unidentified seedlings were classified as non-EcM trees due to high confidence in identification of EcM trees and lianas by their family and functional group characteristics respectively.

Seedling plots were established in July – November 2018 (census 1) and recensused in September – December 2019 (census 2; 10.3-14.0 months later) and February – March 2021 (census 3; 27.3-31.5 months later) to track the demographic fates of seedlings present at census 1.

Droughts (<100 mm rainfall in a 30 day period; Brunig, 1969, Walsh and Newbery, 1999) occurred in early 2019 (between census 1 and census 2) and in early 2020 (between census 2 and census 3), the first of which was associated with an El Niño event (figure S4.1) (SEARRP, 2021). The 2019 drought was followed by a mast fruiting event across Sabah, which had the potential to affect the dynamics of extant seedling cohorts through increased herbivore activity and density-dependent competition for resources across different levels of forest disturbance (Curran and Leighton, 2000). We therefore counted newly germinated seedling populations, in addition to our remeasurements of tagged seedlings at census 2, as an additional predictor in our analyses of the demographic fate of the established seedling community.

In 2018, hemispherical photographs of the canopy were taken above each 1m x 1m seedling plot, using a Nikon D-7000 DSLR and Jintu 180° fish-eye lens (8 mm, F 3.0) held manually at a height of 1.3 m (Origo et al., 2017). To maximise accuracy, photos were taken under diffuse light conditions and without moisture on the lens. Where this was not possible, photos were not taken (15.9% of plots). Images were analysed in CanEye version 6.495 to calculate relative proportions of light and dark pixels as a measure of canopy gap fraction (INRA, 2017).

4.3.3 Data analysis

Seedling density (stems m^{-2}) was calculated at each census for the full seedling community as well as for trees with ectomycorrhizal associations (EcM), trees without ectomycorrhizal associations (non-EcM), and lianas separately. Seedling densities were then compared between forest types at each census by pairwise Mann-Whitney U tests.

For each seedling, relative growth rate (RGR) was calculated for change in height between censuses using Equation 4.1, where $Height_1$ is seedling height at the start of the census interval and $Height_2$ is height at the end of the census interval.

Eq. 4.1 $RGR = (\log_e(Height_2) - \log_e(Height_1)) / \text{Days of interval}$

Generalised linear mixed models were fitted to RGR and likelihood of individual survival (equation 4.2), from census 1 to census 3, using the *glmmTMB* package in *R* (Brooks et al., 2017a). The same predictor variables (fixed effects) were used to model both metrics: functional group (EcM trees vs non-EcM trees vs lianas), forest type (unlogged vs naturally regenerating vs actively restored), canopy openness, initial stem height, initial seedling density, and the density of mast fruited seedlings that germinated shortly before census 2. An interaction between functional group and forest type was included to account for different responses between seedlings with different recruitment strategies. Station and plot numbers (figure 4.1) were included as nested random effects to account for location of individuals within the censused landscape. Initial height was included as a covariate due to its known effect on RGR (Peters, 1983, Umaña et al., 2021). GLMMs for survival used a binomial distribution and GLMMs for RGR used a gamma distribution with a log link function. Best models were selected by lowest AIC using the *dredge* function in the *MuMIn* package in *R* (Barton, 2009). Where best models included canopy openness, seedlings on plots were excluded from the analysed dataset if they lacked canopy openness data. Where best models did not include canopy openness data, the full dataset was used.

Eq. 4.2 $\text{Survival or } RGR_{Height} \sim \text{Functional group} * \text{Forest type} + \log(Height_1) + \text{sqrt(Seedling density)} + \text{sqrt(Masted seedling density)} + \log(\text{Canopy gap fraction}) + (1|\text{Station:Plot})$

To visualise trade-offs between survival and RGR for each functional group, model predictions were plotted against one another. Predictions were made for each model using the full range of initial seedling sizes at each forest type with a resolution of 1 cm between predictions. For predictions of survival (where canopy gap fraction was significant in models), we included the average values for canopy gap factions, as calculated by the *ggeffects::ggeffect* function in *R* (Lüdecke, 2018).

4.4.0 Results

A total of 1506 seedlings (table 4.1) was recorded in the first census, across unlogged (755 seedlings; median density = 2.89 m^{-2}), naturally regenerating (373 seedlings; 2.82 m^{-2}), and actively restored (378 seedlings; 2.47 m^{-2}) forests. Seedling density (m^{-2}) did not differ between unlogged and naturally regenerating forests, nor between naturally regenerating and actively restored forests, at any census (Mann-Whitney U test, $p > 0.05$; Table 4.2). However, median seedling density was higher in unlogged than actively restored forest for the full community at after 10.3-14.0 months at census 2 (2.50 m^{-2} vs 1.82 m^{-2}; U = 2737, p = 0.031) and after 27.3-31.5 months at census 3 (1.95 m^{-2} vs 1.26 m^{-2}; U = 2791, p = 0.011). At census 1, EcM tree seedling density was greater in unlogged than actively restored forests (0.39 m^{-2} vs 0.27 m^{-2}; U = 2652, p = 0.035) but did not differ in later censuses. By contrast, non-EcM trees did not differ in densities between unlogged and actively restored forests at first census (2.17 m^{-2} vs 1.98 m^{-2}; U = 2536, p = 0.160) but had greater seedling densities in unlogged forest at census 2 (1.93 m^{-2} vs 1.44 m^{-2}; U = 2746, p = 0.028) and census 3 (1.54 m^{-2} vs 1.05 m^{-2}; U = 2827, p = 0.007). Lianas followed the same pattern as non-EcM trees, with similar densities between unlogged and actively restored forests at census 1 (0.34 m^{-2} vs 0.22 m^{-2}; U = 2603, p = 0.054) but greater seedling densities in unlogged forest at census 2 (0.29 m^{-2} vs 0.16 m^{-2}; U = 2651, p = 0.038) and census 3 (0.22 m^{-2} vs 0.09 m^{-2}; U = 2691, p = 0.013). Median canopy gap fraction was 3.03% (interquartile range = 2.00-4.94%) in unlogged forest, 3.76% (IQR = 2.31-7.20%) in naturally regenerating forest, and 2.71% (IQR = 1.62-3.51%) in actively restored forest (Figure S4.2).

Of the seedlings tagged at census 1, 82.3% (1239 seedlings) survived to census 2 and 62.4% (940 seedlings) survived to census 3 (table 4.1). For all functional groups, percentage survival was lowest in actively restored forest (table 4.1). Tree seedlings with ectomycorrhizal associations (EcM) had the greatest percentage survival in naturally regenerating logged forest (75.4%) but seedlings of non-EcM trees and lianas had greatest survival in unlogged forest (71.2% and 64.8% respectively).

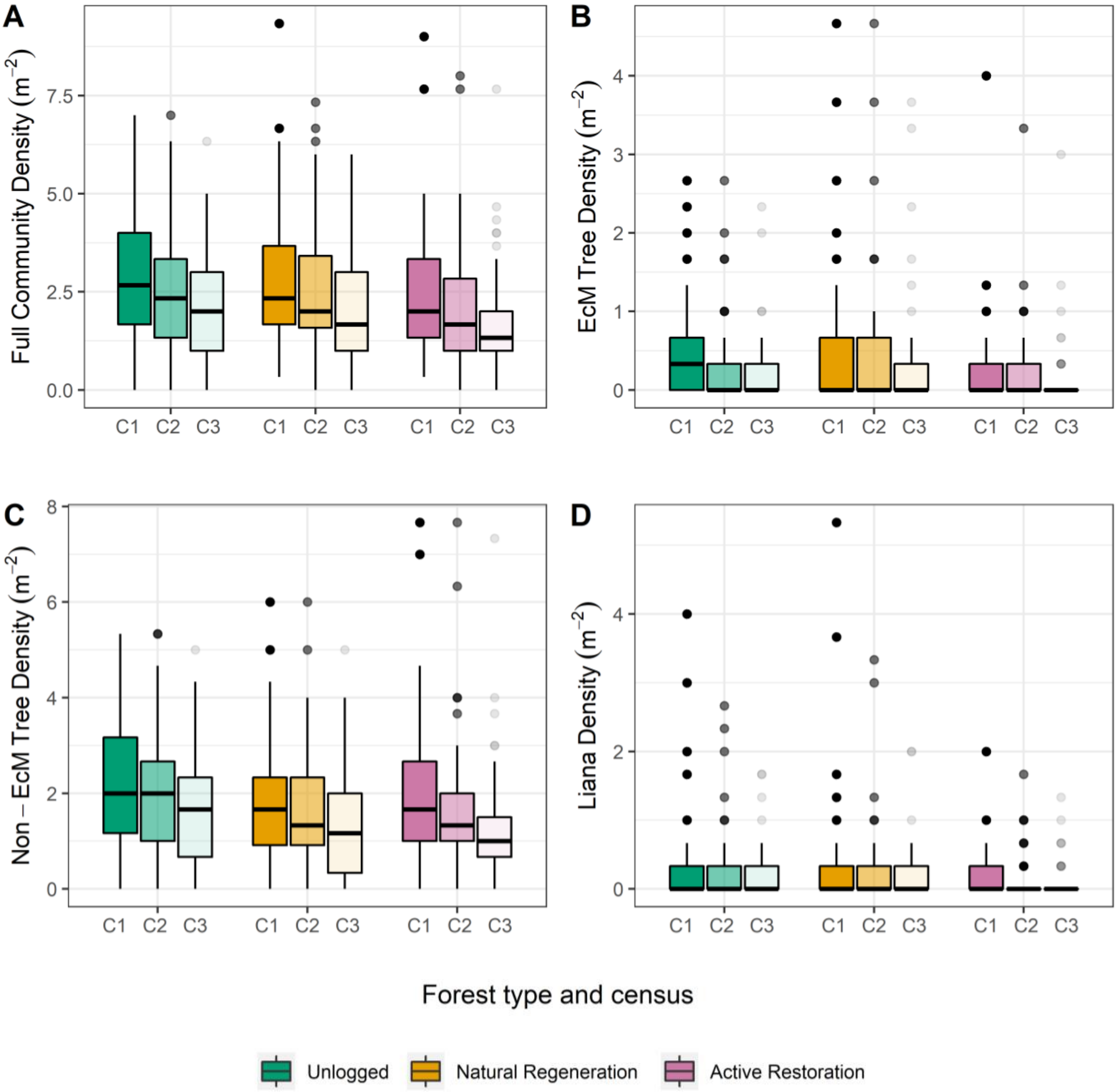


Figure 4.2 *Boxplots of seedling density (m^{-2}) for A) the full seedling community, B) EcM tree seedlings, C) non-EcM tree seedlings, and D) liana seedlings at each census (census 1 to 3 presented left to right with decreasing colour saturation) and forest type.*

Table 4.1 *Counts of seedlings surviving from the census 1 cohort at censuses 1, 2, and 3. Counts are shown for each analysed functional group and forest type. Counts at censuses 2 and 3, are also shown in parentheses as a percentage of the stem count at census 1. Sampling effort for each forest type is shown in parentheses (m^2)*

Forest Type	**Functional group**	**Census 1 (0 months)**	**Census 2 (10.3-14.0 months)**	**Census 3 (27.3-31.5 months)**
Unlogged (261 m^2)	EcM trees	101	74 (73.3%)	49 (48.5%)
	Non- EcM trees	566	504 (89.0%)	403 (71.2%)
	Lianas	88	75 (85.2%)	57 (64.8%)
	Total	**755**	**653 (86.5%)**	**509 (67.4%)**
Naturally Regenerating (132 m^2)	EcM trees	69	61 (88.4%)	52 (75.4%)
	Non- EcM trees	248	200 (80.6%)	156 (62.9%)
	Lianas	56	46 (82.1%)	30 (53.6%)
	Total	**373**	**307 (82.3%)**	**238 (63.8%)**
Actively Restored (153 m^2)	EcM trees	42	33 (78.6%)	19 (45.2%)
	Non- EcM trees	303	221 (72.9%)	160 (52.8%)
	Lianas	33	25 (75.8%)	14 (42.4%)
	Total	**378**	**279 (73.8%)**	**193 (51.1%)**
Total (546 m^2)	All seedlings	1506	1239 (82.3%)	940 (62.4%)

Table 4.2 *Mann-Whitney U test results comparing the seedling density (m^{-2}) of different seedling functional groups between forest types at each census. P values <0.05 and <0.01 are marked '*' and '**' respectively and presented in bold.*

Functional group	**Census**	**Unlogged *vs* Naturally Regenerating**		**Unlogged *vs* Actively Restored**		**Naturally Regenerating *vs* Actively Restored**	
		U	P	U	P	U	P
EcM Trees	1	2067	0.416	**2652**	**0.035***	1222	0.379
	2	2037	0.587	2577	0.099	1207	0.444
	3	1854	0.725	2495	0.124	1277	0.131
Non-EcM Trees	1	2212	0.146	2536	0.160	1106	0.907
	2	2252	0.126	**2746**	**0.028***	1214	0.492
	3	2267	0.084	**2827**	**0.007****	1239	0.380
Lianas	1	1985	0.705	2603	0.054	1279	0.169
	2	1933	0.987	**2651**	**0.038***	1330	0.063
	3	1964	0.784	**2691**	**0.013***	1326	0.055
Full Community	1	2072	0.443	2659	0.052	1261	0.300
	2	2069	0.523	**2737**	**0.031***	1277	0.247
	3	2049	0.512	**2791**	**0.011***	1331	0.119

A binomial GLMM (tables 4.3 & S4.3; figure 4.3) indicated that the likelihood of seedling survival between census 1 and census 3 (2.5 years) was lower for EcM trees than for non-EcM trees (estimate = 1.265, p < 0.001; table 4.3) or lianas (estimate = 1.388, p < 0.001; table 4.3) in unlogged forest. In actively restored forest, these differences between functional groups were the same as in unlogged forest (p = 0.231 and p = 0.864, respectively; table 4.3), however likelihood of survival was found to be lower across all functional groups (estimate = -0.986, p < 0.001; table 4.3). By contrast, EcM trees in naturally regenerating logged forest were more likely to survive than EcM trees in unlogged forest (estimate = -1.075, p = 0.003; table S4.3), and were similarly likely to survive compared to non-EcM trees (p = 0.848; table S4.3). Lianas in naturally regenerating forest had marginally lower survival than trees but not significantly so (p = 0.063; table S4.3). In addition to functional groups and forest types, seedling survival likelihood was predicted to be greater for seedlings that were taller at the first census (estimate = 0.439, p < 0.001; table 4.3).

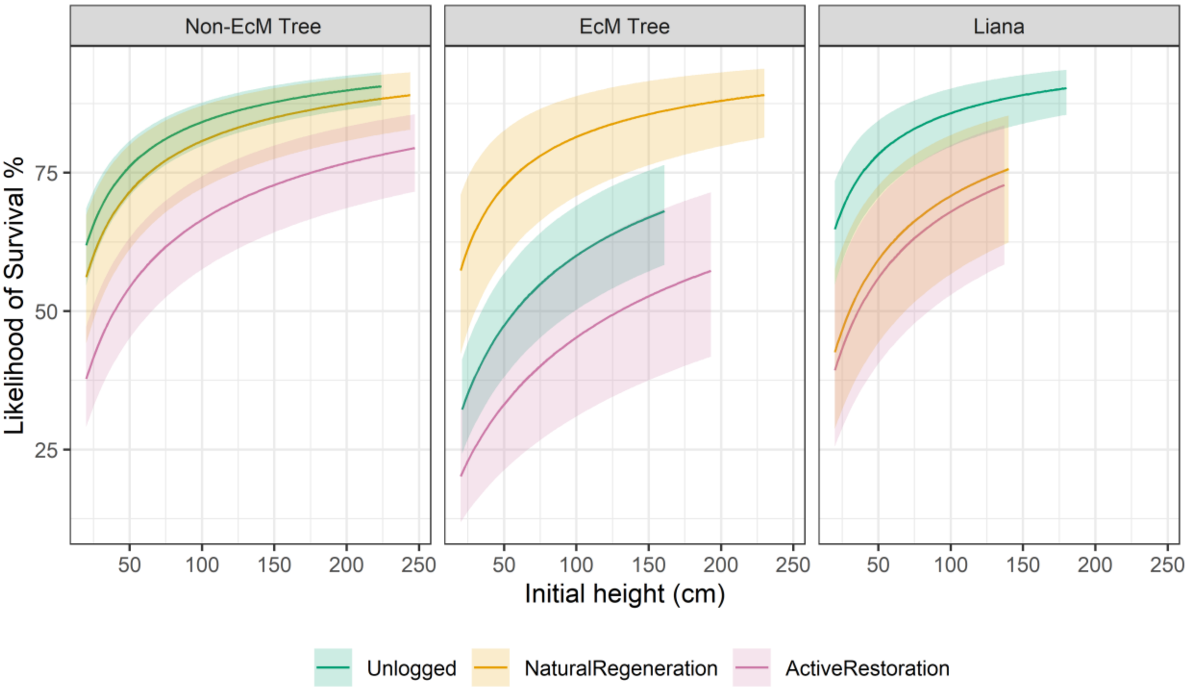


Figure 4.3 *Binomial GLMM for likelihood of seedling survival (%) over a ~2.5 year interval, predicted by seedling height at first census (cm) for Non-EcM trees, EcM trees, and lianas in unlogged, naturally regenerating, and actively restored logged forests (equation 4.2; Table 4.3). Predictions are bounded by 95% confidence intervals.*

A gamma GLMM (tables 4.3 & S4.3; figure 4.4) indicated that seedling RGR was greater in EcM trees than non-EcM trees (estimate = -0.326, p < 0.001; table 4.3) and lianas (estimate = -0.343, p = 0.005; table S4.3) during a ~2.5 year interval in unlogged forest. Likewise, in actively restored logged forest, EcM tree RGR was greater than for non-EcM trees (estimate = -0.703, p < 0.001; table S4.3) and lianas (estimate = -1.481, p < 0.001; table S4.3). For both EcM (estimate = -0.816, p < 0.001; table S4.3) and non-EcM trees (estimate = 0.439, p = 0.002; table 4.3), seedlings regenerating in actively restored forest had higher RGR than those in unlogged forest. In naturally regenerating logged forest however, non-EcM trees had greater RGR than EcM trees (estimate = -0.401, p < 0.001; table S4.3) and lianas (estimate = -0.382, p = 0.019; table S4.3), while EcM trees and lianas did not differ (p = 0.919; table S4.3). For EcM trees, RGR was lower in naturally regenerating forest than in unlogged (estimate = 0.537, p = 0.007; table S4.3) or actively restored forest (estimate = 1.352, p < 0.001; table S4.3). RGR was predicted to be greater in stations with higher canopy gap fractions (estimate = 0.156, p = 0.004; table 4.3). In both models (figures 4.3 and 4.4) EcM tree seedlings were particularly sensitive to forest type, exhibiting greater variation in survival and RGR than the other functional groups.

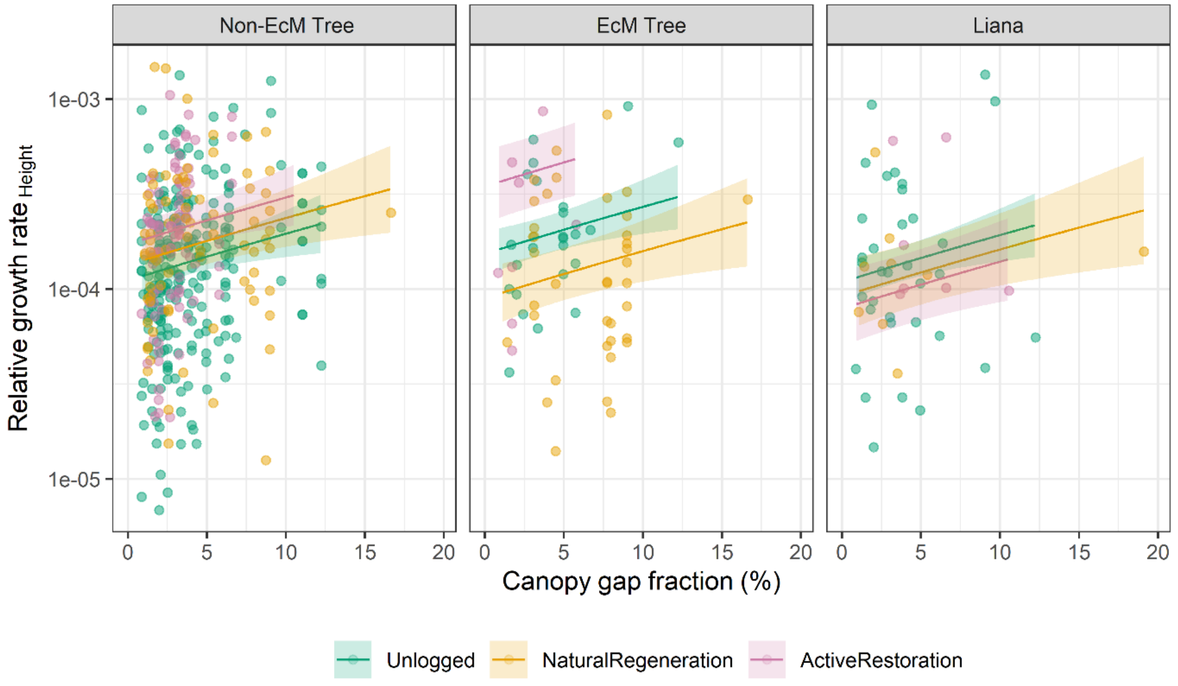


Figure 4.4 *Gamma GLMM with a log link function for relative growth rate of seedling height (equation 4.1) over a ~2.5 year interval, predicted by canopy gap fraction (%) for Non-EcM trees, EcM trees, and lianas in unlogged, naturally regenerating, and actively restored logged forests (equation 4.2; Table 4.3). Predictions are bounded by 95% confidence intervals.*

Table 4.3 *GLMM model summary for the effects of logging and restoration treatment (unlogged vs naturally regenerating vs actively restored), seedling functional group (EcM trees vs Non-EcM trees vs lianas), initial height, initial seedling density, masted seedling density, and canopy gap fraction as predictors of seedling survival and relative growth rate (RGR; equation 4.1) between census 1 and census 3 (equation 4.2). All numeric independent variables are centred, scaled, and transformed as necessary to approximate a normal distribution. Site variance (Site var.) is the variance explained by the nested random effect of seedling stations at each plot location. Best models were selected using the R MuMIn dredge function (Barton, 2009). Results are reported relative to the model intercept (non-EcM trees in unlogged forest). Where variables were not selected as part of the best model, they are still listed but value columns are filled by '-'. Variance inflation factor (VIF) is presented for each variable and conditional (Cond.) and marginal (Mar.)* R^2 *values are presented for the model as a whole.*

	Estimate	**Error**	**Z-value**	**P-value**	**VIF**	**Site Var.**	**R^2**	
							Cond.	**Mar.**
Model 1 (Survival)						1.102	0.333	0.109
(intercept)	1.080	0.141	7.636	<0.001***	-			
Forest type (Nat. Regen.)	-0.238	0.275	-0.865	0.387	1.55			
Forest type (Act. Rest.)	-0.986	0.226	-4.360	<0.001***	1.55			
EcM Trees	-1.265	0.164	-7.705	<0.001***	3.50			
Lianas	0.124	0.179	0.692	0.489	3.50			
Log(Height$_1$)	0.439	0.041	10.785	<0.001***	1.02			
Sqrt(Seedling Density)	0.133	0.073	1.833	0.067	1.02			
Sqrt(Masted Seedling Density)	0.189	0.103	1.842	0.065	1.37			
Log(Canopy Gap Fraction)	-	-	-	-	-			
Nat. Regen. : EcM Trees	1.312	0.296	4.428	<0.001***	3.91			
Nat. Regen. : Lianas	-0.671	0.298	-2.249	0.025*	3.91			
Act. Rest. : EcM Trees	0.389	0.325	1.197	0.231	3.91			
Act. Rest. : Lianas	-0.058	0.337	-0.172	0.864	3.91			
Model 2 (RGR$_{Height}$)						0.310	0.506	0.148
(intercept)	-8.769	0.078	-112.92	<0.001***	-			
Forest type (Nat. Regen.)	0.190	0.162	1.17	0.241	1.71			
Forest type (Act. Rest.)	0.439	0.141	3.12	0.002**	1.71			
EcM Trees	0.326	0.095	3.42	<0.001***	2.86			
Lianas	-0.017	0.086	-0.19	0.846	2.86			
Log(Height$_1$)	-0.238	0.020	-11.67	<0.001***	1.02			
Sqrt(Seedling Density)	-	-	-	-	-			
Sqrt(Masted Seedling Density)	-0.118	0.062	-1.91	0.056	1.50			
Log(Canopy Gap Fraction)	0.156	0.055	2.86	0.004**	1.06			
Nat. Regen. : EcM Trees	-0.727	0.148	-4.91	<0.001***	3.24			
Nat. Regen. : Lianas	-0.365	0.184	-1.99	0.047*	3.24			
Act. Rest. : EcM Trees	0.377	0.225	1.67	0.095	3.24			
Act. Rest. : Lianas	-0.761	0.223	-3.41	<0.001***	3.24			

Examining relationships between model-predicted survival (model 1) and RGR (model 2) (figure 4.5) showed that seedlings displayed a trade-off, with higher growth rates associated with lower rates of survival across functional groups and forest types. While there was substantial overlap in these relationships within tree populations, lianas maintained higher likelihoods of survival in unlogged forest than in either logged forest type and EcM trees had higher growth rates in actively restored forest than other forest types.

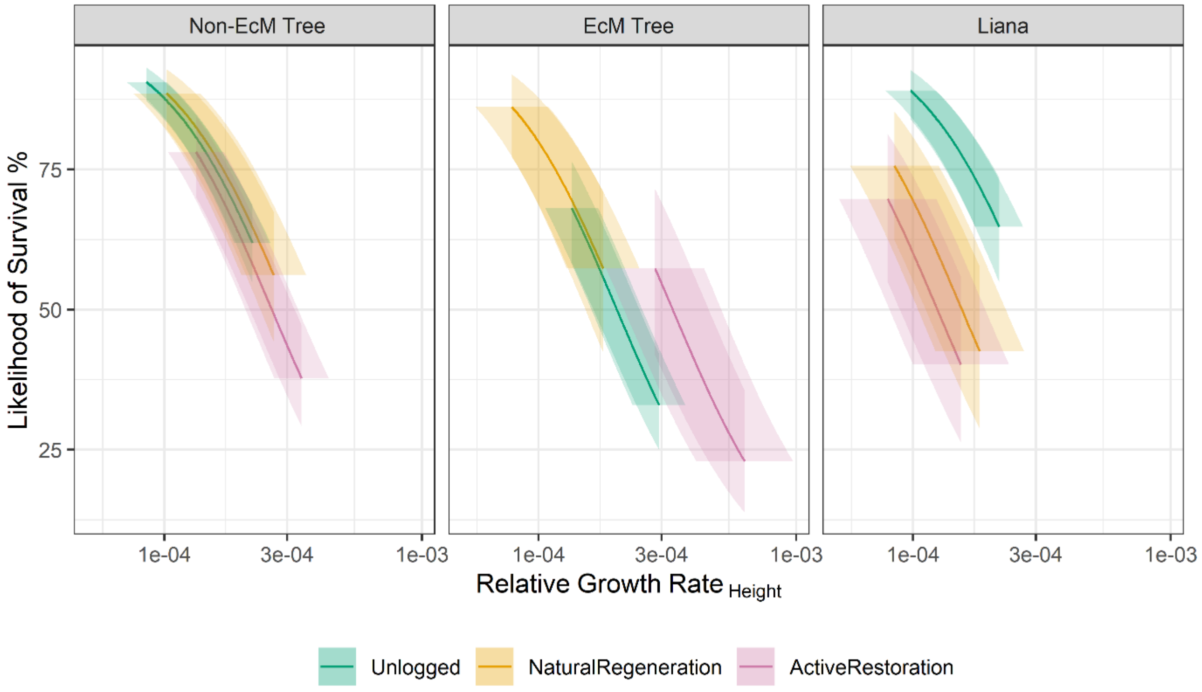


Figure 4.5 *Predicted likelihood of individual seedling survival (model 1) and relative growth rate (RGR_{Height}; model 2) for each forest type and seedling functional group. 95% confidence intervals are presented for survival on the Y axis and for RGR_{Height} on the X axis.*

4.5.0 Discussion

Across all functional groups, the likelihood of seedling survival over a ~2.5 year interval was lower in actively restored logged forest compared to unlogged forest, while seedling relative growth rate (RGR) was higher for tree seedlings in actively restored than unlogged forest. When we assessed the seedlings according to three functional groups, survival of non-EcM seedlings was similar in naturally regenerating and unlogged forests; lianas had lower survival in naturally regenerating than unlogged forests; and EcM trees had a greater chance of survival in naturally regenerating forest than in unlogged forest and actively restored forest, but, in this case, this was balanced by lower RGR. We found that seedlings that were taller at first census were more likely to survive and that seedlings under more open canopies had greater RGR. Seedling density was greatest in unlogged forest but neither density of established seedlings nor of new recruits from mast was a significant predictor of survival or growth. Across functional groups and forest types, there was a trade-off such that higher survival rates were associated with lower growth rates.

4.5.1 Seedling density

At census 1, seedling density of the entire community did not differ among forest types, suggesting that total seedling density combined across functional groups was unaffected by logging, with or without restoration. This matches findings from two sites in Kalimantan, Borneo, which found that selective logging did not affect total tree seedling density 10 years after logging (Arbainsyah et al., 2014) and that, nine years after logging and active restoration, seedling numbers were only marginally lower than in unlogged plots (Pamoengkas et al., 2019). Given that the first census in our study was conducted the year before a mast fruiting event, eight years after the previous large-scale masting event (Oshima et al., 2015), and four years after the most recent mast at Danum (Kanamori et al., 2017), it is likely that many seedlings were either four or eight years old, except for non-masting species such as lianas and early-successional tree species (Kelly, 1994). Evidence from elsewhere in Borneo suggests that seedlings derived from a mast event are able to persist in the understory for over a decade post-germination (Delissio et al., 2002), which is supported by our model predictions showing up to 90.6% likelihood of survival over a ~2.5 year period for the most resilient stems (the largest non-EcM stems in unlogged forest). We conclude that some seedlings within our census were survivors from the cohorts established by the 2014, 2010, or earlier mast events.

EcM tree seedling density (primarily comprised of dipterocarps) was highest in unlogged forest and lowest in actively restored logged forest at the first census, reflecting previous findings from the same study landscape that initially high seedling mortality post-mast results in lower than unlogged seedling densities in restored forest after the first six months of establishment (see thesis chapter 3). Seedling density in naturally regenerating forest did not differ significantly from those in either of the other forest types, suggesting that seedlings occurred at medium densities in naturally regenerating forest, along a possibly related gradient of disturbance from unlogged (low disturbance and high seedling density) to actively restored forest (high disturbance and low seedling density).

4.5.2 Tree seedling survival and growth

Model predictions of seedling survival decreased with increasing RGR, indicating trade-offs for each forest type and functional group. This relationship has been found commonly amongst trees at various life stages, both in Borneo (Philipson et al., 2014) and elsewhere in the tropics (Figueira et al., 2008, Inman-Narahari et al., 2014). Trade-offs between survival (defence) and growth can be exacerbated by drought (Daisuke et al., 2013, O'Brien et al., 2017), particularly within logged forests (Woods, 1989, Qie et al., 2019) therefore the 2019 and 2020 droughts captured by our study (figure S4.1) may have contributed to the differences we see between forest types, particularly amongst EcM trees, which showed lower RGR than other forest types in naturally regenerating forest – the forest type with the greatest canopy gap fraction. Given the likelihood of increasingly frequent droughts in tropical forests under climate change (Coelho and Goddard, 2009), understanding these trade-offs is critically important.

In the ~2.5 years of our study period, seedlings that were taller at census 1 were more likely to survive, with seedlings less than ~1 m tall particularly at risk. RGR decreased with increases in stem height, which matches expectations based on observations of seedling survival and growth from other tropical forests (Queenborough et al., 2007, Johnson et al., 2017) as well as observations that similar absolute growth rates would be recorded as lower relative growth for taller seedlings. Larger seedlings may also be less palatable to herbivores, giving them a greater chance of survival (Karban and Thaler, 1999).

Seedling survival and growth both varied with forest type and with seedling functional group, highlighting that forest management strategies need to consider how responses to intervention may vary among taxa. Non-EcM tree seedlings, which made up the majority of stems in each census and forest type, were equally likely to survive and had similar growth rates in unlogged and naturally regenerating logged forest. Non-EcM seedlings in actively restored forest also had similar RGR to naturally regenerating forest but had accelerated RGR relative to unlogged forest. This suggests a lasting gradient of RGR across disturbance levels (unlogged *vs* logged *vs* logged, cut, and planted). A similar finding has been reported for larger stems, with carbon stocks in selectively logged forests increasing faster than in unlogged forest (Gourlet-Fleury et al., 2013, Poorter et al., 2016) and active restoration accelerating carbon accumulation (Swinfield et al., 2016, Philipson et al., 2020).

In actively restored forest, non-EcM tree seedling survival was lower than in other forest types. During restoration at Danum, only 26 of the 76 tree species planted were non-EcM trees and those were planted less often than seedlings of EcM species (table S4.1) (Face the Future, 2011). Cutting of stems during post-planting silvicultural maintenance operations also targeted non-EcM trees and lianas, in an attempt to give valuable EcM timber trees an advantage for short-term growth and survival (Face the Future, 2011). These actions may accelerate succession and create the microclimatic and local site conditions that favour late successional EcM species whilst also driving up mortality of early-successional non-EcM species (Mahayani et al., 2020), as reflected by our finding of lower canopy openness in actively restored than naturally regenerating forest.

In Bornean forests, the majority of EcM associated trees are from the family Dipterocarpaceae. These late-successional tree species dominate the canopy of undisturbed forests in the region and comprise the majority of timber extracted during logging operations (Face the Future, 2011, Brearley, 2012). Differences in survival and growth in naturally regenerating and actively restored forests compared to unlogged forest were greater for EcM tree seedlings than for other functional groups, however, the direction of this effect was not consistent with levels of disturbance. EcM seedling survival was higher in naturally regenerating than unlogged forest but at the cost of lower RGR. By contrast, in actively restored forest, survival was lower and RGR was higher than in unlogged forest, indicating that restoration efforts may be successful in accelerating EcM recruitment to larger size-classes, despite inevitable trade-offs against survival.

Increased canopy gap fractions were related to increased seedling RGR but had no effect on survival within forest types. Paired with the higher basal area of mature stems observed previously in actively restored forests than unlogged forests in this landscape and elsewhere in Sabah (Philipson et al., 2020, Hayward et al., 2021), this suggests that the established tree community may influence growth and survival of late-successional EcM seedlings. Conspecific negative density dependence (C-NDD) plays a role in maintaining tree community diversity and composition within the tropics (Janzen, 1970, Connell and Connell, 1971, Bagchi et al., 2010, Comita et al., 2014). Direct targeting of EcM trees during both logging and restoration, affects the density of established conspecific EcM stems and may partially explain why we see different patterns of survival and growth across forest types in different tree seedling functional groups. While it has been suggested that EcM associations may help to protect plants from fungal pathogens in the soil, reducing C-NDD limitations (Laliberté et al., 2015), a recent study of Bornean seedlings found weak fungal C-NDD across dominant old-growth species, with no significant effect of mycorrhizal association (Cannon et al., 2020).

Ultimately, the high RGR of EcM tree seedlings in actively restored forest is a promising finding that suggests silvicultural interventions might support ongoing successional processes to restore valuable dipterocarp species within larger size classes to a pre-logging stem density long-term. Conversely, naturally regenerating forest had high survival but reduced seedling RGR which could also delay community succession, matching findings from the Central African Republic and China that biomass recovery of shade-tolerant timber trees (typically EcM trees in Malaysia) lags behind other taxa (Gourlet-Fleury et al., 2013, Xu et al., 2015). Finally, it is worth considering that, due to the long periods for which Southeast Asian tree seedlings are able to persist in the understory and the heterogeneity of growth rates during this time, it is possible that our censuses simply captured disparate periods of suppression and growth across forest types (Delissio et al., 2002). With a longer census interval we may have recorded less distinct RGR between forest types (Delissio et al., 2002).

4.5.3 Liana seedling survival and growth

Survival of liana seedlings was greater in unlogged forest than either logged forest type and there was no difference between survival in naturally regenerating and actively restored forest. Unlike tree seedlings, the mean RGR of liana seedlings did not differ among forest types. This may reflect the high diversity of growth strategies – from disturbance sensitivity to specialism – that is found among Bornean lianas (Addo-Fordjour et al., 2012, Cleary, 2017). Across the tropics, lianas tend to increase in abundance in logged forests, often at the expense of regenerating tree communities (Schnitzer et al., 2004, Magrach et al., 2016, Cleary, 2017). However, in lowland dipterocarp forest lianas may be less prolific following disturbance; for example, a study in Malaysia found lower liana species richness, diversity, and basal area in logged secondary forest relative to unlogged old growth (Addo-Fordjour et al., 2012). Young liana stems in particular may struggle to survive in the more open environments typical of logged forests, where they are vulnerable to hydraulic failure during drought (Schnitzer and Bongers, 2011, Rowe, 2018). Liana cutting is a common management strategy in logged forest, with the intention to prevent lianas from outcompeting more carbon-dense stems (Pérez-Salicrup, 2001, Estrada-Villegas and Schnitzer, 2018, O'Brien et al., 2019). In this study, liana seedling growth and survival did not differ among forest types, suggesting that the tri-monthly cutting during restoration treatments carried out at Danum had no lasting effects on liana seed production or seedling recruitment. Over a similar time period, another study in Malaysia found liana basal area was reduced after 19 years but equal after 42 years in actively restored forest, relative to naturally regenerating forest (Addo-Fordjour et al., 2014). Together with our results, this suggests that liana abundance is capable of recovery following cutting as an active restoration treatment aimed towards tree stems, however the community composition of lianas in restored forests requires further study.

4.6.0 Summary

Our results indicate that seedling responses to selective logging and active restoration, in terms of survival and growth, vary amongst functional groups. Both EcM and non-EcM tree seedlings grew faster in actively restored logged forest than unlogged forest or naturally regenerating logged forest. This pattern was particularly notable for EcM seedlings, which were the primary targets for both timber extraction and subsequent active restoration by enrichment planting. Although seedling survival was reduced in actively restored forest across all functional groups – possibly covarying with canopy gap fractions – no forest type experienced total loss of seedlings from the cohort tracked by our study, indicating the potential of stems to recruit through to larger size-classes. Therefore, following short to medium term successes of active restoration within the Asian tropics (Philipson et al., 2020, Hayward et al., 2021), accelerated growth amongst seedlings suggests recovery of biomass is likely to continue through recruitment of future generations where these techniques have been implemented. However, recovery of community composition in restored forests may still be limited if some species are unable to survive as seedlings.

4.7.0 Acknowledgements

We give thanks to the Sabah Biodiversity Centre for permitting us to complete this study; to our research assistants – particularly Tambi Karolus and the SEARRP 50 ha team – for their invaluable efforts in collecting these data; and to Alex and Ica Karolus for their help with seedling identification. This research was supported by an Iapetus DTP PhD studentship (R.M.H.) and urgency grant (NE/T006552/1 to D.F.R.P.B., L.F.B., D.H.D, and Dr Lucy Rowland) from the UKRI Natural Environment Research Council as well as the Arnold Arboretum Ashton Award (R.M.H.).

4.8.0 Supplementary Materials

Table S4.1 *Species planted in actively restored logged plots within the INFAPRO network (Face the Future, 2011)*

Dipterocarps	Non-Dipterocarp Hardwoods	Fruit Trees	Other Trees
Dipterocarpus applanatus	*Azadirachta excelsa*	*Aglaia squamulosa*	*Agathis borneensis*
Dipterocarpus caudiferus	*Eusideroxylon zwageri*	*Alangium javanicum*	*Aquilaria sinensis*
Dipterocarpus acutangulus	*Intsia palembanica*	*Allophylus cobbe*	*Duabanga moluccana*
Dipterocarpus confertus		*Artocarpus integer*	*Koompassia excelsa*
Dipterocarpus conformis		*Baccaurea angulata*	*Neolamarckia cadamba*
Dipterocarpus gracilis		*Baccaurea latifolia*	*Octomelis sumatrana*
Dipterocarpus lowii		*Dimocarpus longan*	*Palaquium spp.*
Dryobalanops beccarii		*Diospyros spp.*	*Scaphium macropodum*
Dryobalanops keithii		*Durio spp.*	
Dryobalanops lanceolata		*Garcinia parvifolia*	
Hopea beccariana		*Lansium domesticum*	
Hopea dryobalanoides		*Nephelium lappaceum*	
Hopea ferruginea		*Nephelium mutabile*	
Hopea nervosa		*Parartocarpus spp.*	
Hopea nutans		*Walsura pinnata*	
Hopea pentanervia			
Hopea sangal			
Hopea spp.			
Parashorea malaanonan			
Parashorea smythiesii			
Parashorea tomentella			
Shorea acuminatissima			
Shorea agami			
Shorea argentifolia			
Shorea beccariana			
Shorea faguetiana			
Shorea falciferoides			
Shorea fallax			
Shorea flaviflora			
Shorea gibbosa			
Shorea guiso			
Shorea johorensis			
Shorea laevis			
Shorea leprosula			
Shorea leptoderma			
Shorea macroptera			
Shorea macrophylla			
Shorea mecistopteryx			
Shorea ovalis			
Shorea parvifolia			
Shorea parvistipulata			
Shorea pauciflora			
Shorea pilosa			
Shorea pinanga			
Shorea seminis			
Shorea smithiana			
Shorea superba			
Shorea symingtonii			
Vatica albiramis			
Vatica dulitensis			

Table S4.2 *List of taxa classified as non-EcM trees, EcM trees, and lianas. Taxa which could not be identified to family (see ‘unknown’ below) were categorised as non-EcM trees due to high confidence in identification of EcM and liana groups. Seedlings which could not be identified to species are grouped by genus and designated ‘sp.’. Percentage of total stem abundance is presented for each taxon across all plots at first census. Where percentage of total stem abundance is >1%, taxa are presented in bold.*

Non-EcM	**%**	**EcM**	**%**	**Liana**	**%**
Achariaceae Ryparosa acuminata	0.53	*Dipterocarpaceae Anisoptera costata*	0.07	***Combretaceae Quisqualis indica***	**3.32**
Actinidiaceae Saurauia agamae	0.66	*Dipterocarpaceae Dipterocarpus caudiferus*	0.60	***Connaraceae Agelaea sp.***	**2.19**
Anacardiaceae Buchanania sessilifolia	0.53	*Dipterocarpaceae Dryobalanops lanceolata*	0.93	***Fabaceae Spatholobus sp.***	**6.24**
Anacardiaceae Mangifera quadrifida	0.07	*Dipterocarpaceae Hopea ferruginia*	0.07	**Total:**	**11.75**
Annonaceae Anaxagorea javanica	0.33	***Dipterocarpaceae Hopea plagata***	**1.66**		
Annonaceae Goniothalamus uvarioides	0.07	*Dipterocarpaceae Hopea sangal*	0.20		
Annonaceae Goniothalamus woodii	0.46	***Dipterocarpaceae Parashorea malaanonan***	**2.99**		
Annonaceae Huberantha rumphii	0.07	***Dipterocarpaceae Parashorea tomentella***	**2.39**		
Annonaceae Marsypopetalum pallidum	0.07	*Dipterocarpaceae Shorea gibbosa*	0.07		
Annonaceae Monoon erianthoides	0.07	*Dipterocarpaceae Shorea johorensis*	0.66		
Annonaceae Monoon hookerianum	0.33	*Dipterocarpaceae Shorea leprosula*	0.27		
Annonaceae Monoon sp.	0.20	*Dipterocarpaceae Shorea sp.*	0.07		
Annonaceae Neo-uvaria acuminatissima	0.13	*Dipterocarpaceae Shorea parvifolia*	0.66		
Annonaceae Orophea corymbosa	0.46	***Dipterocarpaceae Shorea pauciflora***	**1.53**		
Annonaceae Orophea myriantha	0.40	*Dipterocarpaceae Shorea seminis*	0.60		
Annonaceae Phaeanthus sp.	0.07	*Dipterocarpaceae Shorea superba*	0.07		
Annonaceae Phaeanthus splendens	0.13	*Dipterocarpaceae Shorea symingtonii*	0.07		
Annonaceae Polyalthia cauliflora	0.27	***Dipterocarpaceae Vatica dulitensis***	**1.20**		
Annonaceae Polyalthia insignis	0.07	*Fagaceae Lithocarpus sp.*	0.20		
Annonaceae Polyalthia microtus	0.07	**Total:**	**14.28**		
Annonaceae Polyalthia sp.	0.07				

Annonaceae Polyalthia obliqua	0.07
Annonaceae Polyalthia saprosma	0.13
Annonaceae Popowia hirta	0.07
Annonaceae Popowia pisocarpa	0.27
Annonaceae Pseuduvaria reticulata	0.07
Apocynaceae Kopsia pauciflora	0.60
Apocynaceae Tabernaemontana pauciflora	0.07
Calophyllaceae Calophyllum gracilipes	0.07
Calophyllaceae Calophyllum soullatri	0.07
Cannabaceae Gironniera nervosa	0.20
Celastraceae Lophopetalum javanicum	0.13
Celastraceae Lophopetalum sp.	0.93
Clusiaceae Garcinia sp.	0.07
Combretaceae Terminalia citrina	0.07
Convolvulaceae Erycibe borneensis	0.27
Cornaceae Alangium javanicum	0.20
Dilleniaceae Dillenia sp.	0.60
Ebenaceae Diospyros curranii	0.27
Ebenaceae Diospyros elliptifolia	0.13
Ebenaceae Diospyros frutescens	0.07
Ebenaceae Diospyros sp.	0.93
Ebenaceae Diospyros pilosanthera	0.13
Ebenaceae Diospyros squamifolia	0.13
Euphorbiaceae Croton argyratus	0.13
Euphorbiaceae Croton oblongus	0.27
Euphorbiaceae Dimorphocalyx murinus	0.20
Euphorbiaceae Euphorbia sp.	0.07

Euphorbiaceae Koilodepas longifolium	1.13
Euphorbiaceae Mallotus korthalsii	0.13
Euphorbiaceae Mallotus lackeyi	0.20
Euphorbiaceae Mallotus miquelianus	**15.34**
Euphorbiaceae Mallotus sp.	0.13
Euphorbiaceae Mallotus penangensis	0.07
Euphorbiaceae Mallotus stipularis	0.07
Euphorbiaceae Mallotus wrayi	0.86
Euphorbiaceae Ptychopyxis arborea	0.07
Euphorbiaceae Spathiostemon javensis	0.40
Fabaceae Acacia sp.	0.13
Fabaceae Bauhinia sp.	0.40
Fabaceae Crudia sp.	0.13
Fabaceae Fordia sp.	**1.13**
Fabaceae Fordia splendidissima	0.46
Fabaceae Peltophorum racemosom	0.07
Lauraceae Beilschmiedia sp.	0.13
Lauraceae Cinnamomum sp.	0.07
Lauraceae Eusideroxylon zwageri	0.13
Lauraceae Litsea accedens	0.07
Lauraceae Litsea caulocarpa	0.20
Lauraceae Litsea cuprea	0.07
Lauraceae Litsea sp.	0.20
Lauraceae Litsea oppositifolia	0.07
Magnoliaceae Magnolia candolii	0.07
Malvaceae Brownlowia peltata	0.27
Malvaceae Durio graveolens	0.07

Malvaceae Durio sp.	0.13
Malvaceae Microcos crassifolia	0.13
Malvaceae Microcos sp.	0.13
Malvaceae Neesia synandra	0.13
Malvaceae Pentace adenophora	**1.06**
Malvaceae Pentace laxiflora	0.73
Malvaceae Pterospermum javanicum	0.27
Malvaceae Scaphium macropodum	0.13
Melastomataceae Memecylon laevigatum	0.33
Melastomataceae Memecylon oleifolium	0.07
Melastomataceae Memecylon paniculatum	0.07
Melastomataceae Pternandra coerulescens	0.27
Meliaceae Aglaia luzoniensis	0.07
Meliaceae Aglaia sp.	**3.39**
Meliaceae Aglaia odoratissima	0.07
Meliaceae Aglaia oligophylla	0.27
Meliaceae Chisocheton sp.	0.20
Meliaceae Reinwardtiodendron humile	0.33
Meliaceae Walsura pinnata	0.07
Monimiaceae Kibara obtusa	0.20
Moraceae Ficus beccarii	0.07
Moraceae Streblus glaber	0.13
Myristicaceae Knema latericia	0.13
Myristicaceae Knema laurina	0.13
Myristicaceae Knema sp.	0.13
Myristicaceae Myristica sp.	0.07
Myrtaceae Syzygium hirtum	0.20

Myrtaceae Syzygium kunstleri	0.20
Myrtaceae Syzygium sp.	0.40
Oleaceae Chionanthus pluriflorus	0.40
Phyllanthaceae Antidesma neurocarpum	0.07
Phyllanthaceae Aporosa falcifera	0.20
Phyllanthaceae Aporosa sp.	0.20
Phyllanthaceae Baccaurea lanceolata	0.07
Phyllanthaceae Baccaurea tetrandra	0.27
Phyllanthaceae Cleistanthus hylandii	0.13
Phyllanthaceae Cleistanthus sp.	0.07
Phyllanthaceae Glochidion sp.	0.07
Phyllanthaceae Glochidion rubrum	0.46
Polygalaceae Xanthophyllum adenotus	0.13
Polygalaceae Xanthophyllum flavescens	0.13
Polygalaceae Xanthophyllum sp.	0.46
Primulaceae Ardisia colorata	0.60
Primulaceae Ardisia macrophylla	0.07
Primulaceae Ardisia sp.	**1.59**
Putranjivaceae Drypetes castilloi	0.07
Putranjivaceae Drypetes sp.	0.13
Rhamnaceae Ziziphus angustifolia	0.80
Rhamnaceae Ziziphus sp.	0.07
Rubiaceae Cowiea borneensis	0.33
Rubiaceae Ixora brevicaudata	0.07
Rubiaceae Neolamarckia cadamba	0.07
Rubiaceae Neonauclea sp.	0.13
Rubiaceae Praravinia suberosa	0.13

Rubiaceae Urophyllum glabrum	0.40
Rubiaceae Urophyllum griffithianum	0.07
Rubiaceae Urophyllum sp.	0.07
Rutaceae Clausena excavata	0.20
Rutaceae Glycosmis chlorosperma	0.07
Rutaceae Glycosmis macrantha	0.80
Rutaceae Glycosmis sp.	0.07
Rutaceae Luvunga sp.	0.33
Sabiaceae Meliosma sumatrana	0.13
Sapindaceae Allophylus cobbe	0.13
Sapindaceae Dimocarpus dentatus	0.13
Sapindaceae Dimocarpus longan	0.46
Sapindaceae Guioa pleuropteris	0.13
Sapindaceae Lepisanthes tetraphylla	0.07
Sapindaceae Nephelium ramboutan-ake	0.13
Sapindaceae Paranephelium xestophyllum	0.13
Sapotaceae Madhuca elmeri	0.13
Solanaceae Solanum sp.	0.13
Symplocaceae Symplocos fasciculata	0.20
Violaceae Rinorea bengalensis	0.13
Vitaceae Ampelocissus sp.	0.07
Vitaceae Leea aculeata	**1.33**
Vitaceae Leea indica	0.07
Vitaceae Rinorea sp.	0.07
Vitaceae Tetrastigma sp.	0.20
Unknown	**18.86**
Total:	**73.97**

Table S4.3 *Additional descriptive statistics for models presented in table 4.3, produced using alternative factor variable baselines. Continuous variable estimates and random effects are presented only in table 4.3 as these do not vary dependent upon factor baseline.*

Baseline		**Variable**	**Estimate**	**Error**	**Z-value**	**P-value**
Forest Type	**Functional Group**					
Model 1 (Survival)						
Unlogged	Non-EcM	(intercept)	1.080	0.141	7.636	<0.001***
		Natural Regeneration	-0.238	0.275	-0.865	0.387
		Active Restoration	-0.986	0.226	-4.360	<0.001***
		EcM Trees	-1.265	0.164	-7.705	<0.001***
		Lianas	0.124	0.179	0.692	0.489
		Nat. Regen. : EcM Trees	1.312	0.296	4.428	<0.001***
		Nat. Regen. : Lianas	-0.671	0.298	-2.249	0.025*
		Act. Rest. : EcM Trees	0.389	0.325	1.197	0.231
		Act. Rest. : Lianas	-0.058	0.337	-0.172	0.864
	EcM	(intercept)	-0.185	0.195	-0.949	0.343
		Natural Regeneration	1.075	0.358	3.004	0.003**
		Active Restoration	-0.597	0.360	-1.658	0.097
		Non-EcM Trees	1.265	0.164	7.705	<0.001***
		Lianas	1.388	0.224	6.174	<0.001***
		Nat. Regen. : Non-EcM Trees	-1.312	0.296	-4.428	<0.001***
		Nat. Regen. : Lianas	-1.983	0.389	-5.090	<0.001***
		Act. Rest. : Non-EcM Trees	-0.389	0.325	-1.197	0.231
		Act. Rest. : Lianas	-0.447	0.442	-1.011	0.312
	Lianas	(intercept)	1.204	0.209	5.768	<0.001***
		Natural Regeneration	-0.908	0.370	-2.454	0.014*
		Active Restoration	-1.043	0.375	-2.785	0.005**
		Non-EcM Trees	-0.124	0.179	-0.692	0.489
		EcM Trees	-1.389	0.225	-6.174	<0.001***
		Nat. Regen. : Non-EcM Trees	0.671	0.298	2.249	0.025*
		Nat. Regen. : EcM Trees	1.983	0.390	5.090	<0.001***
		Act. Rest. : Non-EcM Trees	0.058	0.337	0.172	0.864
		Act. Rest. : EcM Trees	0.447	0.442	1.011	0.312
Nat. Regen.	Non-EcM	(intercept)	0.842	0.224	3.755	<0.001***
		Unlogged	0.238	0.275	0.865	0.387
		Active Restoration	-0.748	0.294	-2.543	0.011*
		EcM Trees	0.047	0.247	0.192	0.848
		Lianas	-0.547	0.239	-2.291	0.022*
		Unlogged : EcM Trees	-1.312	0.296	-4.428	<0.001***
		Unlogged : Lianas	0.671	0.298	2.249	0.025*
		Act. Rest. : EcM Trees	-0.924	0.372	-2.480	0.013*
		Act. Rest. : Lianas	0.613	0.372	1.647	0.100
	EcM	(intercept)	0.889	0.291	3.059	0.002**
		Unlogged	-1.075	0.358	-3.004	0.003**
		Active Restoration	-1.671	0.431	-3.878	<0.001***
		Non-EcM Trees	-0.047	0.247	-0.192	0.848
		Lianas	-0.594	0.319	-1.861	0.063
		Unlogged : Non-EcM Trees	1.312	0.296	4.428	<0.001***
		Unlogged : Lianas	1.983	0.390	5.090	<0.001***

		Act. Rest. : Non-EcM Trees	0.924	0.372	2.480	0.013*
		Act. Rest. : Lianas	1.536	0.496	3.100	0.002**
	Lianas	(intercept)	0.295	0.297	0.994	0.320
		Unlogged	0.908	0.370	2.454	0.014*
		Active Restoration	-0.135	0.435	-0.311	0.756
		Non-EcM Trees	0.547	0.239	2.290	0.022*
		EcM Trees	0.594	0.319	1.861	0.063
		Unlogged : Non-EcM Trees	-0.671	0.298	-2.249	0.025*
		Unlogged : EcM Trees	-1.983	0.390	-5.090	<0.001***
		Act. Rest. : Non-EcM Trees	-0.613	0.372	-1.647	0.100
		Act. Rest. : EcM Trees	-1.536	0.496	-3.100	0.002**
Act. Rest.	Non-EcM	(intercept)	0.094	0.186	0.506	0.613
		Unlogged	0.986	0.226	4.360	<0.001***
		Natural Regeneration	0.748	0.294	2.542	0.011*
		EcM Trees	-0.876	0.280	-3.126	0.002**
		Lianas	0.066	0.286	0.232	0.817
		Unlogged : EcM Trees	-0.389	0.325	-1.197	0.231
		Unlogged : Lianas	0.058	0.337	0.172	0.864
		Nat. Regen. : EcM Trees	0.924	0.372	2.480	0.013*
		Nat. Regen. : Lianas	-0.613	0.372	-1.647	0.100
	EcM	(intercept)	-0.782	0.310	-2.523	0.012*
		Unlogged	0.597	0.360	1.658	0.097
		Natural Regeneration	1.671	0.431	3.878	<0.001***
		Non-EcM Trees	0.876	0.281	3.126	0.002**
		Lianas	0.942	0.382	2.469	0.014*
		Unlogged : Non-EcM Trees	0.389	0.324	1.197	0.231
		Unlogged : Lianas	0.447	0.442	1.010	0.312
		Nat. Regen. : Non-EcM Trees	-0.924	0.372	-2.480	0.013*
		Nat. Regen. : Lianas	-1.536	0.496	-3.100	0.002**
	Lianas	(intercept)	0.160	0.317	0.506	0.613
		Unlogged	1.043	0.375	2.785	0.005**
		Natural Regeneration	0.135	0.435	0.310	0.756
		Non-EcM Trees	-0.066	0.286	-0.231	0.817
		EcM Trees	-0.942	0.382	-2.468	0.014*
		Unlogged : Non-EcM Trees	-0.058	0.337	-0.172	0.864
		Unlogged : EcM Trees	-0.447	0.442	-1.011	0.312
		Nat. Regen. : Non-EcM Trees	0.613	0.372	1.647	0.100
		Nat. Regen. : EcM Trees	1.536	0.496	3.100	0.002**
Model 2 ($\textbf{RGR}_{\textbf{Height}}$)						
Unlogged	Non-EcM	(intercept)	-8.769	0.078	-112.92	<0.001***
		Natural Regeneration	0.190	0.162	1.17	0.241
		Active Restoration	0.439	0.141	3.12	0.002**
		EcM Trees	0.326	0.095	3.42	<0.001***
		Lianas	-0.017	0.086	-0.19	0.846
		Nat. Regen. : EcM Trees	-0.727	0.148	-4.91	<0.001***
		Nat. Regen. : Lianas	-0.365	0.184	-1.99	0.047*
		Act. Rest. : EcM Trees	0.377	0.225	1.67	0.095
		Act. Rest. : Lianas	-0.761	0.223	-3.41	<0.001***
	EcM	(intercept)	-8.443	0.116	-72.58	<0.001***
		Natural Regeneration	-0.536	0.199	-2.69	0.007**

		Active Restoration	0.816	0.248	3.30	<0.001***
		Non-EcM Trees	0.326	0.095	-3.42	<0.001***
		Lianas	-0.343	0.123	-2.79	0.005**
		Nat. Regen. : Non-EcM Trees	0.727	0.148	4.91	<0.001***
		Nat. Regen. : Lianas	0.362	0.224	1.61	0.107
		Act. Rest. : Non-EcM Trees	-0.377	0.225	-1.67	0.095
		Act. Rest. : Lianas	-1.138	0.310	-3.67	<0.001***
	Lianas	(intercept)	-8.786	0.108	-81.63	<0.001***
		Natural Regeneration	-0.175	0.225	-0.78	0.438
		Active Restoration	-0.323	0.242	-1.33	0.182
		Non-EcM Trees	0.017	0.086	0.19	0.846
		EcM Trees	0.342	0.123	2.79	0.005**
		Nat. Regen. : Non-EcM Trees	0.365	0.184	1.99	0.047*
		Nat. Regen. : EcM Trees	-0.362	0.224	-1.61	0.107
		Act. Rest. : Non-EcM Trees	0.762	0.223	3.41	<0.001***
		Act. Rest. : EcM Trees	1.139	0.310	3.68	<0.001***
Nat. Regen.	Non-EcM	(intercept)	-8.579	0.136	-63.27	<0.001***
		Unlogged	-0.190	0.162	-1.17	0.241
		Active Restoration	0.248	0.191	1.30	0.192
		EcM Trees	-0.401	0.113	-3.54	<0.001***
		Lianas	-0.382	0.162	-2.35	0.019*
		Unlogged : EcM Trees	0.727	0.148	4.91	<0.001***
		Unlogged : Lianas	0.365	0.184	1.99	0.047*
		Act. Rest. : EcM Trees	1.104	0.234	4.73	<0.001***
		Act. Rest. : Lianas	-0.396	0.263	-1.51	0.132
	EcM	(intercept)	-8.980	0.156	-57.63	<0.001***
		Unlogged	0.537	0.199	2.69	0.007**
		Active Restoration	1.352	0.281	4.81	<0.001***
		Non-EcM Trees	0.401	0.113	3.54	<0.001***
		Lianas	0.019	0.188	0.10	0.919
		Unlogged : Non-EcM Trees	-0.727	0.148	-4.91	<0.001***
		Unlogged : Lianas	-0.362	0.224	-1.61	0.107
		Act. Rest. : Non-EcM Trees	-1.104	0.234	-4.73	<0.001***
		Act. Rest. : Lianas	-1.500	0.342	-4.39	<0.001***
	Lianas	(intercept)	-8.961	0.193	-46.37	<0.001*
		Unlogged	0.195	0.225	0.78	0.438
		Active Restoration	-0.148	0.291	-0.51	0.612
		Non-EcM Trees	0.382	0.162	2.35	0.019*
		EcM Trees	-0.019	0.188	-0.10	0.919
		Unlogged : Non-EcM Trees	-0.365	0.184	-1.99	0.047*
		Unlogged : EcM Trees	0.362	0.224	1.61	0.107
		Act. Rest. : Non-EcM Trees	0.396	0.263	1.51	0.132
		Act. Rest. : EcM Trees	1.500	0.342	4.39	<0.001***
Act. Rest.	Non-EcM	(intercept)	-8.330	0.120	-69.20	<0.001***
		Unlogged	0.439	0.141	-3.12	0.002**
		Natural Regeneration	-0.248	0.191	-1.30	0.193
		EcM Trees	0.703	0.204	3.44	<0.001***
		Lianas	-0.778	0.207	-3.76	<0.001***
		Unlogged : EcM Trees	-0.377	0.225	-1.67	0.095
		Unlogged : Lianas	0.761	0.223	3.41	<0.001***
		Nat. Regen. : EcM Trees	-1.104	0.234	-4.73	<0.001***

		Nat. Regen. : Lianas	0.396	0.263	1.51	0.132
	EcM	(intercept)	-7.628	0.221	-34.52	<0.001***
		Unlogged	-0.816	0.248	-3.30	<0.001***
		Natural Regeneration	-1.352	0.281	-4.81	<0.001***
		Non-EcM Trees	-0.703	0.204	-3.44	<0.001***
		Lianas	-1.481	0.286	-5.18	<0.001***
		Unlogged : Non-EcM Trees	0.377	0.225	1.67	0.095
		Unlogged : Lianas	1.139	0.310	3.68	<0.001***
		Nat. Regen. : Non-EcM Trees	1.104	0.234	4.73	<0.001***
		Nat. Regen. : Lianas	1.500	0.342	4.39	<0.001***
	Lianas	(intercept)	-9.109	0.218	-41.82	<0.001***
		Unlogged	0.323	0.242	1.33	0.182
		Natural Regeneration	0.148	0.291	0.51	0.612
		Non-EcM Trees	0.778	0.207	3.76	<0.001***
		EcM Trees	1.481	0.286	5.18	<0.001***
		Unlogged : Non-EcM Trees	-0.762	0.223	-3.41	<0.001***
		Unlogged : EcM Trees	-1.138	0.310	-3.68	<0.001***
		Nat. Regen. : Non-EcM Trees	-0.396	0.263	-1.61	0.132
		Nat. Regen. : EcM Trees	-1.500	0.342	-4.39	<0.001***

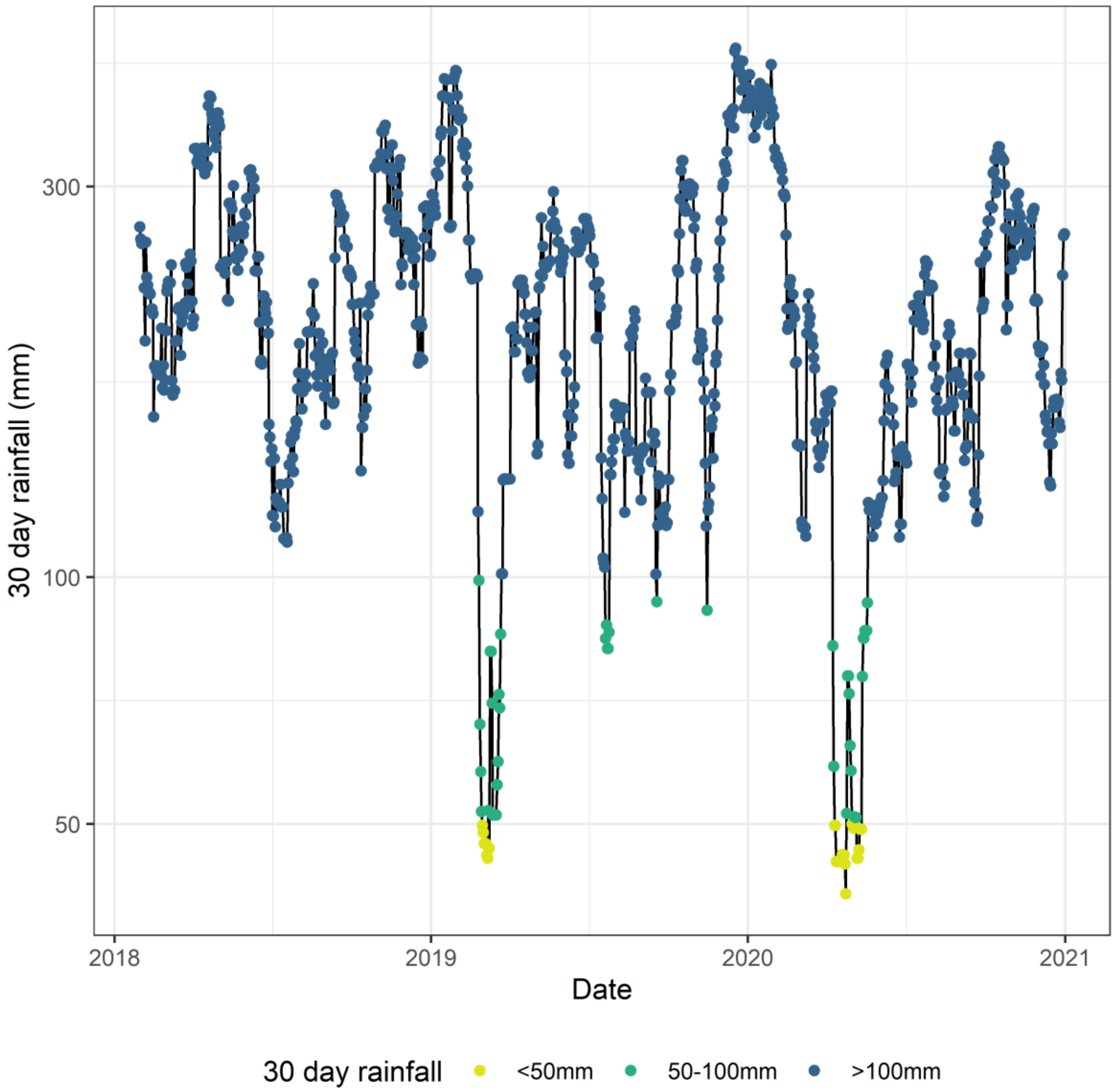


Figure S4.1 *30 day moving sums of rainfall at the Danum Valley Field Centre weather station (SEARRP, 2021). Points are coloured to highlight levels of drought using thresholds of 50 mm and 100 mm rainfall within a 30 day period.*

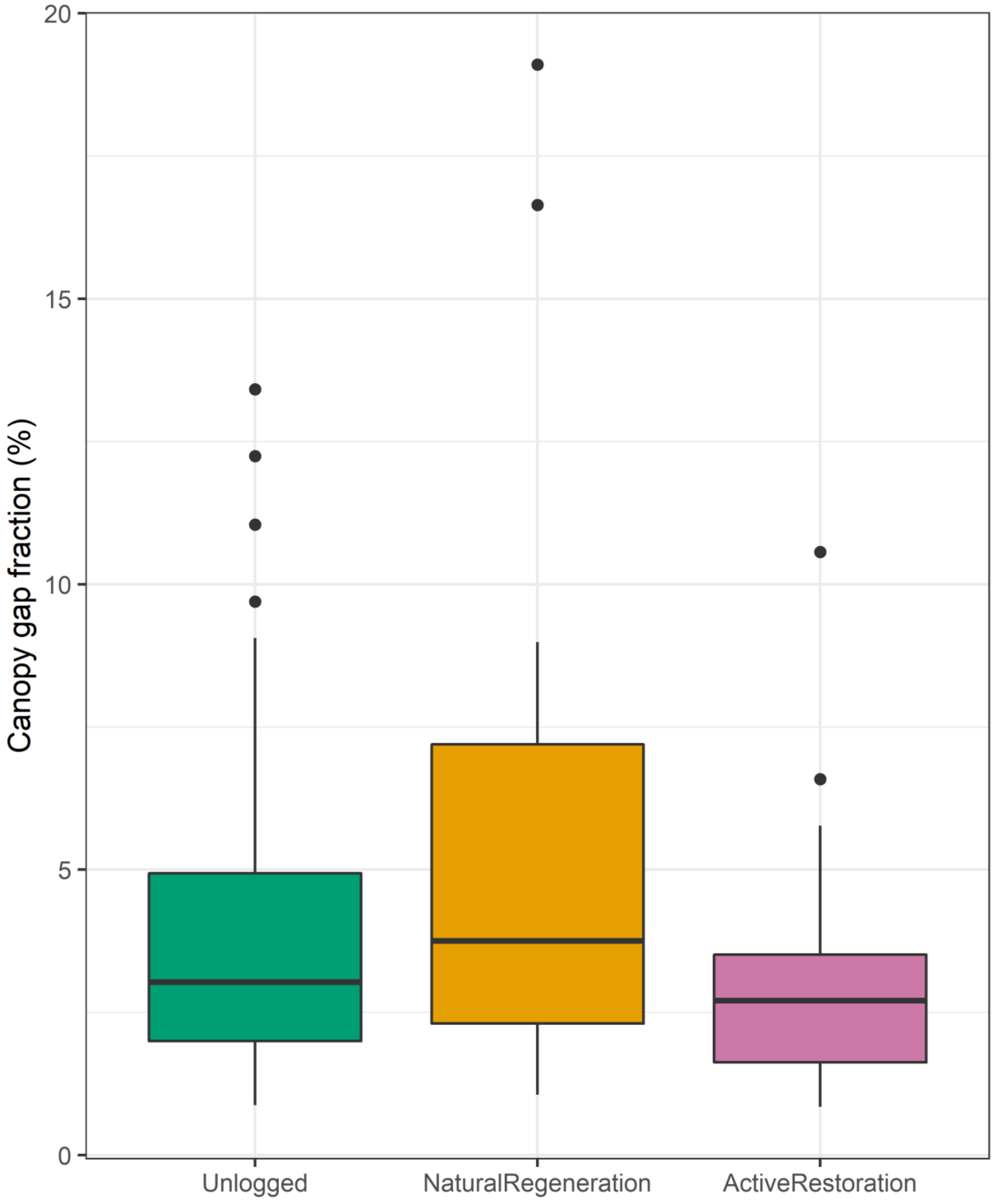


Figure S4.2 *Canopy gap fraction (%) above each seedling station in unlogged, naturally regenerating, and actively restored forest.*

Chapter 5: General Discussion

Photo: Tambi and Yoel leading the way home from our most isolated plots
[credit: Robin Hayward]

Chapter collaborators: Robin Hayward, Lindsay Banin, Daniel Chapman & Daisy Dent.

This chapter was written by RH and all authors commented on a draft of this chapter.

5.1.0 Background

The majority of the forested tropics have been selectively logged (Laurance et al., 2014) and forests in Southeast Asia have been particularly exploited, with 8% of the world's logging concessions (by area) located on the island of Borneo alone (Hansen et al., 2010, Laurance and Edwards, 2014). Old-growth tropical forests are some of the most biodiverse ecosystems on the planet (Dirzo and Raven, 2003) and sequester 2.7 ± 0.7 Pg of carbon each year (Pan et al., 2011), so there is substantial interest in their ability to recover after logging. Selective logging is intended to be carried out at regular intervals, after forests have had a chance to recover valuable timber and ecosystem functioning, but there is pressure to repeat harvests after only relatively brief recovery periods – in Borneo, intervals are frequently <20 years (Reynolds et al., 2011). Active restoration has been used with the aim of accelerating recovery of selectively logged forests. Restoration techniques commonly involve cutting competitive low-value stems to accelerate biomass regeneration, replanting fast-growing timber species, and also planting native species to help restore diversity and richness within the tree community (Moura Costa, 1996, Lamb et al., 2005, Finegan, 2014, Osuri et al., 2019). However, the long-term impacts of these restoration strategies, as well as where and when it is appropriate to apply them, remain unclear (Chazdon et al., 2021). It is therefore vital to study recovery times of biomass and community composition within logged and restored tree communities, to both understand the conservation value of logged forests and to better inform management of production forests.

Natural regeneration of biomass in selectively logged forests leads to higher rates of carbon sequestration, when compared with old growth forests within the same region, because of the greater availability of growth resources (Gourlet-Fleury et al., 2013, Poorter et al., 2016) however, complete recovery of biomass is likely to take >50 years (Foody and Cutler, 2003, Nagaraja et al., 2005, Putz et al., 2012). Using active restoration techniques, biomass regeneration can be accelerated by >50% (Philipson et al., 2020). Tree community composition and biodiversity tend to recover more slowly than biomass (Appanah et al., 1990); late successional species in particular may take hundreds of years to fully recover (Chazdon, 2003) but long-term data regarding tree community change following selective logging are still relatively sparse. The outcomes of active restoration of logged forests have varied, in some cases with logged forest community composition converging on that of nearby unlogged forest (Osuri et al.,

2019) and, in others, causing greater community divergence from unlogged forest than in naturally regenerating forest (de Avila et al., 2015).

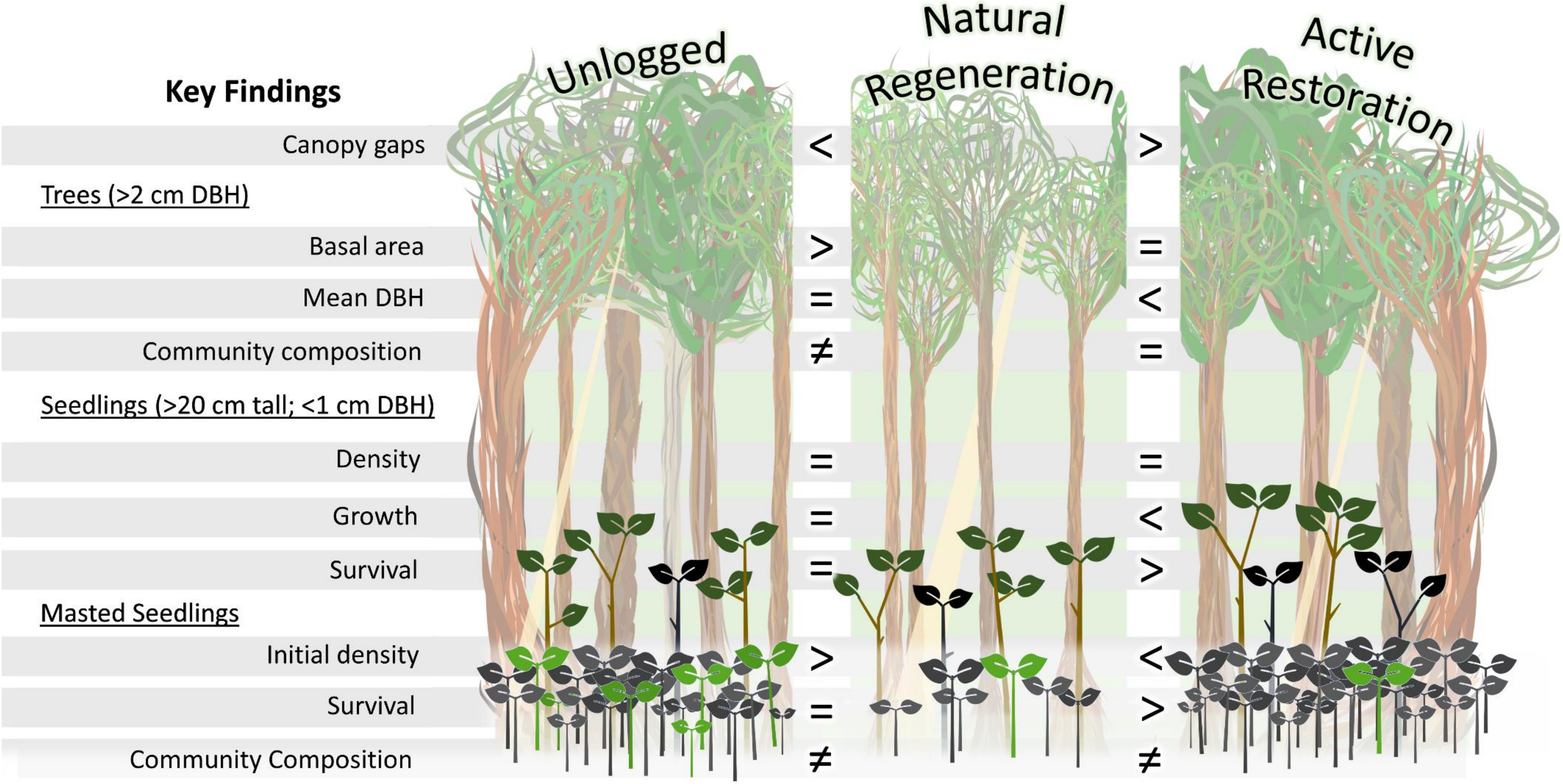
The overall aim of this thesis was to determine how selective logging and active restoration affect tree abundance, dynamics, and community composition across life stages. My research illuminates the ways in which tree communities at each life stage (seeds, seedlings, saplings, poles, and adult trees; see table 5.1) are influenced by selective logging and active restoration. Throughout this thesis I highlight that successful recruitment and growth of trees at every life stage is critical for the long-term recovery of biomass and tree community composition in logged tropical forests, and in this study I found that survival and growth of seedlings varied significantly across forest types.

5.2.0 Discussion and summary of key results

In this thesis I have studied stems across a range of life stages and I have used overlapping terminology to describe stems of differing size (particularly in chapters 3 & 4, which both refer to seedlings). For clarity within this discussion, I will refer to stems by the definitions presented in table 5.1. Likewise, chapters 2 & 3 refer to dipterocarps and non-dipterocarps while chapter 4 refers to EcM trees and non-EcM trees. Only 1.4% of EcM tree seedlings recorded in chapter 4 were non-dipterocarps and no non-EcM trees were dipterocarps, therefore I will simplify this discussion by treating EcM trees and dipterocarps synonymously, and likewise non-EcM trees and non-dipterocarps.

Table 5.1 *Glossary of terms for the stem size-classes referred to in this discussion. Trees ≥60 cm DBH are typically highly fecund in Southeast Asian forests and have therefore been labelled 'parent' trees for the purpose of this discussion (Sist et al., 2003, Tani et al., 2016). The chapter number in which each size-class was studied is also presented.*

Term	Description	Chapter
Parent trees	≥60 cm DBH	2
Trees	≥10 cm DBH	2
Poles	5-10 cm DBH	2
Saplings	2-5 cm DBH	2
Established seedlings	≥20 cm tall and <1 cm DBH	4
Masted seedlings	Germinated in 2019, after a mast fruiting event	3



Key Findings	Unlogged		Natural Regeneration		Active Restoration
Canopy gaps		<		>	
Trees (>2 cm DBH)					
Basal area		>		=	
Mean DBH		=		<	
Community composition		≠		=	
Seedlings (>20 cm tall; <1 cm DBH)					
Density		=		=	
Growth		=		<	
Survival		=		>	
Masted Seedlings					
Initial density		>		<	
Survival		=		>	
Community Composition		≠		≠	

***Figure 5.1** Summary of key findings by size-class: trees (≥2 cm DBH; Chapter 2), established seedlings (≥20 cm tall; <1 cm DBH; tracked over 2.5 years; Chapter 4), and masted seedlings (originating during the 2019 mast fruiting event then tracked for 1.5 years; Chapter 3). Relative values across forest types (unlogged, natural regeneration, and active restoration) are indicated as less than or greater than (>/<), equal to (=), or not equal to (≠) one another.*

5.2.1 Selective logging reduces the density of smaller trees

Saplings, *poles*, and *trees* (see table 5.1) collectively had lower basal area and stem density in naturally regenerating logged forest than in unlogged forest (chapter 2). This finding was primarily driven by *saplings* and *poles*. Density of these smaller stems did not change with forest age along our chronosequence, 23-35 years post-logging. This supports similar findings from the region that naturally regenerating logged forests have reduced above ground carbon density compared to unlogged forests (Philipson et al., 2020). In contrast to other small stems, I found that dipterocarp *poles* increased in density over time, suggesting that dipterocarps may take longer to recover than the plant community as a whole. Unlike smaller stems, *trees* occurred at equal densities in logged and unlogged forest – a finding in agreement with other Bornean forests 5-15 and 22 years post-logging (Slik et al., 2002, Hector et al., 2011). Lower numbers of *parent trees* (see table 5.1) in naturally regenerating logged forest than in unlogged forest however, are a sign that recovery is still ongoing and the rarity of these large, reproductive stems (Sist et al., 2003, Tani et al., 2016) could partially explain why greater densities of *saplings* and *poles* have yet to recruit in naturally regenerating logged forest.

5.2.2 Active restoration accelerates biomass recovery

Saplings and *poles* occurred at lower densities in actively restored than in naturally regenerating logged forest and densities increased with time since logging in actively restored forest, while there was no change with time since logging in naturally regenerating forest (chapter 2). There was no difference in density of *trees* between naturally regenerating and actively restored forest, nor was there a trend of changing density with time since logging in either forest type. Total basal area of *saplings*, *poles*, and *trees* did not differ as a result of restoration, however mean DBH was greater in actively restored forest. Fewer, larger stems in actively restored forest, suggests that forest structure is altered by active restoration with potential for increased aboveground biomass. Active restoration of selectively logged forest in Danum Valley was therefore successful in achieving the primary goals of land managers at the time of intervention: accelerating recovery of aboveground carbon and timber stocks (Moura Costa, 1996, Face the Future, 2011). This finding, from chapter 2, matches broader results from

Sabah (Philipson et al., 2020), which suggest recovery of aboveground carbon could be accelerated by climber cutting and enrichment planting. This study finds that 40 year old actively restored forest has equivalent carbon storage to ~60 year old naturally regenerating forest. Accelerated aboveground biomass accumulation has also been recorded in actively restored forests elsewhere in the tropics, e.g. Costa Rica (6-8 years post-logging; Holl and Zahawi, 2014) and Uganda (18 years post-logging; Wheeler et al., 2016).

5.2.3 Logging affects tree community composition but restoration does not.

Community composition of *saplings*, *poles*, and *trees* differed between unlogged and naturally regenerating logged forest, with unlogged forest showing greater inter-plot community dissimilarity than selectively logged plots. However, density of dipterocarp stems (the most represented family across forest types) was only reduced amongst *poles* and their community composition did not differ between logged and unlogged forest at any size class. There were 23 significant indicator species for unlogged forest but no indicator species for logged forest, demonstrating that there are elements of the community missing in disturbed forests – they may be rarer and take longer to arrive back into a disturbed system or may be more sensitive to the novel microenvironments.

Desirable co-benefits of active restoration to tree community composition, species richness, and diversity, in addition to increased biomass – as targeted by the initial planting of non-timber species (Face the Future, 2011) – were not detected in Danum. *Saplings*, *poles*, and *trees* remained compositionally distinct from unlogged forest in both naturally regenerating and actively restored forest, while being similar to each other. This can be viewed as a positive outcome in light of the potential for enrichment planting to lead to more homogeneous community structures, skewed towards planted species over naturally occurring taxa (Hector et al., 2011, Holl and Brancalion, 2020). *Trees* had marginally increased species evenness in actively restored forest, relative to naturally regenerating forest, suggesting increased homogeneity in the *tree* community of restored forests. However the absence of this effect amongst smaller stems suggests that similar levels of heterogeneity to naturally regenerating forest may yet recruit through to established trees with time.

5.2.4 Logging reduces mast but seedling survival and growth match unlogged forest.

Naturally regenerating logged forest produced an order of magnitude fewer *masted seedlings* (see table 5.1) than intact forest during a mast fruiting event in 2019 (chapter 3). Initial *masted seedling* densities in naturally regenerating logged forest were substantially reduced compared to unlogged forest. The mechanisms behind this remain unclear, however reduced numbers of highly reproductive *parent trees* (Sist et al., 2003, Tani et al., 2016) (for which I found a marginal effect in chapter 2; see section 5.2.1), less favourable environmental conditions to support fruit production, differing community compositions, and differences in seed viability may all have contributed to mast limitation. Seed predators may also play an important role in explaining seedling densities across our sites. A previous study from Kalimantan (Curran and Webb, 2000), which recorded reduced dipterocarp seedling densities following mast in selectively logged compared to unlogged forest, attributed this to earlier and more intensive seed predation than in unlogged forest.

Over the first 1.5 years following mast, *masted seedlings* in unlogged forest and naturally regenerating logged forest faced similar exponential declines in abundance, and were reduced to 5.37% and 7.30% of their original population sizes respectively. *Masted seedling* mortality was greater in plots with higher canopy gap fractions (more direct insolation) across forest types. *Masted seedlings* declined in abundance at similar exponential rates in unlogged and naturally regenerating logged forest (chapter 3), suggesting that abiotic conditions were suitable for *masted seedling* establishment in both forest types and that their predation was constrained sufficiently within these forest types to avoid total consumption of the *masted seedling* community, either by predator satiation (Janzen, 1971) or by food scarcity relative to the surrounding area, causing seed predators to move on.

Established seedlings (see table 5.1) occurred at similar densities in unlogged forest and naturally regenerating logged forest (chapter 4). Likewise, tracked over a period of ~2.5 years, the majority of the *established seedling* cohort (non-dipterocarps) had similar rates of survival and growth in both forest types. Dipterocarps had lower survival and higher growth in unlogged than naturally regenerating forest, while lianas had higher survival in unlogged forest but did not differ in growth between the two forest types. This suggests that different disturbance levels between forest types may still affect seedling dynamics of some taxa 25-37 years post-logging, despite broad similarities in rates of survival and growth across the cohort, that will have knock-on effects on the future tree community. I recorded greater canopy openness in naturally regenerating forest than unlogged forest (chapters 3 & 4), which might help to explain this effect amongst dipterocarps, which can survive long periods of suppression in the understory but grow quickly when canopy gaps are opened (Brown, 1993, Delissio et al., 2002). Decreased survival of late successional lianas – which do not respond so strongly to light availability as disturbance specialist lianas – in naturally regenerating logged forest might be partially explained by the absence of preferred host tree species, as has been observed previously in Malaysian Borneo (Magrach et al., 2016) and matches our findings of distinct *tree* community compositions between unlogged and logged forests (chapter 2; section 5.2.3). There was a trade-off between growth and survival across all functional groups and forest types. In both forest types likelihood of *established seedling* survival increased with height at first census, suggesting that larger *established seedlings* were less challenged by adverse environmental conditions in the naturally regenerating forests.

5.2.5 Restoration increases mast but lowers seedling survival.

Chapter 3 revealed dramatic differences between the *masted seedling* dynamics of unlogged, naturally regenerating, and actively restored forests. An order of magnitude more seedlings were masted in actively restored forest than naturally regenerating forest, approximately matching the *masted seedling* density of unlogged forest. However, actively restored *masted seedling* abundance then declined more rapidly than in either unlogged or naturally regenerating forest, particularly over the first six months post-mast, such that fewer *masted seedlings* remained in actively restored (0.85%) than either unlogged (5.37%) or naturally regenerating forest (7.30%) by 1.5 years post-mast. This suggests that, although established trees had regained fecundity, conditions in restored forest were not conducive to *masted seedling* establishment, possibly due to the combined effects of greater seed predation, lower genetic diversity (Nutt et al., 2016, Tito de Morais et al., 2020, Nef et al., 2021), and differences in local environmental conditions, such as comparatively low light (recorded in chapters 3 & 4), commonly recorded within restored forests.

Low densities of *masted seedlings* in actively restored forest 1.5 years post-mast (chapter 3) reflected densities of *established seedlings* in chapter 4, where density was approximately equal in naturally regenerating and actively restored forests but marginally lower than in unlogged forest. While *established seedling* survival in actively restored forest was lower than in other forest types, this was in trade-off with increased growth. Surviving stems may therefore have gained a competitive advantage by recruiting through to larger size classes, since larger seedlings have both higher survival (chapter 4) and grow more rapidly in response to canopy gaps than smaller individuals (Brown et al., 1992, Brown, 1993). The few surviving *established seedlings* with rapid growth may be sufficient to sustain the canopy community, given the typically low replacement rates of tropical forests (Hubbell, 1979, Zhang and Lin, 1997). However, high mortality amongst seedlings remains a cause for further study, particularly given that responses differ between species and functional groups – as I saw in chapters 3 & 4 – and that mortality causes community composition to diverge amongst forest types (chapter 3).

5.2.6 Logging and restoration drive differences amongst masted dipterocarps.

Masted seedling community composition differed between unlogged, naturally regenerating, and actively restored forests. Community composition of *masted* seedlings in naturally regenerating and actively restored forest converged during the first six months post-mast but became more distinct from unlogged forest (chapter 3), possibly due to high rates of mortality amongst the progeny of stems planted during active restoration. *Shorea johorensis* and *Shorea leprosula* were both planted during active restoration and, as *masted seedlings*, were indicator species of both unlogged and actively restored forest at census 1, then only of unlogged forest by census 2, lending support to this theory. Across all forest types, differences in the seedling community may have been primarily driven by densities of dipterocarps, given that non-dipterocarp stems did not differ in average density across forest types, possibly due to non-obligate association with mast reproduction. However, *Koompassia excelsa* (unlogged), *Pterospermum javanicum* (natural regeneration), and *Buchanania sessilifolia* (active restoration) were all non-dipterocarp indicator species across multiple censuses. Dipterocarps comprised similar percentages of *masted seedlings* in unlogged (88.0%)

and restored forests (79.2%) but were less relatively abundant in naturally regenerating logged forest (50.9%), suggesting that dipterocarp seedlings were more limited by seed production and/or seed survival-to-germination than other taxa in naturally regenerating forest, compared to other forest types. This could be explained by differences in community composition amongst reproductive stems in unlogged and naturally regenerating forests (chapter 2). Although the reproductive tree community of restored forest also differed from unlogged forest, restored forest stems had larger mean DBH than naturally regenerating forest (chapter 2). Larger trees are more fecund, potentially explaining why restored forests produced large numbers of *masted seedlings* (Sist et al., 2003). Across forest types, dipterocarp *masted seedlings* were found at higher densities in plots with a higher basal area of dipterocarp trees >20 cm DBH.

After 1.5 years, dipterocarps remained 90.8% of the *masted seedling* community in unlogged forest and 70.6% in restored forest but were reduced to 35.0% of stems in naturally regenerating forest. Dipterocarps were therefore particularly limited in survival post-mast in naturally regenerating forest. Dipterocarps drove the majority of *masted seedling* mortality across all forest types and mortality was highest for both dipterocarps and non-dipterocarps in actively restored forest. The dipterocarp *Parashorea malaanonan* was a significant indicator of both unlogged and naturally regenerating forest at first census but was lost from naturally regenerating forest by 1.5 years post-mast. Lower survival of dipterocarp *masted seedlings*, relative to other taxa, in naturally regenerating compared to unlogged forest could be explained by greater exploitation from dipterocarp-specific seed predators in naturally regenerating forest, as has been reported previously in Kalimantan (Curran and Leighton, 2000).

5.2.7 Established seedling dynamics are affected by restoration, not logging.

Survival amongst the *established seedling* community was similar in unlogged and naturally regenerating forests, however survival differed within functional groups. Dipterocarp *established seedlings* had higher likelihoods of survival in naturally regenerating forest compared to non-dipterocarps and lianas. This contrasts with our finding of lower survival among dipterocarp *masted seedlings* than non-dipterocarps in naturally regenerating forest, however the *established seedling* community likely contains more stems from species that do not obligately mast and may be driving this difference in mortality rates amongst seedling size classes. The relative palatability of dipterocarp seedlings at different stages of development may also play a role in determining levels of predation, as dipterocarp leaves are more vulnerable to predation during growth than at full size (Howlett and Davidson, 2001). In *established* seedlings, this mechanism may also support the trade-off between survival and growth as actively growing seedlings that produce new leaves are more vulnerable to predators than seedlings with supressed growth (Howlett and Davidson, 2001). Trade-offs between growth and survival have been well documented within the literature (Figueira et al., 2008, Inman-Narahari et al., 2014, Philipson et al., 2014) and I report these trade-offs directly in chapter 4, suggesting that, at early life stages, dipterocarp seedlings grow faster in unlogged than naturally regenerating logged forest. This reduced growth of dipterocarp seedlings in naturally regenerated forest may delay successional change in these forests with repercussions for the rate at which mature tree community composition is able to recover and may feed back into the reduced density of dipterocarp *poles* I observed in naturally regenerating forest in chapter 2.

The representation of different functional groups of *established seedlings* did not differ between actively restored and naturally regenerating logged forest (chapter 4), however at first census, there were fewer *established seedlings* of dipterocarps in actively restored than unlogged forest. After 2.5 years, density of these *established seedlings* did not differ across forest types but non-dipterocarp tree and liana *established seedlings* were less abundant in actively restored than unlogged forest. The majority of *established seedlings* were non-dipterocarp trees across forest types at each census. Across all functional groups *established seedling* survival was lowest in actively restored forest, however this difference was more substantial amongst dipterocarps than non-dipterocarp trees or lianas. For both dipterocarps and non-dipterocarp tree *established seedlings*, trade-offs against growth meant that growth was highest in actively restored forest. High growth amongst trees in actively restored forest and similar rates of liana growth across unlogged and restored forests, suggest that biomass recovery may accelerate into the future, however further evidence is needed to confirm that rates of survival are sufficient for all taxa to recruit. More research is therefore required to uncover and mitigate the mechanisms that limit survival of stems in actively restored forest over other forest types.

5.3.0 Future work

Throughout this thesis I highlight the necessity for greater understanding of long term tree community dynamics following active restoration. In particular, I present for the first time to my knowledge, a study recording levels of in-situ seed production and subsequent mortality of seedlings in actively restored forest following a naturally occurring mast (chapter 3). My results revealed high levels of mortality in actively restored forest, relative to both unlogged and naturally regenerating forest, for both newly *masted seedlings* (chapter 3) and *established seedlings* (chapter 4). I have only been able to speculate about the drivers of these observed differences however, and our understanding of these dynamics would benefit from more focused long term monitoring of *masted seedlings* and the possible biotic (e.g., seed predators and low genetic diversity) and abiotic (e.g., drought) drivers of their fates. I suggest that establishing predator exclusion experiments across forest types and comparing with controls – as conducted in naturally regenerating and unlogged forests in Kalimantan by Curran and Webb (2000) – at a future mast would allow us to ask the question: *does seedling predation following mast fruiting drive higher mortality in actively restored than unlogged forests?* Furthermore, given the extensiveness of selective logging throughout the tropics and the variable techniques and goals of active restoration, these observations should be repeated in multiple locations and in response to a variety of forest silvicultural strategies. Of particular interest would be observations of seedlings across forests with distinct genetic diversity of seedlings planted during restoration. This is relevant to the long-term sustainability of all restored tropical forests, not just those with mast fruiting (Fremout et al., 2021). Studies that pair in-situ measurements of seedling and parent tree genetic diversity with demographic parameters would enable us to address the question: *does low genetic diversity amongst seedlings in actively restored forest drive mortality through increased susceptibility to pathogens?* Further research should also observe relative growth rates of individual seedlings. In chapters 3 & 4 I observed differences in survival between dipterocarp *masted seedlings* and *established seedlings,* but I was only able to record trade-offs between survival and growth in chapter 4 due to the logistical difficulties of rapidly tagging and measuring all seedlings across a landscape, as opposed to simply counting and identifying them. Observations of relative growth rates from immediately post-mast would improve our understanding of why rates of survival amongst seedlings differ across forest types as they become more established in the understory.

Periods of drought are expected to become more common in tropical forests with future climate change (Coelho and Goddard, 2009), so it is important that we understand how drought affects seedling dynamics across forest types. While substantial research has been conducted to determine drought stresses amongst seedlings in tropical wet forests (Bebber et al., 2002a, Delissio and Primack, 2003, O'Brien et al., 2017, Qie et al., 2019), in-situ watering manipulation experiments of seedlings in actively restored forests, by comparison to unlogged and naturally regenerating forests, have not been attempted during droughts. These studies could target the question: *does active restoration of logged forest increase seedling vulnerability to drought?* The results of drought studies could help to guide future restoration strategies to maximise long-term efficacy in a climate changed future.

The results I present in chapter 4 indicate differences in survival and growth between forest types, modulated by functional groups. Although during this thesis I was unable to consider species-specific trade-offs because travel to the local herbarium was prohibited by the Covid-19 pandemic restrictions, understanding how individual species' seedling dynamics of growth and survival are affected, particularly within the Dipterocarpaceae, would give valuable insight to the consistency with which logging and active restoration determine recruitment across species and functional groups.

5.4.0 Is restoration of logged forests worth it?

My research has identified distinct community compositions of trees across unlogged and naturally regenerating forests in Danum Valley, from seedlings to trees of DBH > 10 cm. I show that aboveground biomass is lower in naturally regenerating logged forest than unlogged forest and that active restoration can accelerate its recovery, as has been recorded previously in the region (Philipson et al., 2020). Tree communities were similar in naturally regenerating and actively restored logged forests but distinct from unlogged forest. Increased biomass and higher density of dipterocarp poles in restored forest suggests that some taxa targeted by restoration strategies are able to recruit through to larger size classes but longer-term observations are required to see if the communities recruited will successfully converge with those in unlogged forest.

Seedlings produced by mast fruiting were of distinct community compositions across forest types. While restored forest seedlings had high relative growth rates, seedling survival was substantially lower than in other forest types, raising concerns over the capacity of restored forest to recruit diverse, naturally propagated generations to the future canopy community without further intervention. Further research is required to improve our understanding of how active restoration might affect dynamics and recruitment of future seedling cohorts in Southeast Asian forests and elsewhere in the tropics.

Selective logging remains widespread throughout the tropics and my findings provide new insight to the potential for active restoration of logged forests; something which remains relatively poorly studied, particularly amongst the progeny of trees planted during restoration. I highlight that, although active restoration can accelerate recovery of biomass – and is therefore successful in achieving the goals of some land managers – tree community composition and seedling dynamics remain distinct from unlogged forest 12-28 years after intervention. Although similar tree communities in naturally regenerating and actively restored forest suggest that restoration may not be ‘worth it’ from the perspective of species recovery, acceleration of biomass recovery without further detriment to the tree community, relative to naturally regenerating forest, may still be considered a restoration success. My research supports increasing recognition within the scientific community that, while active restoration has the potential to accelerate biomass recovery (Holl and Zahawi, 2014, Wheeler et al., 2016, Philipson et al., 2020), natural regeneration or minimal intervention strategies may be as good as or better for ecological recovery than active restoration strategies (Crouzeilles et al., 2017, Crouzeilles et al., 2020, Chazdon et al., 2021). Effects of active restoration on tree community composition are likely to differ between sites – depending on site history, landscape context, biogeography, species composition, and logging and restoration strategies used (de Avila et al., 2015, Osuri et al., 2019) – therefore further research is needed to understand the mechanisms driving these differences, and to inform which types of restoration are most suitable for individual forests and management goals. Studies of survival, growth, and recruitment amongst seedlings in actively restored forests remain rare and the dynamics of restored forest systems require further research throughout the tropics. Seedling dynamics will determine long-term trajectories within the canopy community and thus will ultimately decide the ability of forests to recover from selective logging and whether active restoration techniques can meaningfully accelerate recovery to converge with old growth.

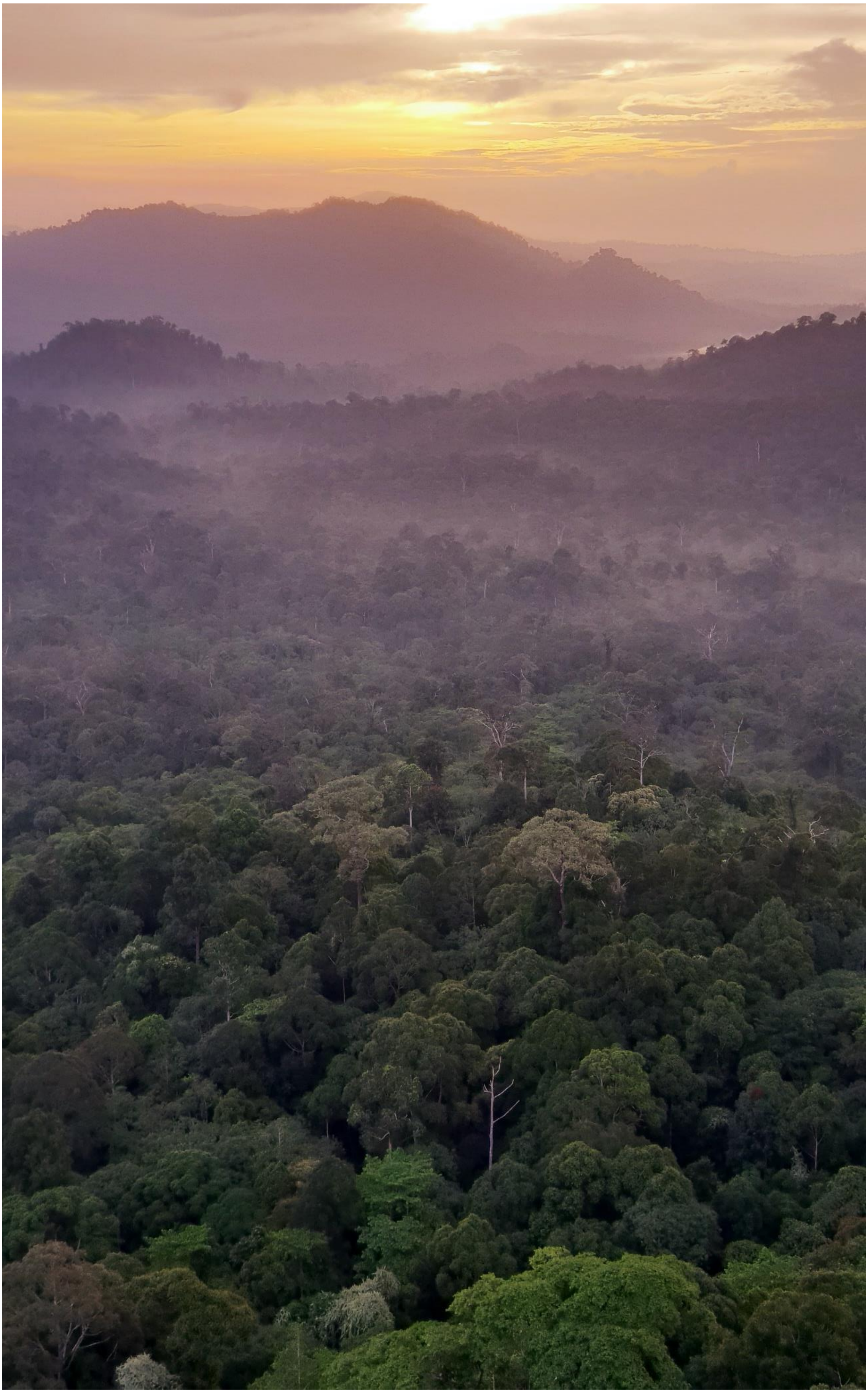


Photo: Sunset in Danum Valley [credit: Robin Hayward]

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“So they all left the path and plunged into the forest together”

– J.R.R. Tolkien, The Hobbit