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Restoring the 3D structure of tropical ecosystems – how important is tree diversity?

Natalie Christiansen

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Masters of Science by Research in the Faculty of Science and Cabot Institute.

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Thesis structure

The overarching goal of this thesis is to explore the extent to which different forest restoration interventions can help speed up the recovery of degraded tropical forests impacted by logging. The thesis itself is structured into three main chapters. In Chapter 1 I begin by providing an introduction to tropical forest ecosystems; their value for biodiversity, climate and people; and the threats they face as a result of tropical forest loss and degradation. I then move onto exploring methods for restoring degraded tropical forests and how best to monitor their effectiveness at scale using emerging remote sensing technologies such as LiDAR. In Chapter 2 I then use one of the world's largest and longest running forest restoration experiments – the Sabah Biodiversity Experiment in Malaysian Borneo – to put these ideas to the test. Specifically, I leverage airborne LiDAR data acquired at two points in time to test how tree planting and liana cutting impact the 3D structure of forest canopies during the initial decades of post-logging recovery. Finally, in Chapter 3 I explore the implication of my results in more detail in the context of tropical forest restoration and climate change mitigation, and discuss how I think these approaches could be developed further through future avenues of research.

Covid-19 Statement

The original design of this project was to collect terrestrial laser scanning (TLS) data of the study site in Malaysian Borneo for more layered insights into the structure and differences within the forest structure. Unfortunately, these plans needed to be altered due to the COVID-19 pandemic resulting in prolonged travel restrictions to Malaysia. Therefore I worked on pre-collected airborne LiDAR data from the years of 2013 and 2020, primarily focusing on changes in canopy height growth and canopy gaps. The addition of TLS data on the understory and below canopy differences between treatments would have greatly enriched this project. Which could have provided a more holistic depiction of the study site and possibly more relevant insights for early stage rehabilitation. Solely leveraging airborne laser scanning provides a top-down view, and because LiDAR cannot penetrate solid objects such as branches and stems this view of the understory is typically occluded. It would also have proved a very novel approach for tropical forest rehabilitation assessment, whilst providing me with valuable fieldwork training. Thus the method of TLS is discussed in further detail in Chapter 3.

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Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic awards. Except when indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

Signed: Natalie Anne Christiansen Date: February 3rd 2023

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Chapter One

1. General introduction

1.1 Introduction

Tropical forests are some of the most biodiverse ecosystems on our planet, supporting over half the world’s known endemic flora and fauna (Pan et al., 2011; Lewis, 2015; Roberts et al., 2021). These functionally diverse hotspots for biodiversity provide an array of essential ecosystem services to local and global communities, and greater ecosystem and planetary functioning alike – ranging from timber stock and global livelihoods to carbon storage and climate regulation (Edwards et al., 2014; Lewis, 2015; Lefeuvre et al., 2022). Despite their intrinsic value these ecosystems are increasingly threatened by anthropogenic disturbances, such as logging, land conversion, and unsustainable agricultural practices (Jacobson et al., 2019). Containing 55% of global aboveground forest carbon stores, the greater ripple effect of this fragmentation and degradation to tropical landscapes not only risks these carbon sinks shifting to carbon sources, but also increases the pace of species loss and extinction (Baccini et al., 2017; Philipson et al., 2020). As such, identifying best practices for the restoration of tropical forest ecosystems is imperative in mitigating the emerging detrimental climatic trends, recovering biodiversity and species abundance, and ensuring the longevity of humanity (Martin et al., 2021).

The irreversible loss of species diversity through the mismanagement and exploitation of tropical forest ecosystems has emphasized the global scale of the issue (Finger et al., 2012; Watson et al., 2018; Zeng & Fischer, 2021). Degradation, caused by logging and land conversion, has been extensive across the world’s tropical forests, leading to observations of vast changes to ecosystems and forest area cover. The intensity of these transformations have been greatly witnessed in Malaysian Borneo where, since the 1970s, 60% of intact tropical forests have been either logged or converted to monoculture plantations, with the most common monoculture being oil palm. Industrial oil palm plantations have replaced large areas of old-growth forest, wherein the 2015 FAO report stated 87% of the world’s palm oil production originated in Indonesia and Malaysia (Margono et al., 2014; FAO, 2015; Gaveau et al., 2016). Another principal driver of forest degradation in the tropics is the practice of selective logging where mature and high value tree species are harvested for their wood. This method can result in a depauperated stand from species loss, whilst also damaging the crowns of neighbouring trees intensifying the extent of the degradation (Pfeifer et al., 2015). In 2011 this intensity of damage was reflected in the estimated loss of 53% of above-ground biomass in the Bornean region of Sabah alone (Raynolds et al., 2011; Saner et al., 2011).

With the emergence of research highlighting the relationship between biodiversity and ecosystem functioning, these anthropogenic changes are considered increasingly concerning (Isbell et al., 2017; Gonzalez et al., 2020). The functioning and habitat qualities of a forest ecosystem are strongly influenced by the levels of structural diversity present. A diverse mosaic is observed to strongly influence the greater functioning, productivity, habitat quality, and resilience of a stand (Kettel et al., 2008; Pfifer et al., 2015; Jucker et al., 2020). Tree species richness has been linked to increased biomass and productivity – supported by a decrease in competition granting more effective nutrients cycling, and complementary effects where interspecies dynamics can support and enhance performance (Hooper, 1998; Chisholm et al., 2013). A multi-story canopy, upheld through tree species diversity and age, have superior structural diversity thus sustaining greater diversity in understory plants which boosts availability of natural subregions increasing fauna diversity (Morin et al., 2011; Morin et al., 2014; Brassard et al., 2014; Wang et al., 2022). Large scale disturbance, such as selective logging, degrades the structural diversity and complexity – decreasing biomass, impacting carbon storage and nutrients cycling, and creating canopy gaps thereby altering the microclimate of a stand and causing warmer and drier conditions. This leaves the ecosystem more vulnerable to pests, diseases, and the unprecedented environmental fluctuations of the changing climate (Kettle, 2010; Alfaro et al., 2014; Jucker et al., 2018; Deere et al., 2020; Senf et al., 2020).

Regardless of the visibly dramatic structural changes, logged tropical forests remain functionally diverse and are still able to provide an array of ecosystem services (Edwards et al, 2014; Lewis et al., 2015). Nonetheless, the continued value and productivity of such forests are often neglected, increasing their vulnerability to repeat logging or agricultural conversion (Reynolds et al., 2011; Lefeuvre et al., 2022). This intrinsic value has influenced the rise in forest rehabilitation and conservation initiatives as a means for restoring biodiversity, and become an increasingly popular topic in the discussions of slowing the impacts of climate change (Isbell et al., 2018; Senf et al., 2020; Zhang et al., 2022). As such, an array of methods from tree planting, to climber cutting management have emerged. Yet, the most effective methods of management and rehabilitation of tropical forest ecosystems have yet to be quantified.

1.2 Restoration methods

Rehabilitating degraded tropical forests is critical for allowing both biodiversity and carbon stocks to recover. Yet, it remains unclear which approaches may yield the greatest results when promoting recovery in tropical ecosystems – passive regeneration through conservation, or active methods that involve tree planting and other management interventions. Moreover, defining and assessing the success of restoration and recovery can be complicated, especially as recovery rates can differ across ecosystems depending on the climate, and extent and intensity of past disturbances, such as clear cutting vs selective logging. As such, there are a multitude of factors and metrics one could use to monitor and measure recovery (Poorter et al., 2021).

Despite the vast research into community succession and assembly, generalisations are challenging to draw especially when biogeographically distinct areas can vary greatly in their species composition (Fukami, 2015). Even between tropical forests, where wet and dry forests can differ in their functional composition, different successional pathways have been observed in their recovery. Nonetheless, they have been noted to still reach similar functional characteristics with stand maturation (Poorter et al., 2020). Thus, without clear baselines, other than undisturbed neighbouring old growth forests for comparison, pin-pointing how a recovered forest ecosystem may function and appear can seem arbitrary, and depends greatly on what one may be assessing for – from canopy cover to soil carbon storage, the variables for assessment can be numerous. Therefore, as traits influence species performance, research is emerging around community composition and assembly based on species-specific traits and ecosystem processes (Garnier et al., 2016; Poorter et al., 2021). By assessing the functional traits of communities, a deeper insight into the processes of succession and recovery over time can aid us in defining baselines to quantify the extent to which a forest ecosystem may be considered recovered or restored (Poorter et al., 2021). As such, data emerging from the 2ndFOR network indicates some of the many layers for assessment into the recovery of secondary tropical forests in predominantly clear-cut landscapes, such as; biomass, biodiversity, plant characteristics, and capacity to sequester carbon, to name a few (Chazdon et al., 2016; Poorter et al., 2019; Rozendaal et al., 2019). Different attributes have been found to recover at different rates in secondary forests, but previous work suggests that three key metrics to assess recovery include: maximum tree size, overall tree size variation and the number of tree species in a forest (Poorter et al., 2021).

In addition to identifying the attributes based on which to assess recovery, reference points for comparison are required in order to best assess the extent to which a forest ecosystems' conditions are deemed as 'restored' and the successes rate of an intervention or rehabilitation method. One option in this regard is to leverage a nearby undisturbed old growth stand as a references site can grant us insights into what the recovering ecosystem would have looked like before being disturbed (Saatchi et al., 2011; Poorter et al., 2016; Rozendaal et al., 2019). An alternative approach when assessing the effectiveness of specific rehabilitation interventions is to have control plots which have been subjected to similar degree of initial disturbance but have then been allowed to recover naturally without any human intervention (Hector et al., 2011; Tuck et al., 2016). We delve into these topics of natural regeneration and active rehabilitation methods in greater detail throughout our study and this paper.

Although it is possible for a forest to naturally regenerate post logging, the extent to which this may emulate the complex and diverse multifunctional system pre-disturbance depends on a multitude of factors, such as intensity of disturbance, remnant species diversity, seed survival and availability, and climatic fluctuations during recovery, to name a few (Poorter et al., 2016; Rozendaal et al., 2019; Philipson et al., 2020). Active restoration methods, such as tree planting, have been shown to increase the pace at which a degraded forest can recover and can supplement for lost species diversity (Philipson et al., 2020). The supplementary management method of climber cutting is considered to enhance recovery by liberating the crowns of restricted remnant trees, whilst decreasing competition and increasing understory light availability for saplings (Garcia & Falck, 2003). However, it remains unclear whether the gains in carbon removal rates obtained from tree planting can offset the high costs of these operations under the current voluntary carbon market (Philipson et al., 2020). Presently, most restoration projects involving tree planting focus on whole deforested areas over restocking forest remnants. This requires significantly higher investment than nurturing existing fragmented forests through enrichment planting and management (Suganuma & Durigan, 2015; Bertacchi et al., 2016; Shoo et al., 2016). Additionally, due to site, seed and financial availability as well as monitoring methods, the vast majority of diversity planting for recovery studies have been approached through short term and small scale projects, computational modelling, or restoring cleared landscapes as opposed to working within an existing matrix of forest (Tuck et al., 2016; Guerrero-Ramirez et al., 2017; Gonzalez et al., 2020; Philipson et al., 2020; Meunier et al., 2021; Wang et al., 2022). As such, the viability of these methods require further field-based assessment to identify the extent of the potential cost – recovery trade-offs.

1.2.1 Natural regeneration

Passive restoration methods, such as conserving degraded forest landscapes, can be a more financially accessible method for landowners and lower income communities than more active approaches of planting (Ashton et al., 1997; Marshall et al., 2021). Such active approaches can, for instance, require planting up to 6000 seedlings per ha, which demands a vast amount of labour and management (Rodrigues et al., 2009; Crouzeilles et al., 2017). Protected fragmented forests have capacity for secondary forest growth, granted significant enough remnant biodiversity. Research monitoring the recovery of degraded forests has indicated their ability to recover up to 80% of the species richness found in old-growth forest within an average of 50 years when under conservation. The equivalent compositional complexity could also be recovered permitting these landscapes are kept undisturbed for centuries- this is due to seed dispersal limitations and the growth pace of late succession species (Rozendaal et al., 2019; Cook-Patton., 2020).

Natural regeneration unfolds through the opportunistic colonising of locally adapted pioneer species and seedling survival of late-succession species (Shoo et al., 2016; Crouzeilles et al., 2017). Although a less predictable recovery process than active planting, these sites have been found to yield higher native and locally adapted flora diversity (Chazdon, 2008; Shoo et al., 2016). Active planting which values diversity during implementation, may also recover a forest’s diversity, however such initiatives have been found to lack the full scope of functional traits present in natural regeneration, oftentimes due to the limited amount of species planted (Minnemeyer et al., 2011; Chazdon & Guariguata, 2016; Chazdon 2017). The pace of landscapes rehabilitated through planting may initially outperform patchy distribution of trees, density, and slower biomass accumulation of naturally recovering forest. Yet, with time the ecological succession could decrease these structural differences by up to 60 years (Crouzeilles et al., 2016; Shoo et al., 2016).

Nonetheless, anthropogenic disturbances, such as logging, are associated with greater canopy gaps and habitat patch development through the loss of whole niches, seed bearing trees and ground seed mortality. Leaving many fragmented forests so depauperated through repeated human disturbance to the extent that natural recovery of aboveground biomass stocks could require up to 70 years, depending on climate and water availability. This further limiting recovery pace and the extent to which former levels of multifunctional complexity can be naturally regenerated. (Poorter et al., 2016; Nichol et al., 2017; Rozendaal et al., 2019). Additional risks of only conserving human-modified forests for passive restoration are the ecosystems’ heightened vulnerability to climatic fluctuations which increases drought conditions, climber invasions and wildfires. Moreover, these conserved sites may be viewed as economic opportunities due to their unused and already exploited appearance. (Aide et al., 2000; Reynolds et al., 2011; Chazdon et al., 2020; Lefeuvre et al., 2022). In such instances, reintroduction of key species can improve the pace and rate of recovery whilst increasing economic value.

1.2.2 Tree planting

Active restoration, such as tree planting, of human-modified landscapes has generally been identified to support the recovery of fragmented ecosystems by accelerating recovery of the greater forest structure and increasing productivity (Chapman & Chapman, 1996; Chazdon et al., 2009). One such method is enrichment planting which has long been considered a viable approach when supplementing for biodiversity loss, and a method to increase density in logged-over tropical forests. This involves planting nurtured saplings within spaces of the forest ecosystem presenting significant canopy gaps, from species which were selected for harvest during logging (Ashton et al., 1997; Millet et al., 2007; Hector et al., 2011). Seedling establishment and greater initial rates of stand density have been attributed to this method, improving canopy complexity and canopy gap filling (Lamb et al., 2005; Chan et al., 2008). This not only optimizes resources through filling forest gaps but can also boost survival rates and decrease the extent of post planting maintenance and management (Ashton et al., 1997). Therefore, supporting the natural recovery of degraded forests can be more cost effective than reforestation initiatives of whole deforested landscapes.

Although previous research has demonstrated the superiority of tree planting as a restoration and climate change mitigation strategy, the oversimplification of widespread tree planting reflected in organization-based initiatives and general media circulation – such as the Trillion Trees Campaign – lack concrete insight for best practices (Bastin et al., 2019). This is reflected, not only in the aforementioned mortality cost sinks, but may further impact the complexity of the greater modified-ecosystem, such as the microclimate, biodiversity, and in some cases human economies (Veldman et al., 2015; Adams et al., 2016; Tuck et al., 2016; Ehbrecht et al., 2017; Bonnesoeur, 2019; Holl & Brancalion, 2020). Tree planting without comprehension of the network shifts within the now-altered mosaic or the knowledge of species which could increase structural complexity and enhance thriving can result in ecosystem disservices otherwise mitigated through conservation for natural regeneration (Shackleton et al., 2016; Veldman et al., 2019; Holl & Brancalion, 2020). Furthermore, without knowledge of best practices the planting project can become a green-washing opportunity as a means for carbon-offsetting, such as some monoculture plantations. Or this could prove a financial cost-sink through planting on incompatible landscapes, or by the lack of maintenance and management optimization. (Martin et al., 2021).

Despite the increased emergence of studies modeling restoration through tree planting, and the tree planting initiatives on the rise, there are few sites in the tropics actively monitoring and assessing the impact of tree planting interventions, how to optimize any benefits, or general planting success rates and conditions (Nunes et al., 2020; Martin et al., 2021). Moreover, the viability of tree planting in the tropics as a methods on its own has come under recent scrutiny, where novel data suggests no significant improvements on pace and extent of canopy cover (Coleman et al., 2021). Further insights indicate the need for supplementary management methods, such as climber cutting, diversity planting, and the importance of a complementary understory granting adequate light availability. This further raises the financial pressures of this active method (Holl & Brancalion, 2020; Coleman et al., 2021; Di Sacco et al., 2021; Marshall et al., 2021). Nonetheless, significant knowledge gaps are present in our general comprehension of how fragmented forest ecosystems may respond in the long term and at larger scales, especially with the increased occurrence of natural disasters and extreme weather fluctuations. Therefore further quantifying these through ecological field-based assessments are a necessary addition to current literature (Nunes et al., 2020; Marshall et al., 2021).

1.2.3 Diversity planting

Partly driven by the cumulative urgency for identifying effective methods of rehabilitation and management in order to conserve global biodiversity and decrease the exacerbation of climate change, the relationship between biodiversity and ecosystem functioning has been greatly researched (Schwartz et al., 2000; Srivastava & Vellend 2005; Eisenhauer et al., 2016; Wang et al., 2022). Loss of biodiversity has been observed to modify the stability and functioning of ecosystems leading to detriment and decline in greater ecosystem services (Reich et al., 2012; Isbell et al., 2017; Isbell et al., 2018). Therefore, planting with species diverse propagules collected from different provinces and multiple seasons of mast seeding could have greater potential to maintain or improve the genetic diversity of a stand than natural expansion (Kettenring et al., 2014; Zeng et al., 2017; Zeng & Fischer., 2020; Zeng & Fischer, 2021). For instance, grassland restoration studies have demonstrated reintroducing diversity can have stabilizing impacts on productivity: lower interannual fluctuations have been observed in grassland systems with higher diversity than those lower in species richness, suggesting a link between species diversity and biomass productivity (Hector et al., 2010; Zavaleta et al., 2010; Loreau & De Mazancourt. 2013; Hautier et al. 2014). Yet, as the pace of change in species abundance and compositional changes can take decades to be notable in forests the drivers identified in these dynamic shifting grassland communities might not be extrapolatable to forest ecosystems (Stephenson & Mantgem, 2005, Gonzales & Loreau, 2009; Jucker et al., 2015). However, the scale and requirements for such ecological studies on tropical forests are significantly more demanding than that of grasslands, and planting initiatives in the tropics are generally not meticulously monitored or assessed. Thus, the majority of ecological research has been on existing systems and impacts from disturbance, or planting on formerly clear-cut landscapes (Tuck et al., 2016; Nunes et al., 2020; Marshal et al., 2021).

At the forest level, ecosystems comprising diverse number of tree species have shown greater productivity than plantations of single trees (Ishii et al., 2004; Ishii & Asano, 2010; Hakkenberg et al., 2016; Zeller et al., 2018; Zeller et al., 2019). Plantation forests of monocultures, although economically beneficial in the short term, have been found to face greater resource competition whilst increasing soil nutrients leaching, thus lacking sustainability. Whereas an ecosystem supporting diversity in tree species has greater variation in resource use which can influence a multitude of forest ecosystem functions, from economic benefits to the productivity levels of the soil, understory and trees (Scherer-Lorenzen, 2014; Paquette et al., 2011; Ruiz-Benito et al., 2014). Stand heterogeneity decreases competition for space due to different levels of shade tolerance granting canopy packing leading to a far denser forest. These multi-layered mixed species tropical forest ecosystems have been found to boast around 38% larger crowns than monocultures due to superior ability in optimising space efficiency, and also improving the canopy’s structural complexity (Morin et al., 2011; Morin et al., 2014; Pretzsch, 2014; Jucker et al., 2015; Juchheim et al., 2019). This greater density equating to more abundance could be a driver for the increased productivity found in highly diverse forests (Fotis et al., 2018; Gough et al., 2019).

Diversity in tree age and species present on average 18% higher understory plant diversity which can support a variety of natural subregions providing niche differentiation (Morin et al., 2011; Brassard et al., 2014; Gong et al., 2021; Wang et al., 2022). The increased complexity and numbers of understory species found in multi-story ecosystems can improve soil nutrients and microclimate; in turn providing further ecological niches facilitating greater coexistence of forest-associated fauna (Larjavaara et al., 2008; Keller et al., 2013; Jucker et al., 2018; Zhang et al., 2022). This niche partitioning impacts the vertical stratification, thereby increasing efficiency of light interception from the higher and multi-layered vegetation density; and increases carbon sequestration, presenting species rich tropical forests as carbon sinks in the global goals of mitigating climate change (Gamfeldt et al., 2008; Hector et al., 2011; Verheyen et al., 2016; Yu et al., 2017; Atkins et al., 2019; Forrester et al., 2019; Riutta et al., 2021; Wilson et al., 2021).

Despite tree species richness and compositional complexity found linked to greater ecosystem productivity, predicting the outcomes of planting a mixture of species is difficult. Due to current limited silvical knowledge on complementary mixtures: in order to plant a greater diversity of species, it is essential to know which species may be appropriate matches for success. Especially when considering the economic pressure faced by rural landowners (Redondo-Brenes & Montagnini, 2016; Hall et al., 2011; Davis et al., 2012; Marshall et al., 2021). Increasing biodiversity and forest productivity depend on an array of factors which can be more sensitive in ecological settings. The functioning, interactions, performance and numbers of species reintroduced are some of the dependent tree trait factors. Whilst ideal mutualistic interactions of the greater ecosystem require deeper site-based knowledge, as seen in those between local tree species and seed dispersing animals, fungi and pollinators (Redondo-Brenes & Montaginig, 2006; McAlpine et al., 2016; Di Sacco et al., 2021; Marshall et al., 2021). Consequently, long-term field-based study on methods for optimised success rates on pace, extent, and longevity coupled with cost trade-off are required for best practices of tropical forest recovery (Thomas et al., 2014; Thomas & Gale, 2015; Philipson et al., 2020; Zhang et al., 2022). However, real-world research on diversity planting has been limited by human monitoring capabilities and economic capacity. As such, both monitoring and maintenance requirements to site and seed diversity availability, have limited capacity for initiatives for study, and opportunity for diversity planting rehabilitation have been restricted (Pérez-Salicrup, 2001; Chazdon et al., 2009; Wang et al., 2022). Therefore, when considering best practices for restoration of fragmented forest ecosystems the level of remaining genetic diversity has been used to determine the level of passive or active intervention methods utilised. Nonetheless, coupling simulated modelling and disturbance effect-based knowledge with field-based studies could lead to greatest success for planting initiatives and carbon stock recovery (Nunes et al., 2020; Philipson et al., 2020; Marshall et al., 2021).

1.2.4 Climber cutting

Often coupled with planting initiatives in the tropics is the method of climber cutting. This has been found to increase survival and optimise establishment of saplings by decreasing competition and increasing light and nutrients availability (Pérez-Salicrup et al., 2002; Grauel et al., 2004; Bertacchi et al., 2016; O'Brien et al., 2019). The removal of climbing vines and lianas has also been shown to liberate remnant trees, improve seedling survival rates, and increase height growth pace of newly planted saplings, thereby facilitating greater canopy packing in disturbed tropical forests.

The swift growth pace and robust root system of climbing plants significantly outperforms that of young trees. In logged and disturbed landscapes these rapidly establishing flora colonise ground space efficiently suppressing the survival rates of seedlings, and stunting saplings (Paul & Yavitt, 2010; Chen et al., 2015). Through the removal of vining plants, saplings and seedlings, have a period of relief from the battle of competing for nutrients, light and space (Pérez-Salicrup et al., 2002; Grauel et al., 2004). This method both lessens competition during initial establishment and decreases height stunting of saplings through the reduction of resistance posed by the weight of dominating vines. Findings of increased height growth have been unanimous, varying between a 5 to 66% increase within the first two years of planting and climber cutting. These great variations in height increase are dependent on differences in site-based infestation severity, fragmentation intensity, and climate (Pérez-Salicrup et al., 2002; Grauel et al., 2004; O’Brien et al., 2019).

Attributed to their sun-seeking nature, vining plants are most often observed in the upper to middle layers of a forest canopy and prioritise length growth, compared to trees which invest the majority of their resources into stem development. After climbing the vertical structure of trees towards the overstory, they proceed to drape across the canopy, placing strain and resistance on the crowns whilst intercepting light (Rodriguez-Ronderos et al., 2016; Media-Vega et al., 2021). This competitive advantage can therefore also suppress crown expansion and height growth of mature trees and decrease understory light availability for saplings (Schnitzer & Bongers., 2002). This stifling impact can have a restrictive effect on seed abundance and fruiting with risk of dramatically decreasing tree recruitment. This is of particular concern post logging for both active and passive rehabilitation methods. In South East Asia, dominant species such as the Dipterocarpaceae, which are regularly harvested, mast fruit every 2-10 years – a phenomenon in which a tree produces a large number of seeds in intervals greater than a year (Janzen, 1974; Ashton et al., 1988; Kelly & Stork., 2002; O'Brien et al., 2013). Liana removal studies in the Americas have documented an increased production of tree fruiting by 150-173% on average, with up to 50% more seeds observed in the canopies of individual trees and a greater number of tree species producing fruits for the first five years post- management (García León et al., 2017). Similarly, were it not for lianas restricting potential canopy expansion, remnant trees would have the freedom to fill canopy gaps created by the process of selective harvesting. Through vine removal management, the crowns are liberated from the constraint and weight facilitating lateral expansion (Alvarez-Cansino et al., 2015; Rodriguez-Ronderos et al., 2016). Despite finding this method to momentarily increase canopy gap size, which can further exacerbate microclimatic fluctuations, risking drought and heat exposure within the fragmented stand. The rapid lateral expansion of remnant trees has demonstrated to recover the lost leaf coverage biomass and light interception formerly contributed by climbers within 2-4 years post removal (Perez-Salicrup et al., 2001; Schnitzer & Carson., 2010; Ehbrecht et al., 2017; O'Brien et al., 2019; Meunier et al., 2021).

Although a seemingly promising strategy to support rehabilitation, liana removal increases canopy gap size which decreases forest density enhancing susceptibility to weather variations. Considering the delicate microclimate of a tropical forest, further stressors such as increased wind exposure, and greater light and heat levels, could heighten damaging and drying effects and a loss of vapour pressure. This in turn impacts survival of saplings and the thriving of already vulnerable remnant flora. (Martines-Garza et al., 2013; Jucker et al., 2018; O'Brien et al., 2019). Furthermore, fluctuations in severity and increased occurrence of unprecedented environmental shifts and natural disturbance from the changing climate could pose greater threat. For instance, when greater canopy openness from cutting coincided with hurricane and El Niño droughts, higher sapling mortality rates followed. In such instances climbers have been observed as 'disturbance-specialist' plants, acting as buffers against damaging effects to the greater forest structure (Garrido- Péres et al., 2008; César et al., 2016; O'Brien et al., 2019). With the increase in severity of weather fluctuations, the benefits and risk indicators of this management method require further assessment.

Although tree planting may present a logical approach to restore human-modified tropical landscapes, the extent of the benefits this resource-demanding method has requires deeper monitoring and assessment. Were planting to increase the pace and extent a landscape can recover, compared to passive methods of conservation, additional insights into management practices which may enhance these benefits could optimise any initiatives.

1.3 Monitoring methods

Quantifying structural shifts and recovery over time is fundamental to comprehending and identifying the impacts of management and rehabilitation methods, yet this can prove laborious and time consuming due to the scale and density of tropical forests. Meanwhile, generally gaining holistic data on the forest structure can be limited and require invasive and time consuming sampling methods (Gower et al., 1999; Sasaki et al., 2018). Limited by human capability, monitoring at scale can therefore prove challenging using traditional field-based approaches.

Passive remote sensing monitoring systems such as multispectral satellite imagery have become useful and accessible tools for multi-temporal monitoring into when and where forest loss occurs due to their heigh refresh rates permitting frequency for monitoring (Richardson & Moskal, 2011) . However, these generally open source datasets are less useful for assessing recovery as their data lack the depth and sensitivity required for assessing complex vertical canopy structures, such as recovery or shifts in biomass. Therefore active remote sensing technologies such as LiDAR have gained increasing popularity by providing efficient, high-quality, and less damaging means for capturing high resolution data on composition and structure (Walter et al., 2021; Camarretta et al., 2020).

Airborne LiDAR is a laser imaging sensor mounted on a drone, airplane or helicopter which uses ultraviolet, visible or near-infrared source to sense objects. The airborne system scans the ground from side to side, sending laser emitted light pulses to the ground, reflecting off that which the pulse touches, such as the canopy’s structure, and can penetrate through multiple layers of vegetation. From this it calculates the return length mapping the variable distance of the objects. Data collection for assessing and monitoring the productivity, recovery, and compositional changes of vast landscapes are thus simplified and optimised.

From these data, deriving high resolution 3D canopy models is made efficient, and provides access to areas of forest canopy formerly inaccessible to human capacity. As such it has been used to capture multi-temporal data to develop 3D information on tree and forest structures - such as canopy height, crown size and shape, stem density and gap size, to name a few. This provides insight into drivers in rehabilitation initiatives or ecosystem shifts post disturbance furthered through repeat-data granting multi-temporal tracking for more comprehensive insights (Lefsky et al., 2002; Dalponte et al., 2019; Senf et al., 2020; Wu et al., 2020).

Yet, leveraging airborne LiDAR does lose out on understory vegetation and insights into below canopy trends and variations. As the pulses cannot penetrate through leaves and stems causing signal occlusion, it can be challenging to adequately detect and map the under and midstory layers of the canopy, risking losing out on data on smaller or young trees. Signal occlusion can pose a challenge for more densely packed canopies, such as those found in the multi-layered stands of tropical forest ecosystems, or when monitoring planting efforts during the early stages of rehabilitation (Richardson & Moskal, 2011; Vauhkonen et al., 2014; Wallace et al., 2016; Crespo-Peremarch et al., 2020). Therefore, ground-based remote sensing methods, such as terrestrial laser scanning (TLS) have been emerging for monitoring individual plants and further structures within the stand, such as deadwood or growth progress of newly introduced young trees (Liang et al., 2016; Disney et al., 2018; Yrttimaa et al., 2019; Seidel et al., 2020). Thus, for a truly holistic image of the complexity of a stand, monitoring and assessment could be most accurately mapped through a combined approach. However, the use of such technologies can be limited by financial resources, training, and permits for use. Moreover, these methods are both sensitive and vulnerable to weather conditions – for instance, movement in the canopy from light breezes can create ‘noisy data’ requiring patience, whilst rain can be extraordinarily damaging to the technology (Disney et al., 2018; Calders et al., 2020).

Nonetheless, remote sensing methods have the potential to support research in best practices for ecosystem recovery and conservation through superior data retrieval on patterns and dynamics in ecosystems. With continuous improvements in the technology and innovation in the use of the datasets, novel methods for analysing the complexity of forest ecosystems emerge rapidly – from calculating shifts in biomass to assessing canopy gap recovery (Armston et al., 2013; Ehbrecht et al., 2017; Disney et al., 2019).

1.4 Summary and project goals

As most effective methods of management and rehabilitation of tropical forest ecosystems have yet to be quantified, the present project aims to explore the efficacy of: planting, diversity planting, and climber cutting management as methods for rehabilitations. To best do so we leverage the Sabah Biodiversity Experiment (SBE), a 500 ha long-term field-scale forest rehabilitation and tree diversity ecological experiment based in Sabah, Malaysian Borneo. Specifically, the experimental set up of the SBE site was developed to test whether enrichment planting a diverse mixture of tree species, combined with climber cutting, can speed up the rate of recovery in logged over tropical forest landscapes. Tree diversity was manipulated through randomised plot planting conditions of monocultures, 4 seed mixture, and 16 seed mixture, alongside unplanted plots for control (Saner, 2009; Hector et al., 2011). This design permits testing for co-beneficial effects between ecosystem functioning and different levels of tree diversity planting (Scherer-Lorenzen et al., 2005).

Presenting airborne LiDAR as a non-invasive tool for multi-spatiotemporal assessment coupled with the experimental design of the SBE, the viability of tree planting as a rehabilitation method in tropical ecosystems, and the extent to which diversity planting and climber cutting may optimise this, can be explored. Therefore, we used repeat airborne

LiDAR data acquired over the SBE to test the impacts of tree planting, diversity planting, and climber cutting as rehabilitation methods for disturbed tropical forests ecosystems.

Chapter Two

2. How important is tree diversity in restoring the 3D structure of tropical forest ecosystems?

2.1 Abstract

Tree planting is increasingly used as a management tool to help the recovery of carbon stocks and biodiversity in logged tropical forest ecosystems. However, it remains to be tested whether planting a diverse mixture of tree species can speed up this pace of recovery of different forest structural attributes, as ecological theory would suggest. In response to this knowledge gap, the Sabah Biodiversity Experiment (SBE) was established in Malaysian Borneo in 2002. The SBE is a landscape-scale (500 ha) experiment in which five treatments were implemented across 124 plots (4 ha each): unplanted controls, single species planting, 4 species mixtures, 16 species mixtures, and 16 species mixtures with the additional treatment of climber cutting. Here we used repeat airborne LiDAR data acquired over the SBE to assess the impacts of tree planting and climber cutting as methods to speed-up the recovery of formerly logged tropical landscapes. To best assess this we analysed airborne LiDAR data from 2013 and 2020 for changes in top-of-canopy height and gap fraction. Our results indicate that tree planting, especially the 16 species mixtures, leads to faster filling of canopy gaps. However, we only found significant effects on the rate of canopy height growth when planting was coupled with liana cutting, while tree planting alone had little impact on this vertical axis of canopy structure. Our results suggest that the effectiveness of diversity planting as a restoration intervention in selectively logged tropical forests may only have marginal benefits on the initial stages of canopy recovery, although the longer term effects of these treatments may take decades to fully manifest.

2.2 Introduction

Tropical forests provide a multitude of vital ecosystem services to humanity, play a crucial role in climate regulation, and are home to around two thirds of the planet's known terrestrial biodiversity (Pan et al., 2013; Lewis et al., 2015; Brancalion et al., 2019). Despite encompassing less than one fifth of the world's land-mass, these biodiverse hubs are among the most productive ecosystems on Earth (Malhi, 2012). Yet, a lot of the world's tropical old-growth forests have been lost to land conversion for monoculture plantations, whereof 87% of the world's palm oil production originates from Indonesia and Malaysia (FAO 2015; Liu et al, 2018). Despite the short-term economic benefits, these monocultures drastically alter habitats and leech soil nutrients, further manipulating and stunting some of the many layers of the ecosystem – such as understory flora abundance and biodiversity, and the mycorrhizal networks – displacing fauna and human communities alike (Morris et al., 2004; Morris, 2010; Subasinghe et al., 2014; Bayrak & Marafa., 2016; Dislich et al., 2017). Were this not reason enough for concern, a large portion of the remaining intact tropical old growth forest has seen rapid degradation and fragmentation through selective logging (Asner et al., 2010; Curtis et al., 2018; Matricardi et al., 2020). This compromises and alters the structural complexity of a canopy which prominently contributes to the loss of global biodiversity, and is a major source of carbon emissions (Ehbrecht et al., 2017; Milodowski et al., 2021). The delicate nature of the microclimate present in tropical forests makes them deeply sensitive to disturbances. This rapid turnover and resulting imbalances from old-growth forest to human-modified landscapes have grave consequences leading to a range of destabilising effects; from climate fluctuations to changes in light coverage, which in turn directly impact the behaviour, abundance and physiology of local flora and fauna (Hardwick et al., 2015; Jucker et al., 2018; Zhang et al., 2022). The practice of selective logging is a prevalent source of disturbance, where mature, high-value timber species are harvested, often damaging the crowns of neighbouring trees resulting in a depauperated stand post-harvest (Pfeifer et al., 2015). These selective, and often intense, losses in trees decreases biomass displacing wildlife and releasing carbon dioxide, creating gaps within the canopy and resulting in canopy height fluctuations which alter the microclimate often leading to drier and warmer conditions (Jucker et al., 2018; O'Brien et al., 2018; Senf et al., 2020; Zhang et al., 2022). Therefore rehabilitating logged forests in the tropics is critical for global biodiversity conservation and mitigating climate change exacerbation.

2.2.1 Methods for tropical forest recovery

Methods of conservation to facilitate natural regeneration and active restoration to discern for heighest efficiency in restoring fragmented tropical forests are being explored. Despite the potential of forest islands forming through fragmentation, significant biodiversity can still be found in the presence of remnant trees, leftover seedlings, and seed dispersing fauna which can facilitate natural expansion within the disturbed landscape (Chazdon et al., 2009; César et al., 2016). Although natural recovery of aboveground biomass stocks can take up to 70 years in secondary forests, depending on climate and water availability (Poorter et al., 2016). Within the first 20 years post-abandonment agricultural tropical landscapes, whereon secondary forests are re-establishing, have potential to recover up to 80% of the species richness levels found in old-growth forest (Poorter et al., 2021). However, the species composition, especially in diversity sparce ecosystems, could take over a century to resemble the complex mosaic found in old growth forests leading to a more varied rather than diverse stand (Rozendaal et al., 2019). Consequently, the extent to which heavily disturbed ecosystems can naturally recover to obtain a complex and diverse multifunctional system, equivalent to that of an old growth forest or the results of active planting methods, is uncertain (Poorter et al., 2016; Rozendaal et al., 2019).

Ecosystem fragmentation is associated with the development of habitat patches and a decrease in species diversity. Through selective logging, entire niches and seed bearing trees can be lost, limiting the success rate of the ecosystem regenerating naturally to its former multifunctional complexity (Nichol et al., 2017; Rozendaal et al., 2019). Genetic diversity in a forest is deemed valuable for long-term sustainability, as such enrichment planting and climber cutting are practiced in active restoration methods to fill canopy gaps more effectively and to support multi-layered tropical forests (Hector et al., 2014; Zeng et al., 2017). Enrichment planting is one method applied in poorly-stocked areas of logged-over forests and associated degraded areas in the tropics (Hector et al., 2011). Enabling seedling establishment aims to recover sparce or patchy forests by supplementing the stock of trees, often times planting the seedlings of the timber tree species that have been selectively logged and early succession species (Chan et al., 2008). Climber cutting, which is supplementary to enrichment planting, involves cutting lianas and climbing plants which would otherwise present competition and cause damage to planted saplings. This enhances forest floor light availability and decreases nutrients, water and below ground competition against the swift growth rate and sturdy root system of vining plants (Pérez-Salicrup, 2001; César et al., 2016; Meunier et al., 2021). Relief cutting has been found to enhances seedling survival, increase biomass gain by around 50% for smaller trees and shrubs, and facilitate rapid canopy growth (Kettle, 2012; César et al., 2016; García León et al., 2017). Planting seedlings in existing gaps and clearing fast growing vines decreases competition granting a greater chance for establishment and faster initial growth (Cesar et al., 2016; Philipson et al., 2020). Additionally the relationship strength between biodiversity and ecosystem functioning has been suggested to increase through time, likewise presenting a rise in biomass productivity

(Cardinal et al., 2007; Guerrero-Ramirez et al., 2017). Although, through influences from elemental and anthropogenic changes, primary forests cannot be returned to their pre-disturbed state, planting a mixture of species could promote reforestation and faunal diversity (Guerrero-Ramirez et al., 2017; Gonzalez et al., 2020; Wang et al., 2022). This work has also demonstrated temporal changes where species rich restoration-oriented plots increased in biodiversity, compared to managed plantations which presented a decrease in general productivity (Gonzalez et al., 2020; Wang et al., 2022). Further discussions have suggested that restoration planting with species diverse propagules collected from different provinces and multiple seasons of mast seeding, can maintain or improve the genetic diversity of a stand more so than natural expansion, whilst mitigating potential genetic drift (Kettenring et al., 2014; Zeng & Fischer, 2020; Zeng & Fischer, 2021).

Despite indicating accelerated aboveground biomass recovery by 50%, it remains unclear whether active restoration interventions can be economically viable given they are costly, time consuming, and labour-intensive to implement (Pérez-Salicrup, 2001; Cardinal et al., 2007; Chazdon et al., 2009; Guerrero-Ramirez et al., 2017; Gonzalez et al., 2020; Philipson et al., 2020 ; Wang et al., 2022). However, considering the pace and extent of anthropogenic land cover change and elemental shifts, field-based multi-temporal studies on the effects of biodiversity could better emulate natural conditions whilst developing current computational models. This presents a clear gap in real-world system knowledge as to the drivers of tree species diversity planting and the extent of its potential in restoring logged tropical forest ecosystems, if at all a viable or cost effective method (Nadrowski et al., 2010; Scherer-Lorenzen, 2014; Amazonas et al 2018; Wang et al., 2022). To explore this very question, the Sabah Biodiversity Experiment (SBE), a long-term forest rehabilitation and tree biodiversity field study, was established in 2000 in Malaysian Borneo (Hector et al., 2011).

The tropical forests of South-East Asia are known for their diversity and complexity with over 2,500 different tree species (Whitmore, 1998; Saner, 2009). Yet, tropical forest ecosystems, such as those of Malaysian Borneo, have been exploited to the point of severe degradation (Marsh & Greer, 1992). For instance, the region of Sabah alone, where our study was undertaken, was documented in 2009 to hold less than 15% of original and undisturbed forest cover (Marsh & Greer, 1992; Saner, 2009). This is predominantly attributed to oil palm plantation conversions and logging due to the economic value of the commercial timber found within Malaysia's mixed dipterocarp forests (Ashton, 2008; Bhagwat & Willis, 2008). Consequently, rehabilitating logged forests in Sabah has become a practice, leading to current enrichment planting methods in Borneo; wherein species of the dominant genus, the Dipterocarpaceae, are restocked or supplemented due to their ecological and economic value (Appanah & Khoo, 1996; Appanah, 2001; Romell et al., 2008). As such, since the 1990's a number of large-scale rehabilitation sites have been developed, such as the INEKIA and SBE projects, in the area of the Sabah Foundation (Garcia & Falck, 2003; Hector et al., 2011).

The SBE, a 500 ha of former production forest, presents a model system in real-world setting, designed to assess management and rehabilitation methods for future efficiency and optimisation of our degraded and commercialised tropical forest ecosystems. The primary interventions of the SBE are enrichment planting, diversity planting, and vine removal. Here the aspect of diversity is manipulated through randomised plot planting conditions of monocultures, 4 seed mixture, and 16 seed mixture, alongside unplanted plots (Saner, 2009; Hector et al., 2011). This design permits testing for co-beneficial effects between ecosystem functioning and different levels of tree diversity planting (Scherer-Lorenzen et al., 2005; Saner, 2009).

2.2.2 Monitoring large landscapes using remote sensing

Whilst the SBE provides a platform to test efficiency for restoring degraded tropical forests, the scale and density of tropical forest landscapes undergoing large-scale rehabilitation can prove laborious and time intensive (Lefsky et al., 2002). Physical capacity can limit the amount and extent of site based monitoring, as well as the capacity for longitudinal investigations. As such monitoring and assessing for leading variables within methods of management, restoration and recovery can be limited to samples whilst requiring some invasive methods (Gower et al., 1999; Sasaki et al., 2018). Remote sensing technology such as global satellite imagery and LiDAR offer a less destructive, more time efficient means for capturing high resolution data on landscape structures (Walter et al., 2019). Airborne LiDAR, a laser imaging sensor mounted on a drone, airplane or helicopter, is more sensitive to changes and less error-prone than field data. Although field data has been found to be accurate when assessing foundational metrics like diameter at breast height, it is further down the chain of analysis where error is more probable, for instance when assessing more complex metrics such as top of canopy height (Lefsky et al., 2002; Sexton et al., 2009). Leveraging higher resolution remote sensing technology, such as areal LiDAR, not only decreases the amount of systematic errors found in field measurements for more complex metrics, but also provides access to hard to reach canopy and thus novel perspective to field data, by granting a birds-eye view of the desired landscape, such as the top of trees and the size and shape of canopy gaps (Sexton et al., 2009; Goodbody et al. 2020). For instance, mapping and monitoring canopy gaps through manual methods was until recently limited due to high financial and time demands. The development of remote sensing methods such as aerial LiDAR has greatly increased the scope and range we can now monitor and characterising such canopy dynamics (Asner et al., 2013; White et al., 2018; Goodbody et al., 2020). As highlighted, this grants the ability to collect data across vast landscapes, airborne

LiDAR generates large scale high resolution 3D canopy models wherefrom landscape compositional changes, such as canopy height and gap size, can be assessed for multi-temporal insights into drivers in rehabilitation initiatives or changes post disturbance (Lefsky et al., 2002; Dalponte et al., 2019; Senf et al., 2020; Wu et al., 2020). Remote sensing methods therefore have the potential to support research in best practices for ecosystem recovery and conservation through patterns of observational dynamics in ecosystems.

2.2.3 Project aims

The present project aims to assess the impacts of the aforementioned methods of rehabilitation by leveraging repeat airborne LiDAR surveys from 2013 and 2020 over the SBE. The objective is to observe and investigate how enrichment planting a diverse numbers of sapling species impacts the recovery of canopy structural complexity. More specifically, we examine whether the canopy height and canopy gaps recover faster through (i) the introduction of diverse enrichment planted populations compared to natural regeneration, and (ii) the use of advanced climber cutting management. Specifically, we hypothesise that (i) planting will lead to faster growth leading to a greater mean canopy height by 2020 and smaller canopy gaps, (ii) greater diversity planted will fill gaps in the canopy faster and more efficiently, and (iii) climber cutting will facilitate sapling establishment filling canopy gaps and increasing the canopy height mean.

2.3 Methods

2.3.1 Study site: the Sabah Biodiversity Experiment (SBE)

The study was conducted over the Sabah Biodiversity Experiment (SBE), 500ha of the 35,000ha Malua Forest Reserve, a selectively logged production forest located in the southern part of Malaysian Borneo (Figure 2.1). This field-scale forest rehabilitation project was established in 2000 to facilitate the assessment of restoration practices and management strategies utilised in fragmented tropical forest ecosystems, and to investigate the impacts of biodiversity on greater forest ecosystem multi-functionality. The scope and scale of the SBE, spanning from sapling to adult tree, make it one of the world's largest landscape-scale ecological experiments on ecosystem functionality, tree biodiversity, and forest rehabilitation. This provides a means to evaluate and monitor a range of ecological questions in tropical forest ecosystems and their rehabilitation through a controlled experimental set up in a real world setting. Presenting an ideal study side, it was selected due to the unique opportunity for assessing the drivers in reforestation through the relationship of tree diversity on ecosystem functioning.

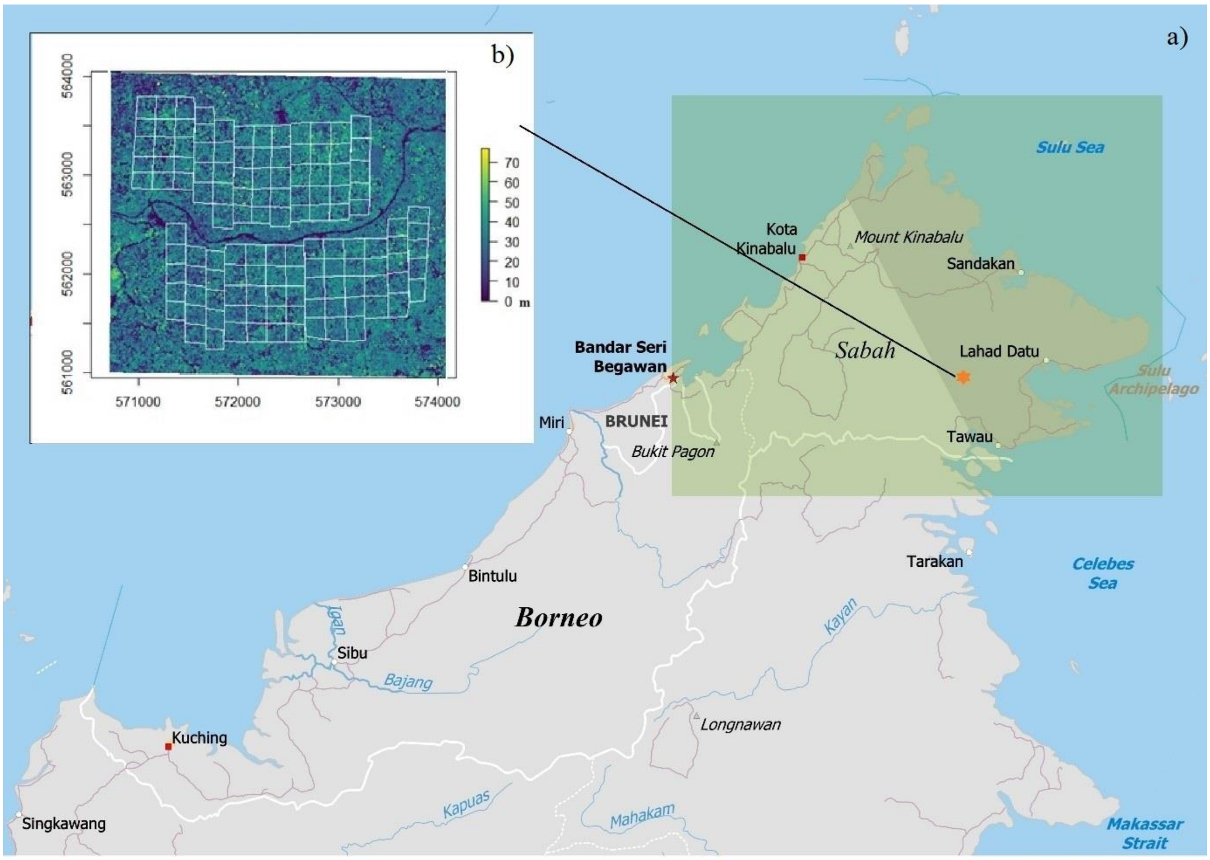


Figure 2.1: Map establishing location and layout of the Sabah Biodiversity Experiment in Sabah, Malaysian Borneo. Section a) provides an overview of Sabah and the approximate location of the SBE. Section b) depicts the 124 plots as a CHM from 2020, where the colour scale portrays the canopy height in m.

Despite undergoing logging once, compared to more frequent harvesting common for timber production stands, the vegetation of the SBE was classified to have a mixture of poor to very poor forest with some cloud forest (Saner, 2009). When designing the SBE the approach was thus to best imitate the mosaic of the forest prior to the disturbances of the 1980s. Therefor a mix of up to 16 different Dipterocarpus species, the dominant tree genus of Malaysian Borneo and the tree family originally selectively logged, were line and enrichment planted in the canopy gaps (Table 2.1). The SBE combines restoration initiatives with management practices by integrating a multi-species enrichment planting design founded in the biodiversity theory; suggesting an increase in diversity can improve ecosystem functioning (Scherer-Lorenzen et al., 2005; Saner, 2009; Watson et al., 2018).

There are two dominant treatments for restoration leveraged in regions such as Sabah, practiced in accordance with local sustainable forest management (Sabah Forestry Department, 2017). Enrichment planting, one treatment, where selectively planting a number of native trees within canopy gaps or along lines is considered to enhance the poorly stocked forest. Holding space for planted seedlings to regenerate adequately generally 3 m planting lines are carved into the degraded forest at 10 m intervals; often maintained up to five years later to ensure establishment success (Adjers et al., 1995; Garcia & Falck, 2003). The other treatment is that of climber cutting, wherein climbing plants and vines are removed from the overstory liberating the crowns of restricted mature trees and decreasing overhead shade (Garcia & Falck, 2003).

Planting for the SBE was thus conducted in compliance with the aforementioned enrichment planting standards to increase sapling establishment and survival. The primary cohort of seedlings were planted between January 2002 and September 2003, followed by a secondary set planted between September 2008 and August 2011, to account for initial mortality rates. The 500 ha was divided into 124 x 4-ha plots separated into two blocks, one on each side of the river (Figure 2.1). In each plot the composition and diversity of enrichment planted dipterocarp seedlings were manipulated and approximately 1300 seeds were line planted in existing gaps of remaining vegetation. 108 plots contain one of four randomised groups of enrichment planted seedlings: 1 species, 4 species mixture, and 16 seed species mixture. The remaining 12 plots serve as unplanted controls (Table 2.1). As removal of vines and lianas can be beneficial in decreasing competition, increasing success rates of establishment and the pace of sapling growth, the method of climber cutting was added to 16 plots of the 16 species mixture treatment as a sub-condition (César et al., 2016; Medina-Vega et al., 2021). For more in depth descriptions of the SBE experimental design and the pre-planting species composition see Saner (2009), and for layout of the randomised plot treatment conditions see Hector et al. (2011) figure 1(b) and Tuck et al. (2016) supplementary materials 3 and 4.

Tabel 2.1: List of treatment conditions and the corresponding number of plots, as well as additional information, implemented in the SBE.

Treatment condition	**Number of plots**	**Additional information**
Control (unplanted)	12	Control plots were allowed to naturally regenerate after selective logging without any human intervention.
Monoculture (1 species)	32	Two replicate monocultures of each of the 16 species listed in Table S2.1. listed in Table S2.1.
4 species mixture	32	Plots contain different mixtures of 4 of the 16 species listed in Table S2.1. The composition of these 4 species was designed to generate 16 possible treatment combinations (each replicated 2 times): (1) mixtures of species from 2 genera that form low complexity canopies; (2) mixtures of species from 4 genera that form low complexity canopies; (3) mixtures of species from 2 genera that form high complexity canopies; (4) mixtures of species from 4 genera that form high complexity canopies. For further detail see Hector et al., (2011) and Tuck et al. (2016).
16 species mixture	32	Plots containing a mix of all 16 species listed in Table S2.1.
16 species mixture with climber cutting	16	Plots containing a mix of all 16 species listed in Table S2.1, as well as undergoing liana cutting across the plot.

2.3.2 Airborne LiDAR data acquisition and processing

Airborne LiDAR data were collected over the SBE in 2013 and 2020. These airborne LiDAR surveys were conducted by Ground Data Solutions R&D (GDS), a private Malaysian registered company. The data were collected using GDS's MATRIX LiDAR system, which incorporates multiple RIEGEL sensors, mounted on a helicopter flown at 350 m altitude with a 60 ° scanning angle producing a ground swath width of 284 m with a 30% side and 60% front flightline overlap. With an average ground points spacing of 1-3 m over vegetated terrain, a laser points relative accuracy of 2 – 3 m RMSE, and an average pixel resolution of 10 cm. The point cloud data from both surveys, which were pre-processed by GDS, were processed using LAStools (https://rapidlasso.com/lastools). After classifying the ground returns of the point cloud we produced a digital elevation model (DEM), this is a numeric representation of the terrain's surface containing terrain details such as the slope. Thereafter, the elevations of non-ground points were subtracted from the DEM to produce a normalised canopy height model (CHM) using a locally adaptive spike-free algorithm (Fisher et al., in preparation). The resolution of the CHMs was 1m.

2.3.3 Data metrics and rationale

To test the hypothesis previously outlined, we used the airborne LiDAR-derived CHMs from 2013 and 2020 to quantify a range of canopy structural complexity metrics related to canopy height and openness. Although we did not assess all metrics of structural complexity we expected canopy height and canopy openness to be indicators of early stage recovery when leveraging enrichment planting.

To test whether enrichment planting accelerated the rate of canopy height growth relative to control plots, we used the CHMs to calculate the mean top-of-canopy height (TCH) of all 124 plots in both 2013 and 2020, as well as the difference in TCH between the two surveys (ΔTCH). Our hypothesis is that the TCH of plots which received the 4 or 16 species mixture treatments will have faster growth rates than those of the unplanted controls and monoculture plots and will consequently have reached a greater mean height by 2020 thus resulting in greater values of ΔTCH.

In addition to these canopy height metrics, we also used the CHMs to calculate the gap fraction (GF) at multiple height tiers above-ground, including 5 m, 10 m, 15 m, and 20 m. Once again, our hypothesis was that tree planting will lead to the more rapid filling of canopy gaps compared to control plots. Assessing GF at multiple height tiers allowed us to test where within the vertical profile of the canopy the biggest effects of tree planting can be observed in the first two decades of enrichment planting. In addition to the effects of tree planting, GF also allows us to test the hypothesis that liana cutting will facilitate the establishment of tree saplings, allowing them to more rapidly close canopy gaps (César et al., 2016; Meunier et al., 2021). For the purpose of the GF analysis only data from the 2020 airborne LiDAR survey was used. For the purpose of the GF analysis, only data from the 2020 airborne LiDAR survey was used. This was chosen due to the potential of gaps forming during the time between the acquisition of the 2013 and 2020 data. These potentially notable mortalities and new gaps developing in the canopy by 2020 would be related to the trees predating the SBE and already established in the canopy cover, from natural causes such as branch fall, tree mortality and wind throw, and therefore unrelated to the interventions of the SBE (Bonnet et al., 2015; Goulamoussène et al., 2017; Goodbody et al., 2020). Any larger disturbance events creating canopy gaps, such as the El Niño of 2015/2016, would most likely primarily be reflecting any impacts on the remnant stand (O’Brien et al., 2019). As such, in order to mitigate noisy data, wherein it would be impossible to discern between the old and new gaps, the gap dynamics would need tracking by delineating the gaps in the two datasets. This is because simply comparing and overlaying the amount of gaps of the two datasets would not be specific enough to provide any information other than the percentage of gaps in the canopy. From this one cannot deduce what has shifted in the gaps calculated from the 2013 data and any gap expansions or new gap openings could suggest a worsening effect. However, to truly assess this a completely separate form of analysis would need to be conducted. This would require not only defining and applying height thresholds to CHMs in order to differentiate between gap and non-gap pixels, but also characterising properties of detected gaps, such as gap area and shape index to calculate the gap shape complexity (Goodbody et al., 2020). This would need to be done for both datasets. Thereafter methods to assess for gap dynamics would need to be developed by calculating a variety of gap properties, like the gap fraction, areas of novel gap openings, any gap size shifts such as expansions, and any gap closures (Vepankomma et al., 2008). The gaps of the 2013 dataset would also require tracking in order to pinpoint how much they close by 2020, this would allow us to exclude any new or expanding gaps. Therefore, a less complex approach providing a more basic overview is the method we utilised by simply assessing the gap fraction in the 2020 data. This gives us a cumulative view of how the canopy cover has changed in the treated plots relative to the control since the start of the implementation of the SBE 20 years prior.

2.3.4 Data analysis and hypothesis testing

To test how the different SBE treatments impacted the canopy height and openness metrics described above, we used an analysis of variance (ANOVA) to compare mean values of each metric across the various experimental treatments. The response variables in the ANOVA are the metrics described above (TCH_{2020}, ΔTCH, GF_{5m}, GF_{10m}, GF_{15m} and GF_{20m}) whilst the main explanatory variable is the experimental treatment (factor with five levels: unplanted control, planting of monocultures, 4-species mixtures, 16-species mixtures and 16-species mixtures with climber cutting). In the case where significant ANOVA effects were identified, post-hoc pairwise comparisons among treatments were undertaken using a Tukey test to further identify which of the treatment conditions were presenting the greatest difference to the control, and their extents.

2.4 Results

2.4.1 Canopy height and height growth rate

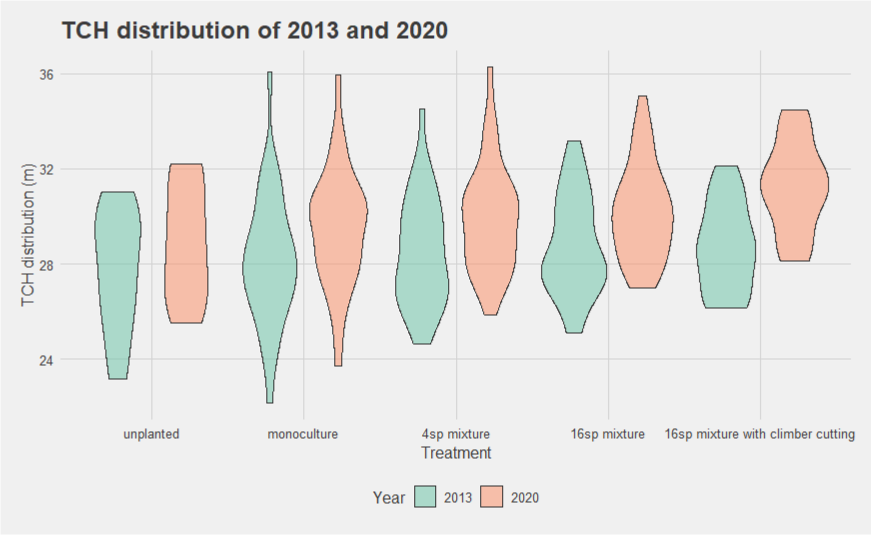


Figure 2.2: Overview of TCH distribution across conditions in 2013 and 2020. Although no significant results were found from the treatment conditions on the 2020 TCH, a slight difference can be noted between the years and conditions, suggesting planted plots may have more notable gain with time compared to unplanted plots.

By 2020, almost 20 years after enrichment planting, we found no statistically significant difference in mean canopy height between any of the treatments across the SBE ([F(4,119) = 2.35, p = 0.058] (p > 0.05); Figure. 2.3b). Nonetheless, on average TCH2020 was 1.3 m taller in plots treated with the 16 species mixed tree planting with climber cutting compared to the control plots. This difference is further noted in the significant result found from the 16 species mixture with climber cutting treatment in ΔTCH ([F(4,119) = 7.16, p = 3.36e-05] ($p < 0.05$); Figure. 2.3d).

Although no significance was found of treatments on TCH by 2020, visible differences can be observed across treatments and between 2013 and 2020 (Figure 2.2). Figure 2.2 demonstrates both the variation in distribution range between treatments, and the impact of time on recovery with and without intervention. Interestingly one can note through Figure 2.2 that the overall mean TCH did indeed increase in all planted conditions whereas the unplanted conditions seemed less variable. The differences in range, as well as the increase in the minimum, median, and maximum ΔTCH suggests that planting was somewhat more effective. Observing these same differences and the smaller range in the 16 species mixture and the 16 species mixture with climber cutting suggests that diversity and relief cutting may prove somewhat more effective than simply planting. Curiously, the range of the monoculture conditions presents a greater range than the other planted conditions. As planting started in 2002 and the second round was completed in 2011, this could indicate rehabilitation and changes starting to build already prior to the 2013 survey. This range could possibly also be reflecting differences between the 16 different planted species, something we were not aware of and thus did not consider when first assessing our data. We expect this could be verified through additional LiDAR data acquired at later dates, as well as through field based verification of planting success rates. This larger range, albeit slightly smaller, can also be observed in the condition of the 4 species mixture. We once more theorise this could be due to the 16 different compositions of the 4 species mixture condition, species compositional differences were a variable we had not considered to assess outside of the scope of diversity; as such we first explain and delve further into this and the monoculture planting conditions in section 3.3. This suggests intervention may have more of an accumulative effect requiring more time for significant observation. Whilst Figure 2.3b shows a clear difference between unplanted plots compared to combining diversity planting with climber cutting management.

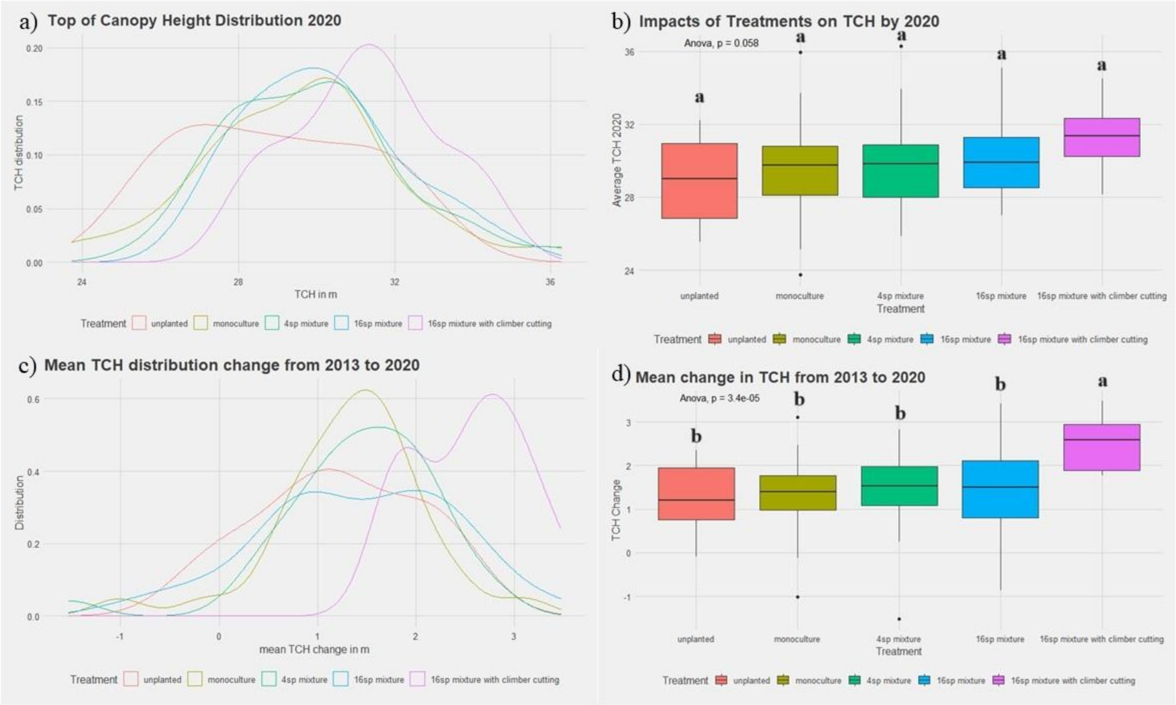


Figure 2.3: TCH distribution in 2013 and 2020, impacts of treatment on TCH by 2020, and ΔTCH results. Figure a) shows the distribution of TCH for each treatment condition by 2020. Figure b) depicts the extent to which the treatment conditions have impacted TCH by the year 2020. Figure c) shows the distribution of ΔTCH for each treatment condition. Figure d) denotes the mean change of TCH from 2013 to 2020, demonstrating the significant difference in ΔTCH from the treatment of planting a mixture of 16 species with climber cutting management.

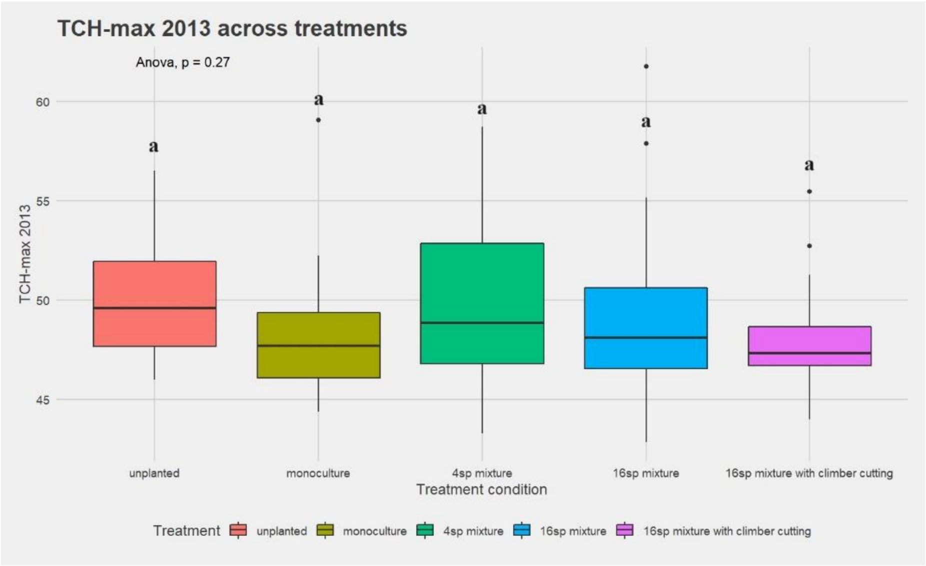
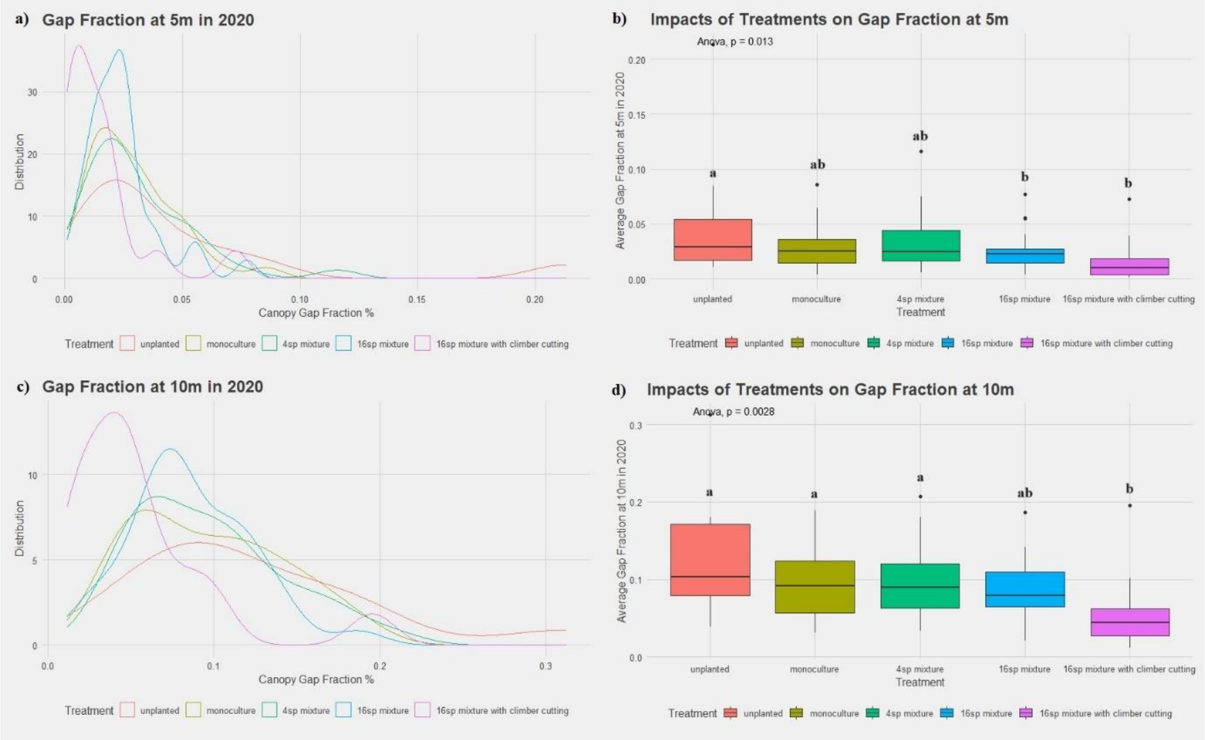


Figure 2.4: Demonstrates the range of max top of canopy height of the plots across the different treatments in 2013. Here we can see the variability of maxTCH across and between treatment conditions, affirming the randomised nature of the SBE's planting.

As the SBE is a randomised experiment, we consider the planting of the plots to be equally variable, thus we expect there to be no observable systematic differences between treatments directly after implementation. Yet, observing the long tails of figure 2.2, as well as considering the possible impacts of topography on canopy gaps, we reflected on the potential of the remnant trees in the stand influencing the ΔTCH, thus we assessed the maximum top of canopy height of the 2013 data (maxTCH). Whilst also being an adequate metric for assessing for past disturbance, analysing the maxTCH can highlight any variability in past logging intensity across the different treatment conditions (Battles et al., 1995). As expected, after running this analysis, we discovered no statistically significant difference in maxTCH between treatments ([F(4, 119) = 1.31, p = 0.269] ($p > 0.05$); Figure 2.4). We did however note the visibly smaller maxTCH range of the 16 species mixture with climber cutting condition. We speculate this could most likely be due to the smaller sample size, where only 16 plots received the sub-treatment of climber cutting compared to the other four planting conditions being assigned 32 plots each (Table 2.1).

2.4.2 *Canopy gap fraction*

We found a significant effect of tree planting across all observation levels of the canopy height profile. Specifically, we found that planting a mixture of 16 species significantly reduced the GF size across all height profiles. The post-hoc Tukey test indicated that most significant differences were found between the unplanted control condition and the 16 species mixture with climber cutting (notable in Figure 2.5). A significant impact from planting monocultures and a mixture of 4 species was only detectable in the 5m profile.



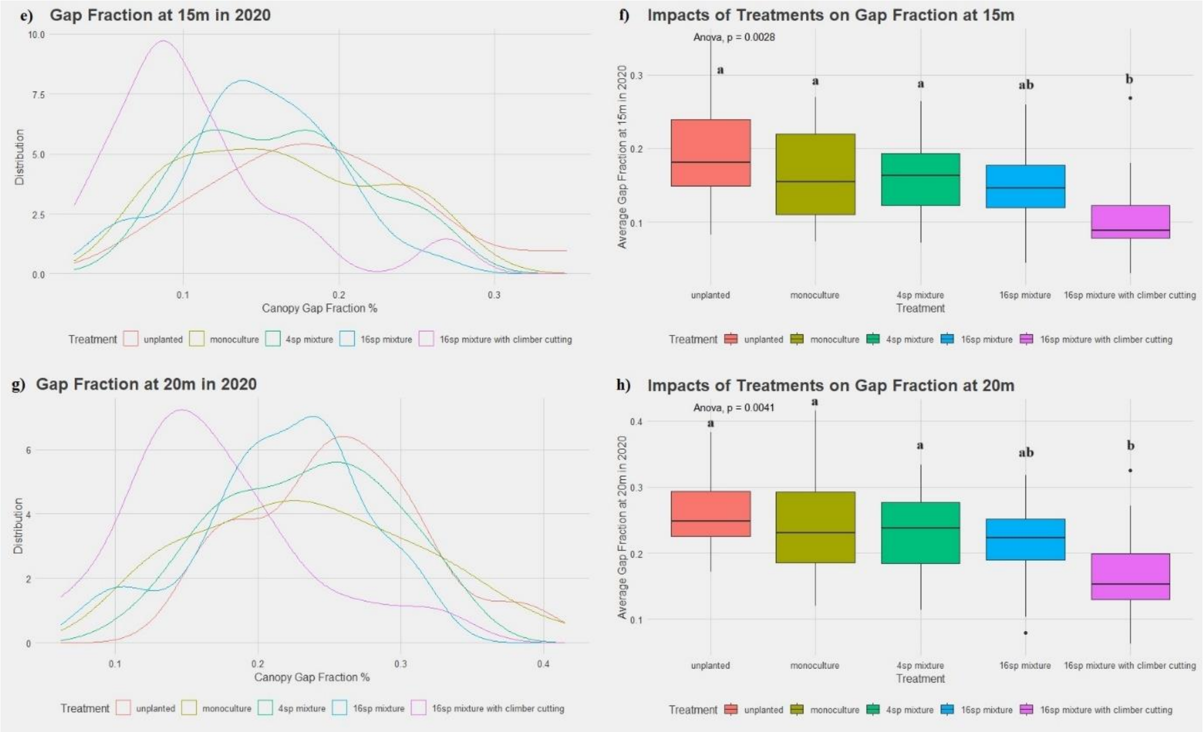


Figure 2.5: The distribution of the percentage gap remaining in the canopy for each treatment condition at their respective observed distances (5m, 10m, 15m, and 20m) are presented next to the equivalent box plot. These box plots portray the extent to which the various treatments have had in filling the canopy gaps by how much gap in the canopy remains. A difference in variation of gap size can be observed between the different heights, yet all distances can be observed to contain statistically significant differences on the size of the GF ($p < 0.05$), with observational differences between the control and monoculture plots compared to the 16 species mix both with and without climber cutting with increase in distance.

2.5 Discussion

Through the use of airborne LiDAR, we were able to track canopy recovery across the SBE affirming this method of remote sensing to be an effective tool (Lefsky et al., 2002; Dalponte et al., 2019; Walter et al., 2019; Senf et al., 2020; Wu et al., 2020). Overall we discovered canopy recovery rates to vary considerably across the SBE and that the restoration initiatives implemented can in part explain these differences. Although only some results yielded statistical significance, at this early stage we found planting to be superior to no planting – specifically when combined with liana cutting.

The results indicated a positive effect of climber cutting management on canopy gap filling compared to control plots and those in the monoculture and 4 species planting conditions. This supports current research and management practices for sapling establishment and success rates, with additional insights into the pace and extent to which these gaps may start to pack (Gonzalez et al., 2020; Wang et al., 2022). Considering the SBE’s design limitations and without ground data we have deduced three potential drivers for these results – sapling establishment, liberation effects, and diversity planting.

Conversely these findings suggest tree planting and diversity have limited statistical significant impact on the mean height of the canopy in the initial 18 years post enrichment planting, especially if planting a larger diversity of species is paired with climber cutting. Moreover, these early results suggest with time more significant shifts may be notable as our results presented a form of ramping-up effect. Nonetheless, our ΔTCH results differ from current go-to management practices where tree planting is considered a viable strategy (Sabah Forestry Department, 2017). As such, further multi-temporal investigations into the top of canopy height growth, leveraging additional remote sensing methods for more holistic data of the forest layers, could be clarifying.

2.5.1 Canopy gaps and coverage

Our results showed climber cutting had strong significance, particularly on the pace of canopy gap closure. The climber cutting plots superior gap filling generated notable results across all four height tiers; with the greatest differences observed between the unplanted control condition and that of the 16 species mixture with climber cutting management. These gap fractions were also significantly smaller when compared with the monoculture and 4 species planting conditions. Yet, due to limitations of the SBE and the lack of ground data for a holistic image, the driving factor(s) for these findings are not clear cut. Consequently, we have identified three leading drivers for these canopy gap results: i) climber cutting increased sapling success ii) liberation effects on remnant trees granted canopy expansion and iii) canopy packing optimised by high species diversity.

i. Climber cutting and sapling success rates

Due to lianas prioritising growth length compared to trees which invest in developing large stems, liana removal has demonstrated to increase sapling establishment and height (Schnitzer & Bongers, 2002; O'Brien et al., 2019). Logging and large disturbances in a forest grant these swiftly growing vines more freedom to colonise, paired with their hardy root system and rapid growth pace their rate of establishment significantly outperforms that of young trees (Pérez-Salicrup, 2001; Kettle, 2012; César et al., 2016; Meunier et al., 2021). Our results depict a significantly smaller gap fraction in the lower height tiers (Figure 2.9) potentially supporting the success rate and height growth of the planted saplings in filling the gaps. These results were especially significant when compared with the unplanted and monoculture conditions which did not undergo this sub-treatment.

ii. Liberation effect on remnant trees

Lianas are most often observed in the upper to middle layers of the forest canopy, rapidly growing up the trees' vertical structures seeking sunlight, which restricts a tree's canopy and height growth (Schnitzer & Bongers., 2002; Media-Vega et al., 2021). As such, liberation cutting has been found to release adult trees from the suppressive effects of lianas permitting canopy lateral expansion (Alvarez-Cansino et al., 2015; Rodriguez-Ronderos et al., 2016; García León et al., 2017). This could explain the significant gap fraction results observed at the higher tiers (Figure 2.5).

iii. Response of canopy gaps to diversity planting

Mixed species stands have demonstrated the efficiency of crown plasticity due to variability in nutrient requirements and shade tolerance (Jucker et al., 2015; Gong et al., 2021; Wange et al., 2022). Diversity planting could therefore optimise space through canopy packing filling gaps more effectively. Through the unique opportunity of leveraging the SBE's real-world experimental system, our results support the structural equation models suggesting planting a mixture of species can drive reforestation (Guerrero-Ramirez et al., 2017; Gonzalez et al., 2020; Wang et al., 2022). Our results suggest diversity planting does play a significant role in filling canopy gaps, wherein the 16 species mixture plots without climber also demonstrated significantly greater gap filling compared to the monoculture and 4 species planting conditions.

iv. Limitations and future research

Further assessment is required through combined airborne LiDAR and TLS multi-temporal data for a comprehensive insight into where in the canopy compositional change is most notable to identify main drivers of canopy gap closing – be it liberation effects or sapling success rates from climber cutting or diversity planting. Until further analysis, we derive that planting a highly diverse number of tree species coupled with relief cutting fills canopy gaps more rapidly in the first couple of decades than possible through natural regeneration.

2.5.2 Canopy height and height growth

Our results do not support current literature and management practices – suggesting that planting had no significant impact by 2020 compared to control plots, yet a notable difference was observable across treatments between 2013 and 2020 (Philipson et al., 2020; Zeng & Fischer, 2021). However, the significant ΔTCH results of 16 mixture planting, especially when combined with climber cutting, suggest that significant results may emerge with time.

Nonetheless, finding limited significant effect of enrichment planting is further surprising due to the vast literature on the relationship between biodiversity and ecosystem functioning, and the satellite data emerging from the SBE indicating higher remote sensed vegetation in planted conditions (Philipson et al., 2020; Wu et al., 2020). The lack of significance at this stage of recovery supports natural regeneration of fragmented tropical forests to be more cost-effective, especially should the remnant forest hold a significant abundance of biodiversity (Chazdon et al., 2009; Cesar et al., 2016).

The climate and tall canopies found in tropical forest ecosystems hold capacity for vast species abundance and greater canopy complexity through canopy packing (Morin et al., 2011; Pretzsch et al., 2014; Jucker et al., 2015). TCH was initially selected as a metric for reliable indication of ecosystem functions, such as biomass productivity and species diversity, as it summarises vertical patterns of distribution over time (Asner et al., 2014; Tao et al., 2016; Mao et al., 2019). Since tree height is propelled by carbon dioxide uptake and light competition, and the SBE's enrichment plating involved line planting saplings of species previously harvested during selective logging, noted as poorly stocked within the site (Hector et al., 2011). Coupled with further optimising growth conditions for saplings from climber cutting increasing canopy openness thus enhancing light penetration (Pérez-Salicrup, 2001; César et al., 2016; Meunier et al 2021). We had reason to predict a more rapid growth in planted plots, expecting this to best be indicated through significant increases in mean TCH, especially in the treatments involving diversity and climber cutting (Gamfeldt et al., 2008; Haase et al., 2015; Tao et al., 2016 ; Yu et al., 2017). Yet, these results indicate that TCH may not be a worthwhile measure for impacts of planting on canopy recovery and productivity for another few decades, unless mapping Dipterocarpaceae recovery dynamics. Particularly when taking into account the potential growth stunting impacts the El Niño drought's climatic stressors may have had on the saplings (O'Brien et al., 2019).

Despite the statistical insignificance, a 1.3m difference in height variation of TCH distribution can be noted in the 16 species mixture planting with climber cutting management compared to the control. This could be interesting to follow up on once the planted trees have matured. Considering the average growth pace of Dipterocarpaceae expecting a significant increase in mean TCH less than 20 years post planting may be ambitious. Within Malaysian Dipterocarp Forests, their growth has been observed to require longer to achieve natural equilibrium in stand dynamics (Mendoza et al., 1986). Smaller changes in average tree size were found during the first 100 years (Ingram et al., 1996; Bischoff et al., 2005). Therefore, further assessing the plots through TLS could prove more beneficial as compositional developments may be more notable in the understory and lower canopy at this stage (Liang et al., 2016; Disney et al., 2018). These TCH findings could however potentially have provided insights, were further decades of multi-temporal airborne LiDAR data collected. This would offer clarity, should there be a timeline for significance of impacts from intervention and diversity insights into the pace and rate at which a restored and managed Dipterocarp stand might progress, and add understandings to limited Dipterocarp dynamic literature.

2.5.3 Conclusion

Our findings indicated active methods of planting higher numbers in tree species, especially when combined with relief cutting, fills canopy gaps more rapidly in the first 20 years than passive methods of conservation. This supports previous findings on the value of liberation cutting for ease and establishment success rate of tree sapling, whilst adding insights into the pace and extent to which canopy gaps may start to fill post planting and climber cutting management (O'Brien et al., 2019; Wills et al. 2021).

Although the predominant drivers of canopy closing require further research for clear cut insights, airborne LiDAR has proven an efficient and effective tool for monitoring canopy recovery through diversity planting and relief cutting (Lefsky et al., 2002; Dalponte et al., 2019; Senf et al., 2020; Wu et al., 2020). Evaluating restoration methods through airborne LiDAR highlighted the layers of investigation required in such vast tropical forest field-scale experiments. For instance, following the progression of the growth over further time intervals, and harnessing TLS for lower canopy dynamic depictions and biomass productivity not obvious through the airborne LiDAR data (Wu et al., 2020).

Conversely, almost 20 years following enrichment planting found limited statistically significant difference on the mean top of canopy heights across treatments, wherein a significant difference from the control was only notable in ΔTCH of the 16 species mixtures, particularly when combined with climber cutting. This diverges from current management interventions practiced in already existing systems, suggesting tree planting for rehabilitating tropical forest ecosystems may require a more site specific approach, or may require more time to display changes in TCH (Sabah Forestry Department, 2017; Zeng & Fischer, 2021). Nevertheless, a slight TCH difference, albeit insignificant, was observed in planted conditions compared to controls. Nonetheless, at this stage TCH may not be a worthwhile measure for assessing the impacts of planting on recovery and assessing for shifts in leaf area index may be more relevant. Additionally investigating lower canopy trends through terrestrial laser scanning could prove more insightful into the early stages post-planting for density and carbon stock recovery (Liang et al., 2016; Disney et al., 2018).

Chapter Three

3. General discussion and future research

3.1 Overview

The degradation of tropical forest ecosystems, caused by logging and land conversion, has been extensive, leading to observations of vast changes to ecosystems and global tropical forest cover. The fragmentation of tropical forest ecosystems has emphasized the global scale of the issue leading to irreversible loss to species' diversity due to their mismanagement and exploitation (Finger et al., 2012; Watson et al., 2016; Zeng & Fischer, 2021). Although left depauperated post selective logging, the emerging literature on the intrinsic value of fragmented tropical forests has influenced the rise in forest rehabilitation and conservation initiatives aiming to restore biodiversity. Moreover, recovering and secondary tropical forests are increasingly considered an important factor in slowing the impacts of climate change due to their potential to sequester and store carbon (Isbell et al., 2017; Senf et al., 2020; Zhang et al., 2022). Therefore, to mitigate climate change and to promote the recovering biodiversity and species' abundances, it is increasingly crucial to identify best practices for recovery of tropical forest ecosystems (Martin et al., 2021).

Despite enrichment planting being a predominant management method for active restoration of logged-over or otherwise degraded tropical forests, evidence for its success in an existing metric of forest is lacking. The laborious challenge posed by the density and scale of such landscapes paired with the additional financial cost of efficient tools like airborne LiDAR limit capacity for monitoring the success rates, let alone assessing the management methods. Consequently, the vast majority of knowledge on canopy complexity dynamics, changes and trends stem from post-disturbance observations, small-scale short-term field studies, and planting on cleared land (Nadrowski et al., 2010; Scherer-Lorenzen, 2014; Amazonas et al 2018; Wang et al., 2022). The additional concern of the increasing severity and frequency of natural disasters linked with the rise in global temperatures can be challenging to study. The changes in the complexity of a fragmented recovering stand and their response to such unprecedented shifts coupled with various management interventions may be challenging to predict. Consequently, there is a great value and knowledge gain in long-term observations of field-scale ecological experiments wherein the efficacy of a multitude of management methods are measured and assessed (Guerrero-Ramirez et al., 2017; Gonzalez et al., 2020; Wang et al., 2022).

This project aimed to start filling these knowledge gaps by comparing airborne LiDAR data from 2013 and 2020 over the Sabah Biodiversity Experiment (SBE) to assess the effectiveness of the restoration method of tree planting, and the extent diversity planting may optimise this. To test if enrichment planting accelerated the rate of canopy height growth relative to the control, we used canopy height models (CHM) to calculate the mean difference in top of canopy height (ΔTCH). We hypothesised that plots planted with the 4 or 16 species mixtures would present greater change in mean heights than the monoculture planted plots and unplanted controls by 2020 (Chisholm et al., 2013; Jucker et al., 2015; Riutta et al., 2021; Wilson et al., 2021). The CHMs were also used to calculate the gap fractions (GF) at multiple height tiers: 5 m, 10 m, 15 m and 20 m above-ground. We predicted that tree planting would increase the pace of canopy gap filling, expecting a greater difference between the plots planted with higher numbers of diversity than the control. Evaluating the GF at multiple height tiers allowed us to assess where within the vertical profile of the canopy the greatest effects of tree planting could be observed (César et al., 2016; Meunier et al., 2021).

3.2 Summary of main findings

Our results indicated tree planting had limited impact on ΔTCH almost 20 years post intervention. A significant impact on ΔTCH was found only in the 16 species mixture conditions, namely when combined with climber cutting management. However, no significant results were found from the different treatments in the 2020 TCH. Nonetheless, trends of accumulative change in the data suggest effects are ramping up, indicating a 1.3m difference in height variation of TCH distribution by 2020 between the 16 species mixture planting with climber cutting management and the control. These results suggest that the TCH recovery pace through enrichment planting may build with time to outperform that of unplanted plots. Therefore, TCH may not be a worthwhile measure for impacts of planting on canopy recovery and productivity at such an early stage. Conversely, our results showed diversity-tree planting led to significantly smaller GF across all height tiers, where the 16 species mixture plots showed a significant decrease in GF size compared to all other conditions. Based on this, we infer that planting a highly diverse number of tree species coupled with relief cutting fills canopy gaps more rapidly in the first couple of decades than possible through natural regeneration.

3.3 Canopy height

Previous research reveals trees in tropical forests prioritise height for establishment in the first decade of growth, as a result of strong light competition and driven by fast growth in tropical climates. These tall canopies hold capacity for a multi-layered stand in a species diverse forest ecosystem owing to differences in shade tolerance and resource needs, granting space optimisation through canopy packing (Morin et al., 2011; Pretzsch et al., 2014; Jucker et al., 2015; Chanthorn et al., 2017; Fischer et al., 2020). Consequently, tree planting is extensively leveraged as a means for management and restoration in disturbed and fragmented stands. Therefore, it would be reasonable to expect some increase in the mean top of canopy height, at least in the diversely planted conditions. Additionally, the enrichment planting was conducted with saplings of species previously harvested during selective logging, most of which are classed as endangered (Hector et al., 2011). As they differ to the remnant trees, one might assume the saplings would rapidly re-establish, presenting some notable increase to ΔTCH. As diverse systems use resources more efficiently, taller growth could be stimulated, yielding the assumption of a greater mean height within diversely planted plots compared to the control (Gamfeldt et al., 2008; Hector et al., 2011; Haase et al., 2015; Yu et al., 2017).

Conversely, our results only indicated a significant ΔTCH result in the 16 species mixture treatments, especially when coupled with climber cutting. Despite a 1.3m difference between the heights of the aforementioned condition and that of the control in 2020, no significant impact was found across all treatment conditions on the 2020 TCH. This suggests that enrichment planting may have a build-up effect with time, and more time may be required for notable differences to be present from intervention. Although the limited significance presented in our results differ from current literature and management practices, we suggest, until further knowledge emerges, that this may be due to the slow growth timeline of Dipterocarpaceae.

In Malaysian Dipterocarp Forests, the Dipterocarpaceae are known for their height and density, finding some to grow over 70 – 90 m tall, depending on the region. However, their growth pace is far less impressive, taking on average up to 100 years to reach even 30 m of height, and have been observed to require longer to achieve natural equilibrium in stand dynamics (Mendoza et al., 1986; Appanah et al., 1990; Ingram et al., 1996; Bischoff et al., 2005). After considering this slow growth pace, expecting planted saplings to significantly impact the ΔTCH less than 20 years post planting may be ambitious. Therefore, assessing the plots through terrestrial laser scanning (TLS), in addition to airborne LiDAR, could prove more beneficial as compositional developments may be more notable in the understory and lower canopy at this stage (see section below 3.5 for more on this; Liang et al., 2016; Disney et al., 2018).

TCH is the single most common metric we can derive from LiDAR, and underpins most models of forest biomass. We initially selected TCH as a metric for reliable indication of ecosystem functions and a factor within canopy complexity recovery, as it measures the aboveground vegetation and summarises the vertical patterns of distribution through the canopy over time (Goets et al., 2007; Tao et al., 2016; Mao et al., 2019). Thus we expected the plots which received the 4 or 16 species mix treatment would have more rapid lower canopy growth rates from the introduced trees, than those of the unplanted and monoculture plots, which would consequently reach a greater mean height by 2020. Moreover, TCH captures the dynamics of the whole canopy, including mature trees. Mature trees tend to remain unaffected by tree planting in the first few decades as the majority of changes are occurring lower in the canopy. ΔTCH examined to what degree tree planting and, more specifically, tree diversity affected the mean canopy height growth rates over time, expecting this mean would increase as planted trees would fill the gaps within the canopy. However, this was better assessed through the GF metric, and our limited significant results suggest TCH may not be an ideal metric for capturing early effects of restoration.

Limited significant effects on 2020 TCH thus suggest natural regeneration of fragmented tropical forests to be more cost effective, especially should the remnant forest hold a significant abundance of biodiversity (Chazdon et al., 2009; Cesar et al., 2016). These findings could however potentially provide insights were further decades of multi-temporal airborne LiDAR data collected. This could offer clarity should there be a timeline for significance of impacts from planting and diversity. As well as insights into the pace and rate at which a restored and managed Dipterocarpaceae stand might progress, adding understandings to limited silvicultural Dipterocarpaceae literature. Nonetheless, our results indicate a build up towards the potential for significant differences. Therefore we suggest additional multi-temporal airborne LiDAR data collection to see if effects have stabilised or continued on the upwards trajectory.

In hindsight, a more appropriate metric for tracking the canopy recovery than TCH would have been measuring the leaf area index (LAI). LAI, defined as the area of leaf material per unit ground area, measures the vertical distribution of vegetation in a stand for light interception, and is used as a measure of forest growth and productivity (Alvarez-Cansino et al., 2015; Rodriguez-Ronderos et al., 2016). This could provide a more relevant and clearer insight into the impacts of tree planting on the recovery of the canopy structural complexity during the initial couple of decades post planting.

3.4 Canopy gaps

We found planting a highly diverse number of tree species paired with relief cutting initially supports more rapid canopy gap filling than natural regeneration. We have three theories for these findings: i) climber cutting increased sapling success ii) liberation effects on remnant trees led to canopy expansion of remnant trees and iii) canopy packing optimised by high species diversity.

Climber cutting is applied as a means to increase survival chances of seedlings, the establishment of saplings, and in order to liberate adult trees (Schnitzer & Bongers, 2002). No longer outcompeted by the rapid growth pace and robust root systems of lianas and climbing vines, and liberated from the resistance their weight poses, sapling height stunting is decreased (Pérez-Salicrup, 2001; César et al., 2016; Meunier et al., 2021). Prior research are unanimous on liana cutting leading to increased height growth rate of newly planted saplings. However, the reports on the extent differ greatly expressing a growth rate increase anywhere between 5 to 66% within the first two years of planting and climber cutting, where variations in climate and site based climber infestation severity differed between studies (Pérez-Salicrup et al., 2002; Grauel et al., 2004; O'Brien et al., 2019). Our findings thus supports current research and management practices for sapling establishment and success rates, with additional insights into the pace and extent to which these gaps may start to pack. However, climber cutting has also been found to detrimentally impact the delicate microclimate of the forest ecosystem (O'Brien et al., 2019). Through the initial increase in canopy gap size the ecosystem is more exposed to intensities and fluctuations in weather conditions, such as winds, temperature and light. Namely, the amount of light penetrating to the forest floor is heightened, raising the temperature and risking damaging drying effects resulting in a loss of vapour pressure. This in turn impacts survival of saplings and the thriving of already vulnerable remnant flora (Martines-Garza et al., 2013; Jucker et al., 2018; O'Brien et al., 2019). This invokes the question of the extent to which the canopy cover truly was impacted by sapling success and height from climber cutting, and if this management method may present greater damage to the stand in the long term. This is particularly relevant with current global fluctuations in severity and increased occurrence of unprecedented environmental shifts and natural disturbance from the changing climate. For instance, when greater canopy openness from cutting coincided with hurricane and El Niño droughts, higher sapling mortality rates followed. In such instances climbers have been observed as 'disturbance-specialist' plants, acting as buffers against damaging effects to the greater forest structure (Garrido- Péres et al., 2008; César et al., 2016; O'Brien et al., 2019). With the increase in severity of weather fluctuations the benefits and risk indicators of this management method require further assessment.

The canopies of the remnant trees in a stand are also liberated through liana removal (Schnitzer & Bongers, 2002). Unless disturbance caused to the stand presents significant enough gaps in the canopy, which has been observed in areas exposed to pervasive or intense logging, vining plants are not commonly found to dominate the understory (Media-Vega et al., 2021). This is due to their light demanding nature, preferring to grow vertically towards the overstory where they will proceed to drape across the canopy (Schnitzer & Bongers., 2002). This can have a stifling impact on the adult trees, as they not only compete with the climbers for light, water and nutrients, but also have their canopy expansion restricted and their seed fruiting stunted (García León et al., 2017). Therefore, liberation cutting is also leveraged to free the crowns of remnant trees from the restrictive effects of lianas. With more canopy space to fill and less constraint from the weight of the vines the canopies would expand to dominate more space. The swift lateral expansion of liberated remnant trees has been demonstrated through temporal tracking of LAI and biomass changes (Alvarez-Cansino et al., 2015; Rodriguez-Ronderos et al., 2016). This work indicated that liberated trees require 2-4 years to recover the biomass and compensate for light interception formerly contributed by climbers (Perez-Salicrup et al., 2001; Schnitzer & Carson., 2010; O’Brien et al., 2019; Meunier et al., 2021). Thus, the significant results of the canopy gap filling observed in our data could result from liberation effects.

However, the design of the SBE left climber cutting as a sub-treatment for only 16 of the 16 species mixture plots. Disentangling the effects of liana cutting from tree planting is required. Were this implemented as a sub-treatment across all conditions, or presented as a treatment on its own, this management method could be better assessed for the extent to any benefits it may present. Our results indicated that gap fraction decreased significantly across both 16 species mixture conditions also presenting diversity as a driver. Previous findings have indicated the value of heterogeneity for increasing resilience of a variety of tree species seedlings, assisting in their survival and performance (Graudal et al., 2014; Jalonen et al., 2018). Similarly, mixed species stands have demonstrated efficiency of crown plasticity as a result of their variability in needs; such as differences in nutrients requirements negating the potential of soil leaching and shade tolerance facilitating vertical stratification (Jucker et al. 2015). With even slight differences in needs between species, the competition for resources decreases, granting optimisation of space which can lead to more effective canopy packing, consequently optimising nutrient cycling (Jucker et al., 2015). This diversity provided through species and tree age sustains larger understory plant diversity, boosting availability of natural subregions and increasing canopy complexity (Morin et al., 2011; Brassard et al., 2014; Gong et al., 2021; Wang et al., 2022).

To better discern the extent to which each driver is influencing these significant results, we suggest a combination of additional monitoring and analysis methods. Further metrics, such as LAI to assess temporal fluctuations in physiology and function within the canopies across conditions paired with multi-temporal TLS for a deeper multi-layered image of the canopy, could indicate where in the vertical profile of the canopy increases in vegetation are dominant. The use of TLS could provide a more complete picture of the forest and canopy structure granting an integrative view. These additional insights into the understory and layers within the stand could discern whether the canopy gap closure is driven by the liberation effects on the remnant trees, or through a difference in the height of the saplings between treatment conditions. With the limitation of the SBE’s design in mind, potential effects from diversity and climber cutting management cannot yet be decoupled. The addition of TLS data could depict the extent to which diversity-planting has impacted density and canopy packing at this stage. However, until paired with further exploration into the impacts of climber cutting in plots with no tree planting, the true effects of climber cutting as a method on its own are yet to be uncovered. Finally, for greater comprehension of ecosystem multifunctionality, delving into the long-term impacts of climber cutting and how they impact the greater ecosystem is required. Both from other local species and to quantifying if the carbon store loss from vine removal is more than compensated by the tree growth.

3.5 A bottom-up perspective of tropical forest restoration

Ground-based remote sensing methods, such as terrestrial laser sensing (TLS), a ground based LiDAR, have been emerging for monitoring individual plants and understory vegetation otherwise missed by airborne LiDAR. Adding TLS data has been found to generate more holistic datasets, providing deeper insights into below canopy trends of the structures and variations within the stand, such as deadwood or growth progress of newly introduced young trees (Liang et al., 2016; Disney et al., 2018; Yrttimaa et al., 2019; Seidel et al., 2020). TLS captures large amounts of 3D points rapidly, allowing for high-resolution mapping and data capturing of terrain and vegetation over a range of 50 – 300 m (Vosselman & Maas, 2010). The much higher point density of TLS dataset means that it can be used to detect and determine important tree-level quality attributes, such as biomass components and stem volume, whilst also allowing for time series analysis for longitudinal analysis (Srinivasan et al., 2014; Liang et al., 2016; Walsh et al., 2018). The addition of TLS would provide below-canopy assessment, filling the blind-spots of airborne LiDAR, whilst addressing common attributes like tree height, canopy density, tree species, and diameter at breast height (DBH) (Hiker et al., 2012; Disney et al., 2018). As LiDAR generally cannot penetrate solid objects such as branches and stems the addition of bottom-up mapping could have provided us with a more holistic depiction of the SBE, and possibly more relevant insights for early stage rehabilitation and tree recruitment (Wills et al., 2021). Moreover, using TLS to monitor tropical forest ecosystems is relatively novel. Leveraging TLS could therefore provide further insights in best methods for use as well as its ability to monitor and quantify forest rehabilitation within tropical ecosystems.

Leveraging TLS would also provide a closer look at the differences in the 4 species mixture variations. The design of the SBE contained 16 different mixtures in the 4 species planting condition – two plots per mixture – to test if light targeted species would yield greater impact than a generic mixture, and to assess for optimisation of species compositions (Saner et al., 2009; Tuck et al., 2016). Similarly the monoculture condition also consisted of 2 plots per species planted, resulting in 16 different monoculture conditions (Tuck et al., 2016). These two sub-conditions are factors we did not analyse the difference in from our airborne LiDAR data. This could have been insightful for further comprehension into which species might boost early-stage rehabilitation, if there are optimal species pairings, or if there are species which may have out-performed or had greater survival and establishment successes than others. This could further decouple the potential drivers on the effects within the GF analysis, and possibly explain the greater TCH range observed in the monoculture and 4 species mixture conditions. Although neither condition presented significant TCH results, we speculate that within condition assessment could have suggested otherwise for the 4 species mixture. Assessing if there are differences between the conditions in the lower canopy and understory with TLS could potentially further indicate which species may lead to faster canopy recovery. The combination of TLS data and the sub-experiment in the two aforementioned conditions could potentially provide insight into which, if any, species could be more successful in establishment and resource optimisation.

Furthermore, monitoring for recruitment success at the SBE has not been conducted since planting and species cannot be identified in our airborne LiDAR data. As such, field data is required in order to survey the survival and success rates of the planted trees. Field data covering the growth pace could also support insights into species success differences and their response to being planted amongst a diverse mixture of species and climber cutting effects. Such silvicultural field data, such as deeper knowledge of plot based composition could also add to current silvical knowledge on complementary mixtures for diversity planting initiatives (Redondo-Brenes & Montagnini, 2016; Marshall et al., 2021). Although we have found airborne LiDAR to be a time efficient tool, cross-validating the results could further quantify the benefits. Whilst supplementing remote sensing monitoring with field data to validate these results could also permit us to better understand the underlying mechanisms of the patterns presented from the airborne LiDAR data.

Field data covering the growth pace could also support insights into species success differences and if their success and responses differ when planted amongst a diverse mixture of species or are supported by any climber cutting effects. Such silvicultural field data, such as deeper knowledge of plot based composition could also add to current silvical knowledge on complementary mixtures for diversity planting initiatives (Redondo-Brenes & Montagnini, 2016; Marshall et al., 2021). However, this would once again be a significantly smaller sub-study with only two plots per species in the monoculture condition, and two plots per species mixture for the 4 species condition, possibly making it more challenging to eliminate topographic differences. Nonetheless, this ground data could be fascinating to delve into especially combined with field surveys should there be survival and establishment differences.

3.6 Conclusion

Although the pace of planted plots filled canopy gaps faster than the unplanted, and high levels of diversity coupled with climber cutting proved most impactful, there are vast avenues to explore within the SBE. Namely, the scalability and transferability of the knowledge, should methods of enrichment planting a diverse number of species and the climber cutting management prove viable methods to speed-up the rehabilitation of disturbed tropical forest. As such we recommend cross assessing SBE results with recovering tropical forests of other regions, alongside a three pronged data collection approach of airborne LiDAR, TLS and field data. This would enlighten current literature to if tropical forest restoration can be conducted at scale whilst providing clearer insights into the underlying mechanisms. This may contribute to silvical knowledge into complementary species mixtures for diversity planting, greater ecosystem impacts of climber cutting, and layered insights into the potential shifts within the canopy by combining bottom-up and top-down mapping. We have also identified TCH to be a less insightful metric when assessing early stages in rehabilitation and suggest more particular assessment methods such as LAI.

Appendix

Appendix A

Tabel S2.1: List of 16 dipterocarp species planted in the SBE. Containing species name, taxonomic group (Tuck et al., 2016), and the recent IUCN Red List status (downloaded June 2023 from www.iucnredlist.org) many of which have changed from critically endangered to least concern since SBE establishment.

Species name	**Taxonomic group**	**IUCN Red List**
Dipterocarpus conformis Slooten	Sister to Shoreae	Endangered
Dryobalanops lanceolata Burck	Shoreae	Least concern
Hopea ferruginea Parij	Shoreae	Critically endangered
Hopea sangal Korth.	Shoreae	Vulnerable
Parashorea malaanonan (Blanco) Merr.	Shoreae	Least concern
Parashorea tomentella (Blanco) Merr.	Shoreae	Least concern
Shorea argentifolia Sym.	Shoreae, Shorea, Mutica sect., Mutica subsect.	Least concern
Shorea beccariana Bruck	Shoreae, Shorea, Pachycarpae sect.	Least concern
Shorea faguetiana Heim.	Shoreae, Shorea, Richetioides sect., Richetioides subsect.	Endangered
Shorea gibbosa Brandis.	Shoreae, Shorea, Richetioides sect.	Critically endangered
Shorea johorensis Foxw.	Shoreae, Shorea, Brachypterae sect.	Critically endangered
Shorea leprosula Miq.	Shoreae, Shorea, Mutica sect., Mutica subsect.	Near threatened
Shorea macrophylla Ashton	Shoreae, Shorea, Pachycarpae sect.	Least concern

Shorea macroptera King	Shoreae, Shorea, Mutica sect., Auriculatae subsect.	Least concern
Shorea ovalis Korth.	Shoreae, Shorea, Ovalis sect.	Least concern
Shorea parvifolia Dyer	Shoreae, Shorea, Mutica sect., Mutica subsect.	Least concern

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