The role of biodiversity in Southeast Asian tropical forest restoration

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Supplementary materials

Additional supplementary materials, including coding scripts and data required to reproduce the figures used within each chapter of this thesis, are available to view at http://bit.ly/3TKgKOo.

Thesis abstract

Tropical forests in Sabah, Malaysian Borneo, are threatened by land use change and continued overexploitation. Active restoration of dipterocarp-dominated forests is used to increase the restoration value of these landscapes, and knowledge of the ecological mechanisms that promote tropical forest functioning is critical to realising this goal.

In this thesis, I use a long-term, field-scale experiment to investigate the effectiveness of active restoration techniques in a once-logged lowland dipterocarp forest. I show that enrichment planting of dipterocarp seedlings increases satellite-derived metrics of aboveground biomass, canopy cover, and leaf area index. I then show a clear relationship between ecosystem functioning and the biodiversity of enrichment planted seedlings. This relationship is likely driven by species-specific niche differences which generate stronger complementary effects through a more functionally diverse seedling cohort and is unlikely to be generated via stochastic processes as hypothesised under neutral theory.

At the local scale, I demonstrate that the survival of enrichment planted seedlings in a selectively logged forest may benefit from increasing densities of the surrounding tree matrix as a result of potential positive density-dependence. I also add to the evidence base that light is a primary driver of growth and survival within selectively logged dipterocarp forests. More data concerning the seedling environment, including microclimate variation, will help to provide a more comprehensive assessment of logged forest dynamics.

Finally, I show that survival and growth of enrichment planted seedlings are similar for most investigated species across an old-growth and secondary forest, demonstrating the capacity for old-growth forests to provide restoration target information from which to

compare active restoration success. I also identify a growth-survival trade-off in both primary and secondary forests and demonstrate that my studied selectively logged dipterocarp forest is in an early successional stage and has not experienced a collapse in seedling growth and recruitment. However, I call for more work to understand the variables underlying species-specific responses to habitat perturbation.

This thesis helps to inform future restoration design, implementation, and monitoring across Sabah. To maximise the benefits of forest restoration to climate security, economic growth, and social wellbeing, a data-driven approach to forest restoration projects that utilises current ecological theory will become increasingly important.

Chapter 1: General introduction

The history and current state of Southeast Asian tropical forests

The lowland tropical forests of Southeast Asia are globally known as some of the most diverse in the world (Davies et al., 2005), hosting forest global biodiversity hotspots and many endemic species across several taxa. Southeast Asian tropical forests provide goods and services to the communities who depend on them, across all aspects of ecosystem services (Huu Loc et al., 2020) including carbon sequestration, hydrological functioning, timber and non-timber products, and cultural enrichment (Abram et al., 2014; Harrison et al., 2016; Pattanayak, 2004; Philipson et al., 2020). Their value is equalled only by the threats they face following recent decades of extensive tropical deforestation and degradation driven by logging and agricultural expansion (Curtis et al., 2018; Hoang & Kanemoto, 2021). The majority of recent deforestation has occurred in the tropics (Ometto et al., 2022) but has been particularly acute in Southeast Asia, with an estimated annual deforestation rate of approximately 1% of total land area (Achard et al., 2002; Miettinen et al., 2011)

Timber production in many Southeast Asian countries over the past few decades has shown a classical trend of rapid increase followed by a peak and then decline (Shearman et al., 2012), which is often observed in the extraction of non-renewable resources (Fig. 1.1; Gallagher, 2011). The *de facto* treatment of timber products as a non-renewable resource is attributed to the fact that tropical forest recovery times are often far longer than the 30-35 year logging cycles typically applied to logging concessions (Poorter et al., 2016, 2021; Shearman et al., 2012), often resulting in premature rounds of further logging (Reynolds et al., 2011). Overall, the International Tropical Timber Organisation (ITTO) estimated in

2010 that around 10% of permanent forest estate in the Asia-Pacific region was managed sustainably (Blaser et al., 2011).

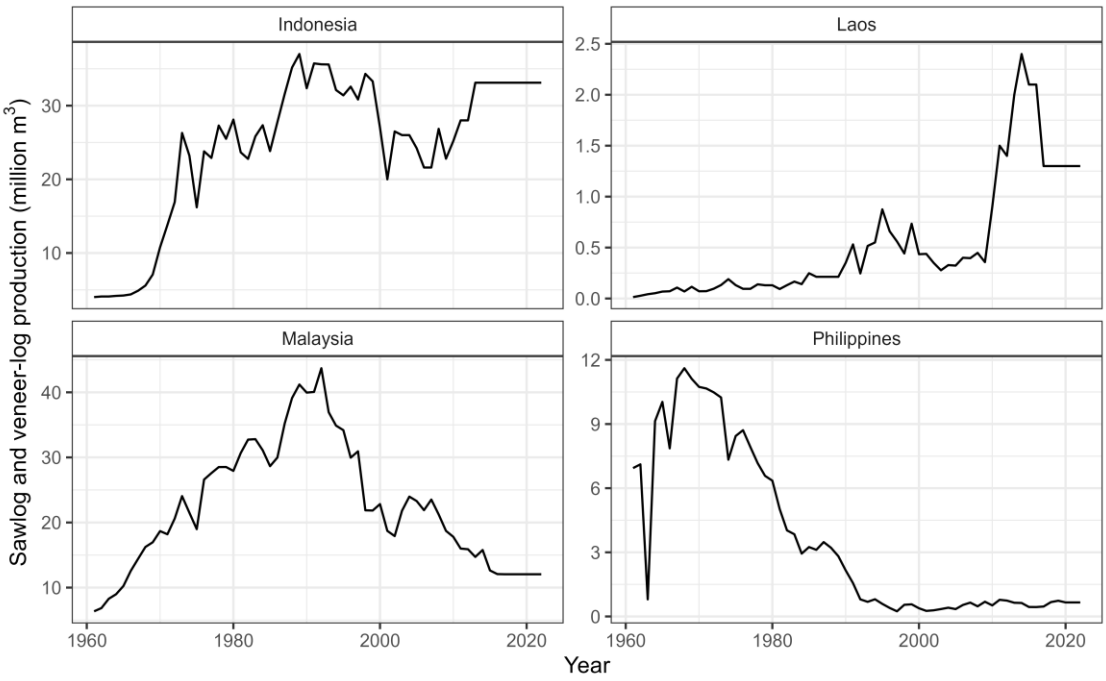


Figure 1.1 Sawlog and veneer-log production for four countries within Southeast Asia. Each curve shows characteristics of boom-and-bust cycles typical for exploitation of non-renewable resources (derived from FAOSTAT, 2022).

Whilst timber exploitation is a leading cause of forest degradation, agricultural expansion is an increasingly important driver of deforestation in Southeast Asia (De Koninck et al., 2011). One driver of this is population expansion, as the population of Southeast Asia is expected to increase from 660 million in 2020 to over 720 million by 2030 (Asia Development Bank, 2015). As well as improved farming efficiency, more land will be needed to meet future agricultural requirements. Another driver is policy initiatives over the past 50 years across Southeast Asia, which have focussed on economic integration and development through promoting large-scale agricultural infrastructure development. For

example, in Sabah, Malaysian Borneo, conversion to oil palm agriculture is attributed to the reduction of forest extent from 86% in 1953 to approximately 59% by 2020 (Asner et al., 2018; McMorrow & Talip, 2001). The pressure for agricultural expansion, combined with prior perceptions that degraded tropical forests lack any real environmental value and are simply a by-product of logging, make degraded lowland tropical forests prime candidates for conversion (Pain et al., 2021). As a result of this pressure, tropical forest science has made considerable progress in the last 30 years in assessing the value of recovering secondary forests in Southeast Asia, in terms of ecosystem functioning and the services secondary forests can provide on local and global scales.

The value of secondary forests – biodiversity, carbon, and wider ecosystem functions

It is well documented that land use change can have negative impacts on both landscape biodiversity and ecosystem functioning (Newbold et al., 2015; Williams & Newbold, 2020). Recent work has also warned that, after a threshold level of disturbance is hit, a tropical forest may never fully recover and instead exist in an 'alternative stable state' (Hirota et al., 2011) or collapse fully, shifting to a new ecological equilibrium with reduced biological diversity and ecosystem functioning such as low-diversity savannah and grasslands. Whilst this effect has already been observed across the tropics globally (Styger et al., 2007; Veldman & Putz, 2011) there is growing concern for the climate-driven impacts of fire and drought on forest degradation and loss across Southeast Asia (Chen et al., 2024; Hamilton et al., 2020), especially as fine resolution analyses of these drivers are lacking within the literature (Chen et al., 2024).

Biodiversity and ecological surveys originally focused on high-diversity intact ecosystems (Fazey et al. 2005), but more recently secondary tropical forests in Southeast Asia have

been shown to support more biodiversity than previously expected. For example, within Southeast Asia, Edwards et al. (2011) showed that 75% of bird and dung beetle species were conserved between primary and twice-logged forests. Berry et al. (2010) analysed over 100,000 observations of over 2,500 species across 20 years within lowland forests of Sabah, Malaysian Borneo, and showed that floral species richness was higher in degraded tropical forests, and whilst faunal species richness was lower, the difference was no more than around 10%. However, forest specialist species, which are more likely to be endemic and of high functional value (Brockerhoff et al., 2017; Dee et al., 2019), are more often lost post-disturbance (Barlow et al., 2007). Southeast Asia contains the highest mean proportion of country-endemic bird and mammal species and the second highest for vascular plant species compared to other tropical regions (Sodhi et al., 2010), and the impacts of these losses should be further studied. Beyond species richness, community structure can change drastically even with a similar level of species richness, with early successional and disturbance-resistant species, such as lianas, increasing in relative abundance (Cleary, 2017).

Not only is biodiversity sustained, but ecosystem services are also largely maintained in secondary forests. Globally, Putz et al. (2012) showed that once-logged forests retained 76% of total carbon, and Heinrich et al. (2023) found that regrowing degraded and secondary forests accumulated 107 Tg C $year^{-1}$ from 1984 and 2018, offsetting 26% of carbon emissions associated with humid tropical forest loss over the same time period. Within Southeast Asian tropical forests, there is evidence that selectively logged forests are still effective carbon stores (Philipson et al., 2020; Rozak et al., 2018). Work by Berry et al. (2010) showed that, during recovery, logged forest in Borneo accumulated carbon at five times the rate of primary forests, and Heinrich et al. (2023) authors specifically found

that Bornean forests showed recovery rates 45% higher than in Central Africa and 58% higher than the Amazon (Heinrich et al., 2023), demonstrating the strong potential of Bornean forests as effective carbon stores despite their extensive logging history.

Secondary forests provide additional ecosystem services beyond carbon sequestration, although these services have received comparatively limited attention. For example, the Amazon rainforest influences rainfall patterns within South America (Boers et al., 2017; Costa & Pires, 2010) to such an extent that reducing deforestation could result in US $1 billion in avoided agricultural losses in the Southern Brazilian Amazon (Leite-Filho et al., 2021). Secondary forests still retain the capacity to regulate the water cycle, and one study in Brazil showed that secondary forest fragments a decade old have water retention and capturing capacities similar to mature forests (Zimmermann et al., 2013). More widely, one meta-analysis showed that restoration of agricultural land improved supporting ecosystem services (including soil physical and chemical quality) by 42% and regulating ecosystem services (including pollination and biological control) by 120%, reaching similar levels of supporting and regulating ecosystem service provision as reference ecosystems (Barral et al., 2015). Secondary forests provide additional ecosystem services beyond carbon sequestration, although these forests have received comparatively limited attention. Bruijnzeel (2004) investigated the impact of forest cover on regional rainfall, flooding and erosion in Southeast Asia and found that secondary forests have less than the predicted 8% average rainfall decrease from conversion to grasslands and reduce the severity of flooding. As assessment of local people's use of secondary forests in Borneo revealed that even highly degraded forests still provided a range of provisioning, regulating, and cultural services to local communities, which included pollution and flood prevention, clean water sources, climate control, and spiritual value (Abram et al., 2014). However, the capacity of

secondary forests to provide non-carbon ecosystem services in Southeast Asia is still poorly understood and requires more dedicated research (Mertz et al., 2021).

It is becoming increasingly clear that biological carbon sequestration via forest restoration will be crucial in climate change adaptation and mitigation (Seddon et al., 2020). For example, the Bonn Challenge aims to restore 350 million ha of forest globally by 2030 (Stanturf et al., 2019). Within Southeast Asia there is a strong potential for regenerating forests to contribute towards climate mitigation. Zeng et al. (2020) showed that Southeast Asia has 121 million ha of degraded land, and that reforestation would contribute 3.43 ± 1.29 $PgCO_2e$ yr^{-1} to climate change mitigation through 2030. However, the authors note the relatively low achievability of this mitigation potential (0.3 to 18%).

Active versus natural restoration of degraded tropical forests

There is a growing debate concerning the overall effectiveness of tropical forest restoration in accelerating forest recovery (Crouzeilles et al., 2017; Philipson et al., 2020). Restoration measures are expensive to implement, costing approximately US \$2000 ha^{-1} across Southeast Asia but ranging from \$400 to \$8000 ha^{-1} (Philipson et al., 2020), and a preference in policy for active over passive restoration (Chazdon & Guariguata, 2016) can give forest restoration a particularly high price tag. The 121 million ha of land suitable for restoration in Southeast Asia estimated by Zeng et al. (2020)(Fagan et al., 2020) would cost, at \$2000 ha^{-1} (Philipson et al., 2020), approximately \$242 billion if achieved exclusively via active restoration. Given the high potential costs of tropical forest restoration, it is therefore vital that the effectiveness of active restoration be fully maximised.

Evidence on the effectiveness of active restoration is mixed. A global meta-analysis of 133 studies suggested that ecological success is higher for natural regeneration relative to active restoration in terms of biodiversity and vegetation structure (Crouzeilles et al., 2017), although the authors warn against making regional conclusions based on this global dataset. A more recent meta-analysis focused on Southeast Asia by Banin et al. (2023) showed that, based on community-level data from 11 landscapes in Southeast Asia, active restoration results in faster accumulation of tree basal area and structural properties relative to naturally regenerating sites, and actively restored forest landscapes exhibit more similarities to old-growth reference sites. In terms of carbon, Philipson et al. (2020) used LiDAR (light detection and ranging) data to estimate that aboveground carbon recovery rates in naturally regenerating and actively restored tropical forests in Sabah were 3.5 and 4.8 Mg C ha^{-1}, respectively, suggesting active restoration increases recovery success. However, they note that current carbon prices in the voluntary carbon market would need to increase by 2-10 times to meet the current costs of active restoration. Very few other studies have linked carbon gains to the cost of restoration (Holl & Zahawi, 2014; Wheeler et al., 2016) to demonstrate that the projects, if successful, are also sufficiently cost-effective to make them viable solutions.

One clear consensus is that there is high variability observed in responses to active restoration (Banin et al., 2023; Crouzeilles et al., 2016), which is generally regarded as being due to variation in the type and severity of initial habitat disturbance across spatial scales. This heterogeneity influences the average recovery time for tropical forests as well as their biomass accumulation speed. Poorter et al. (2021) showed that some tropical forests in the Americas and West Africa can recover 90% of old-growth values for soil and plant functioning in under 10 and 25 years, respectively, but Moreno-Mateos et al. (2017)

predicts a much slower recovery time with a continued 'recovery debt'. Additionally, the metrics of recovery used are inherently variable in their recovery rates. Poorter et al. (2021) noted that whilst soil functioning recovers quickly, forest structure and species diversity can take between 25 and 60 years to achieve 90% recovery, and biomass and species composition could take beyond 120 years. Separately, Spake et al. (2015) found that epiphytic lichen could take up to 180 years to reach 90% of old-growth species richness levels. Judging the success of restoration measures is therefore dependent on both the extent of degradation experienced as well as the taxon studied and the metric of recovery used.

Although there is growing evidence that active restoration can increase overall levels of functioning within Southeast Asian logged forests, the effectiveness of the replanting method itself is equally important. By understanding what influences the success of active restoration, policymakers can seek to maximise the cost-effectiveness of restoration initiatives carried out.

Biodiversity and ecosystem functioning within tropical forest systems

There is now a considerable amount of evidence that biodiversity itself is a strong predictor of ecosystem functioning (Cardinale et al., 2012; Isbell et al., 2017; Lefcheck et al., 2015; Tilman et al., 2014), with the earliest experiments being referenced by Charles Darwin (Hector & Hooper, 2002). Modern research into the relationship between biodiversity and ecosystem functioning stems from a conference in 1991 in Germany, where researchers argued that more diverse communities are more productive (Schulze & Mooney, 1994). Shortly afterwards, experiments showed that increased species diversity results in higher primary productivity (Naeem et al., 1994, 1995) and resilience (Tilman & Downing, 1994).

This work was initially almost exclusively carried out in grassland communities and focused on species richness (Hector et al. 1999; Tilman et al. 1996), but research into the relationship between biodiversity and ecosystem functioning has since been extended to forests. TreeDivNet (https://treedivnet.ugent.be/), for example, is the world's largest network of biodiversity experiments, encompassing over 1.2 million trees across over 850 ha of land and producing dozens of peer-reviewed reports per year.

Within forest literature concerning the biodiversity-ecosystem functioning relationship, recent meta-reviews have shown that more diverse forests are often more productive in terms biomass (Messier et al., 2021; Verheyen et al., 2016). In China, a large biodiversity-productivity experiment involving over 150,000 trees found that species richness strongly increased stand-level productivity (Huang et al., 2018). After eight years, 16-species plots had accumulated more than twice the carbon of single-species plots (referred to as overyielding). A study in Panama showed that mixed tree plots displayed significant aboveground biomass overyielding relative to single-species plots after 16 years (Guillemot et al., 2020). Further, several meta-analyses have identified overyielding in mixed-species forests and have shown that productivity can exceed single-species stands by 15-23% (Jactel et al., 2018; Zhang et al., 2012). However, this increase in biomass does not necessarily result in increased yields of harvestable products. A study on Douglas-fir restoration in Oregon showed that when maximising for a single ecosystem service (e.g., timber), some monocultures can outperform more species-rich sites (Puettmann et al., 2016).

More diverse forests are also less susceptible to pest outbreaks (Pretzsch & Forrester, 2017). A meta-analysis based on over 600 studies found that insect herbivory was, on average, lower for multi-species stands (Jactel et al. 2021), and this effect was stronger if

stands contained more phylogenetically distinct trees, resulting in reduced host abundance and accessibility. In contrast, tree plantations in Malaysian Borneo have had to shift away from planting *Acacia mangium* due to the rapid and extensive spread of a wilt and canker disease caused by the fungal pathogen *Ceratocystis manginecans* and now only plant two species of tree within plantations (Sabah Softwoods Berhad, 2022). More diverse forests are also less sensitive to more extreme weather events through increased resilience (Messier et al., 2021) and better support hydrological functioning (Keller et al., 2023a). Finally, species-rich forests seem to be better at maximising multiple ecosystem functions simultaneously relative to species-poor forests (Isbell et al., 2011). Although carbon sequestration is a metric policymakers often prioritise to achieve carbon emission goals (Aguirre-Gutiérrez et al., 2023), different species affect different ecosystem processes, so focusing on how a single ecosystem functions in isolation risks underestimating the level of biodiversity required to achieve high ecosystem multifunctionality (Hector & Bagchi, 2007).

Mechanisms driving the biodiversity-functioning relationship

Neutral theory (Hubbell, 2001) and associated concepts (Adler et al., 2007; Rosindellet al., 2011) assume that all species are ecologically identical or near-identical and that all species assemblages are a "random walk", which predicts an absence of a biodiversity-functioning relationship. However, although neutral theory can reproduce patterns observed in communities (Hubbell, 2001) and is a valuable null model for community ecology, in the decades since its formulation the theory has received criticism on its assumption that individuals have equal fitness (Purves & Turnbull, 2010). Coexistence theory has since focused more on how density-dependence and competition can describe community assemblages.

Early models describing competition between species provided insights into how competition can result in the maintenance of biodiversity and also how species richness can support higher levels of ecosystem functioning (Loreau et al., 2022). Models that do not explicitly explain the process underlying competition, such as the Lotka-Volterra model, describe the impacts one species can have on the population size of another (Loreau et al., 2022). When intraspecific competition is weaker than interspecific competition, the Lotka-Volterra model suggests that the total carrying capacity, and thus yield, is greater than any proportion between each individual species' carrying capacity, producing overyielding effects (Loreau et al., 2022). Models that explicitly describe interspecific competition as driven by resource competition come to similar conclusions. Tilman et al. (1982) described interspecific competition driven by resource competition and gave an example where two species compete for a single resource. They argue that the species which can sustainably reduce a resource to the lowest level will have a higher resource use efficiency and can competitively exclude the other species. As a result, Tilman et al. (1982) argue that competition results in higher community functioning, defined as the efficiency of resource utilisation.

The above models show that species interactions can promote greater ecosystem functioning, and the literature has since clarified two broad sets of processes that drive the biodiversity-ecosystem functioning relationship, namely *complementarity effects* and *selection effects* (Loreau & Hector, 2001). Complementarity effects occur when species perform better on average growing in a mixture than if they were in a monoculture. This effect can arise from species differing in their resource requirements and usage, such that they exploit different resources within a community, collectively reduce interspecific competition, and ultimately maximise community-level functioning (Tilman et al., 1997).

This connects back to Darwin's principles of divergence, in that species will evolve towards specialised niches under stabilising selection pressures (Hector & Hooper, 2002). Facilitation can also lead to complementarity effects, where the presence of another species actively increases the functioning of another species. In contrast, selection effects describe scenarios where a diverse community is more likely to include and be dominated by species with a high productivity (Loreau et al., 2022). This is distinct from a sampling effect, a purely statistical observation that more biodiverse communities will include a highly productive species, as the most productive species must also dominate in order for selection effects to be realised (Loreau et al., 2022; Loreau & Hector, 2001).

Complementarity and selection effects are not mutually exclusive, and in fact current consensus is that both are important to ecosystem functioning (Cardinale et al., 2012; Cavanaugh et al., 2014; Hooper et al., 2012). Work has since shifted to better understanding the relative importance of each in natural ecosystems. Whilst temperate forest experiments generally show positive relationships between biodiversity and ecosystem functioning in natural communities, tropical forests show a mix of positive, negative and neutral effects (van der Plas, 2019). Attempts to identify the presence of complementarity or selection effects involve modelling the loss of species from a wider ecosystem's functioning, such as investigations identifying individual species contributions to overall ecosystem functioning (Balvanera et al., 2005) and correlation studies between biodiversity and ecosystem functioning (Vilà et al., 2007). Overall results are mixed (e.g., Laughlin 2011; Liang et al. 2016; Lin et al. 2016; Mensah et al. 2016; Prado-Junior et al. 2016; Wu et al. 2015), which some have attributed to local climate not being regularly accounted for which masks potential relationships (Cavanaugh et al., 2014) and plot sizes being relatively small (Cardinale et al., 2011). As relationships between plant diversity and ecosystem functioning

are typically non-linear and asymptote out at higher levels of plant diversity, the hyper-richness of plant species in the tropics is also argued to make it harder to detect such effects without sufficiently large and long-term experiments (Cardinale et al., 2011). Meta-analyses that have tried to account for this are beginning to agree that complementarity and selection effects are both present in the tropics, with some analyses suggesting that each attribute contributes approximately 50% towards the relationship between biodiversity and ecosystem functioning (Cardinale et al., 2011).

It is also important to note that the relative importance of complementarity and selection effects is likely to be temporally dependent. Pacala & Tilman (2002) showed that over time the mechanism driving biodiversity-ecosystem functioning shifts from selection to complementarity effects. Although one species may be dominant in the short term, we may see different species dominating over the long term, resulting in a long-term complementarity effect driven by transient selection effects in the short term. The relative importance of complementarity and selection effects can also be spatially dependent. If a local community is dominated by a single well-performing species, but a different local community under different environmental conditions has an alternative species dominating, on the regional scale we observe different species operating within their preferred niche to maximally extract resources, effectively describing a complementarity effect (Loreau et al., 2022). More research is needed in the tropics to identify the relationship between biodiversity and ecosystem functioning, as well as the underlying mechanisms driving the relationship.

Complementarity and selection effects can also help explain the predicted effect of biodiversity on ecosystem stability. As previously mentioned, more biodiverse forests are considered to have more stable functioning (Messier et al., 2021). One main mechanism

which may drive this relationship is the differences in species' fundamental niches, which results in asynchrony in population changes in response to environmental perturbations as well as how quickly populations respond to perturbations (Loreau & de Mazancourt, 2013). This asynchronous response between species produces more stable aggregate ecosystem properties (Loreau, 2010) and is thought to be most effective within a community of specialists (Yachi & Loreau, 1999) as this maximises asynchronous environmental responses. An extension of this idea is the insurance hypothesis (Yachi & Loreau, 1999), which posits that some species are functionally redundant in a community as they have similar functional traits or niche requirements, such that the loss of some species does not result in large decreases in functional diversity. Loreau & de Mazancourt (2013) also suggest that overyielding itself contributes towards ecosystem stability and that increasing the mean total biomass reduces the relative strength of demographic stochasticity in population dynamics. Together with complementarity and selection effects, the increased stability and functioning supported by biodiversity is becoming more important in nature-based solutions (Seddon et al., 2020), and the concept of utilising biodiversity as a means to achieve global climate change goals is becoming increasingly understood (Mori et al., 2021).

Effects of the existing forest matrix in tropical forest restoration

Enrichment planting takes place within a living ecosystem, so we should expect the surrounding environment to impact the effectiveness of enrichment planting. As the existing matrix of trees will likely compete with enrichment planted seedlings, the parameters that dictate this relationship will also influence the success of enrichment planting.

One mechanism that influences the relationship between seedlings and the surrounding matrix is negative density-dependence, where increases in the number and size of neighbours reduces growth and survival rates as a consequence of increased competition (Peters, 2003). This was first described by Janzen (1970) and Connell (1971) who described how natural enemies could reduce seedling recruitment near similar trees at higher local densities. Historically, this concept has been applied to conspecific trees, but the theory can be applied at the genus level, family level, or beyond. In the tropics, there is evidence that conspecific tree seedlings growing closer to conspecific adults can perform worse than seedlings growing nearer heterospecific adults (Bagchi et al., 2011; Metz et al., 2010; Paine et al., 2012a). For instance, Liu et al. (2012) found that seedlings faced increased mortality when in soil below conspecific trees compared to heterospecific trees due to the presence of species-specific soil pathogens. In tandem with negative density-dependence, we may see positive density-dependent effects through facilitation by neighbours (Bruno et al., 2003). Secondary logged forests have a reduced canopy, and so an established canopy may ameliorate extreme effects of temperature and humidity, reducing drought-related mortality (Mackay et al., 2015). Given the range of possible outcomes from interactions between enrichment planted seedlings and the matrix they are planted within, there is a need for a mechanistic understanding of what factors drive these relationships, so that forest management practices can consider them in optimising their replanting strategy.

Liana removal in tropical forest restoration

Active restoration methods include other techniques beyond just the enrichment planting of seedlings. One common additional treatment is the removal of lianas from within a restored forest. Lianas and climbing bamboo (referred to in this thesis collectively as lianas) act as structural parasites, considered an evolutionary adaptation driven by competition for

light (Tang et al., 2012). They impact forest dynamics by increasing tree-fall rates and canopy-gap formation, keeping habitat heterogeneity and consequently species diversity high as a result. However, their parasitic nature is linked to the structural damage they cause mature trees (Schnitzer, 2005), as well as how they compete for limited resources such as water, nutrients, and light (Estrada-Villegas & Schnitzer, 2018).

The effect of liana removal has received increasing attention in recent decades. In one sense, lianas increase the species richness of the community they are in. They also increase community functional diversity, as lianas are a separate functional group. Under biodiversity-ecosystem functioning theory, we might expect an overall greater level of functioning with the inclusion of lianas, particularly in the long-term. For example, liana leaves have a relatively high phosphorus content and short lifespan (Cao, 2010) so, given the general phosphorus limitation within tropical forests (Vitousek, 1984), lianas have been theorised to increase the phosphorus content of leaf litter and enhance nutrient cycling within tropical forests (Tang et al., 2012). Additionally, lianas may lead to additional ecosystem stability; O'Brien et al. (2019) found that forest plots that underwent liana removal directly before an El Niño-induced drought experienced reduced seedling and tree growth relative to control plots. They suggest that lianas provide a facilitative effect to understory seedlings during drought by reducing local temperatures and evapotranspiration rates.

However, in the context of forestry, we are primarily interested in timber provisioning, and current consensus is that lianas negatively impact the growth and survival of seedlings in the tropics (Magrach et al., 2016; O'Brien et al., 2019; Schnitzer & Carson, 2010; Wright et al., 2015). Even if increased functional diversity increases overall productivity, growth of non-timber lianas within forestry plots, facing a positive selection effect, would be

predicted to reduce the overall levels of carbon accumulation in dipterocarp stocks. Lianas can be particularly harmful in gap environments, where they can inhibit the establishment of non-pioneer tree species and reduce biomass accumulation (Ledo & Schnitzer, 2014). These negative impacts are also expected to increase over time, driven by increased liana abundance related to climate change-related decreases in rainfall (Cai et al., 2014; DeWalt et al., 2010).

Liana cutting is proposed as a management solution in some Southeast Asian forest regions to promote seedling and adult tree growth and survival through removing competitive effects with lianas. There is evidence supporting the practice of liana removal that coincides with felling operations (Campanello et al., 2007; Estrada-Villegas & Schnitzer, 2018), but experimental research investigating the effects of post-felling liana removal management (O'Brien et al., 2019) and the community-level functional impacts of liana removal are more limited.

Thesis research objectives and structure

This thesis aims to add to the evidence base surrounding pure and applied ecological questions relating to tropical forest functioning. My research covers a range of methods used to assess the recovery of a secondary tropical forest site within Sabah, Malaysia, at a long-running experiment which has been recovering from a logging event in the 1980s.

Given the history of the experiment and the substantial work conducted to date, I will begin by giving a comprehensive summary of forest land use and management within Sabah, as well as the history of the experimental site (Chapter 2). I will also provide readers with

context on the Sabah Biodiversity Experiment and the forest reserve it sits within and summarize the wider body of forest restoration science being conducted within Sabah.

Research objective 1 (Chapter 3) – Do actively restored dipterocarp forests result in increased ecosystem functioning, and is this improvement related to the species richness and functional diversity of enrichment planted seedlings?

In Chapter 3, I use satellite-based remote sensing data to estimate the recovery of an enrichment planted tropical forest in its first decade of replanting and test for an overall effect of enrichment planting compared to naturally regenerating controls. I also test for a relationship between restoration success and species richness of enrichment planted seedlings, to identify a biodiversity-ecosystem functioning trend in a tropical forest system. I then test for an effect of functional diversity to identify potential mechanisms for the biodiversity-ecosystem functioning relationship and assess how satellite-derived measures of forest restoration differ between sites that underwent additional liana removal treatments. Chapter 3 was published in *Science Advances* in September 2023.

Research objective 2 (Chapter 4) – How does a forest's surrounding tree matrix impact the growth and survival of enrichment planted seedlings?

In this chapter, I make use of ground-based FieldMap technology to spatially map mature trees within 10 m of planted seedlings within a secondary logged forest. I investigate how the level of density-dependence, asymmetric competition, and confamilial density-dependence impacts the growth and survival of enrichment planted seedlings and how this is affected by light availability within the understory. Chapter 4 will be submitted to *Ecology and Evolution*.

Research objective 3 (Chapter 5) – How do enrichment planted seedling growth and survival rates compare between those planted in old-growth and selectively logged tropical forests?

In this chapter, I compare the survival and growth rates of enrichment planted seedlings in a selectively logged forest with enrichment planted seedlings in a separate experiment within an old-growth forest. I take a species-specific approach to identify which species, if any, show sensitivity to logging-induced perturbation. Finally, I test for evidence of a growth-survival trade-off between species and investigate how this relationship varies across logging conditions. Chapter 5 will be submitted to *Ecology and Evolution*.

Statement of authorship

The chapters of this thesis are published or draft manuscripts. I was a lead contributor for all of the work, and the contributions of co-authors are outlined at the start of each chapter alongside details of publication or planned manuscript submission.

Chapter 2: Sabah, the Sabah Biodiversity Experiment, and the Danum Gaps Experiment

The Sabah Biodiversity Experiment exists within a complex landscape of forest classifications, government agencies, non-governmental organisations, research bodies, and large-scale restoration projects. The objective of this chapter is to provide background and context to the Sabah Biodiversity Experiment and all affiliated and relevant parties.

This chapter begins in Southeast Asia, where we focus on the Malaysian state of Sabah. We explore the state and describe the lands that are managed by the Sabah Forestry Department, a state-run organisation managing Sabah's public forests. We will look more closely at the Yayasan Sabah Forest Management Area as one of these public forested regions. Within this management area, we will explore the selectively logged Malua Forest Reserve, which contains the Sabah Biodiversity Experiment. We then will look at the nearby Danum Valley Conservation Area, an old-growth forest reserve, within which we will explore the Danum Gaps experiment as an experimental contrast to the Sabah Biodiversity Experiment. We will provide more general context on the infrastructure required to support both experiments as well as surrounding restoration projects and experiments which have the potential for collaboration and comparison with the Sabah Biodiversity Experiment. For a summary of key terminology, see Table 2.1.

Table 2.1 Key terminology.

Term	Definition
Borneo	Large island in Southeast Asia, occupied by Brunei, Indonesia, and Malaysia.
Sabah	Malaysian state occupying the northern region of Borneo.
Yayasan Sabah	Also known as the Sabah Foundation. A state-sanctioned organisation developed to promote educational and economic opportunities for residents of Sabah.
Innoprise Corporation	The commercial wing of Yayasan Sabah. Income generation was at first exclusively in wood-based sectors including forestry but now includes tourism, agro-plantation, and oil and gas sectors.
YSF Management Area	Yayasan Sabah Forest Management Area. A large (approximately one million ha) concession managed by Yayasan Sabah to provide socio-economic benefits to residents of Sabah.
Sabah Forestry Department	The department within the state of Sabah responsible for managing all public forest reserves.
SEARRP	Southeast Asia Rainforest Research Partnership. A non-governmental organisation established to promote scientific research in Borneo, who are key facilitators for research at Danum Valley Conservation Area and the Sabah Biodiversity Experiment.
Danum Valley Conservation Area	A region of primary lowland dipterocarp rainforest within the YSF Management Area. Classified as a Class I Protection Forest by the Sabah Forestry Department.
Malua Forest Reserve	A forest reserve to the north of Danum Valley Conservation Area. Contains the Sabah Biodiversity Experiment in its southern portion. Currently classified as a Class I Protection Forest.
Danum Valley Field Centre	A field station on the eastern edge of Danum Valley Conservation Area, used for conducting research at Danum as well as coordinating research within the YSF Management Area.
Malua Field Camp	A satellite field camp of the Danum Valley Field Centre near the Sabah Biodiversity Experiment, established to support research at the site. Managed by SEARRP.
Sabah Biodiversity Experiment	A large biodiversity experiment established in 2001 and located within the Malua Forest Reserve. Designed to test the relationship between tree diversity and ecosystem functioning within tropical forests.
Danum Gaps-Understory Experiment	An experiment established with the seedlings remaining after the completion of the Sabah Biodiversity Experiment. Aims to investigate the growth and survival of seedlings within naturally occurring canopy gaps and understory of a primary lowland dipterocarp forest.
Ulu Segama Forest Reserve	A forest reserve to the west of Malua Forest Reserve and Danum Valley Conservation Area. Currently classified as a Class I Protection Forest.
USM Forest Reserve	Ulu Segama-Malua Forest Reserve. A large district containing 11 smaller individual forest reserves, including both Malua and Ulu

	Segama forest reserves. Contains exclusively Class I and Class VI forest reserves, all of which are designated as Totally Protected Areas by the Sabah Forestry Department.
INFAPRO	Innoprise-FACE Foundation Rainforest Rehabilitation Project. A large-scale (12,000 ha to date) rehabilitation and restoration project in the northeast corner of the Ulu Segama Forest Reserve. Provided the seedling stock used in the establishment of the Sabah Biodiversity Experiment and the Danum Gaps-Understory Experiment.
INIKEA	The Innoprise-IKEA project, also known as the Sow-A-Seed project. Located in the central-south region of the YSF Management Area which has restored approximately 18,500 ha of forest to date.
The SAFE Project	The Stability of Altered Forest Ecosystems (SAFE) Project. A large forest fragmentation experiment located primarily in the Kalabakan Forest Reserve, south of the USM Forest Reserve, and covers a range of habitat modifications.

Sabah

Sabah is one of 13 states within Malaysia and one of only two states on the island of Borneo. Sabah, originally British North Borneo, occupies the northern tip of Borneo and makes up nearly 10% of the island's landmass (Hutchison, 2005). Similar to wider Southeast Asia, Sabah has experienced some of the most intense tropical forest degradation globally over the past 50 years, losing nearly 1.9 million ha of its forest (roughly 25% of its land area) from 1973 to 2015 (Gaveau et al., 2016). Within Sabah, land is managed by two organisations: the Sabah Forestry Department and the Sabah Lands and Surveys Department. The Sabah Forestry Department is responsible for managing all forest reserves, whilst the Sabah Lands and Surveys Department is responsible for the issuance of titles for all land that does not belong to forest reserves. Currently, the Sabah Forestry Department manages nearly 3.6 million hectares of forest reserve (almost 50% of Sabah's land mass; Fig. 2.1). These reserves are split into seven classes (see Table 2.2), ranging from complete protection forests to forests assigned to commercial use. Of these classes, three (I, VI, and VII) are deemed Totally Protected Areas, where no logging is permitted. In total, Totally Protected Areas of forest reserve make up almost 1.7 million ha. Besides

forest reserve space, additional Totally Protected Area spaces exist that are managed by Sabah Parks and Sabah Wildlife Department (around 275,000 ha) for a sum area of Totally Protected Area space of nearly two million ha, or 26.4% of Sabah's total land mass. The remaining 1.9 million ha (25.9%) of the land managed by the Sabah Forestry Department is used for logging or other purposes. Although no data exists on the extent of illegal logging within Sabah (i.e., felling that does not result in clearance or land use change), this was estimated to be minimal as of 2011 according to the Chief Conservator of Sabah Forests at the time, Sam Mannan (Reynolds et al., 2011).

Table 2.2 Seven forest reserve classes managed by the Sabah Forestry Department. Forests also classed as Totally Protected Areas include (TPA) in their class name. Source: Sabah Forestry Department (2022).

Class	Management function	Approximate area (ha)	% of total area
I – Protection Forest Reserve (TPA)	Maintenance of forest essential on climatic or physical grounds. Logging is not permitted.	1,421,717	39.8
II – Commercial Forest Reserve	For supply of timber and other produce to meet the general demands of trade.	1,655,483	46.3
III – Domestic Forest Reserve	For supply of timber and other produce for local consumption.	4,634	0.1
IV – Amenity Forest Reserve	For local amenity and arboretum work.	11,403	0.3
V – Mangrove Forest Reserve	For supply of mangrove timber or other produce to meet the general demands of trade and for eco-tourism activities.	234,680	6.6
VI – Virgin Jungle Reserve (TPA)	For forest research purposes. Logging is not permitted.	107,048	3.0
VII – Wildlife Reserve (TPA)	For protection of wildlife. Logging is not permitted.	139,503	3.9
Total	-	3,574,468	-

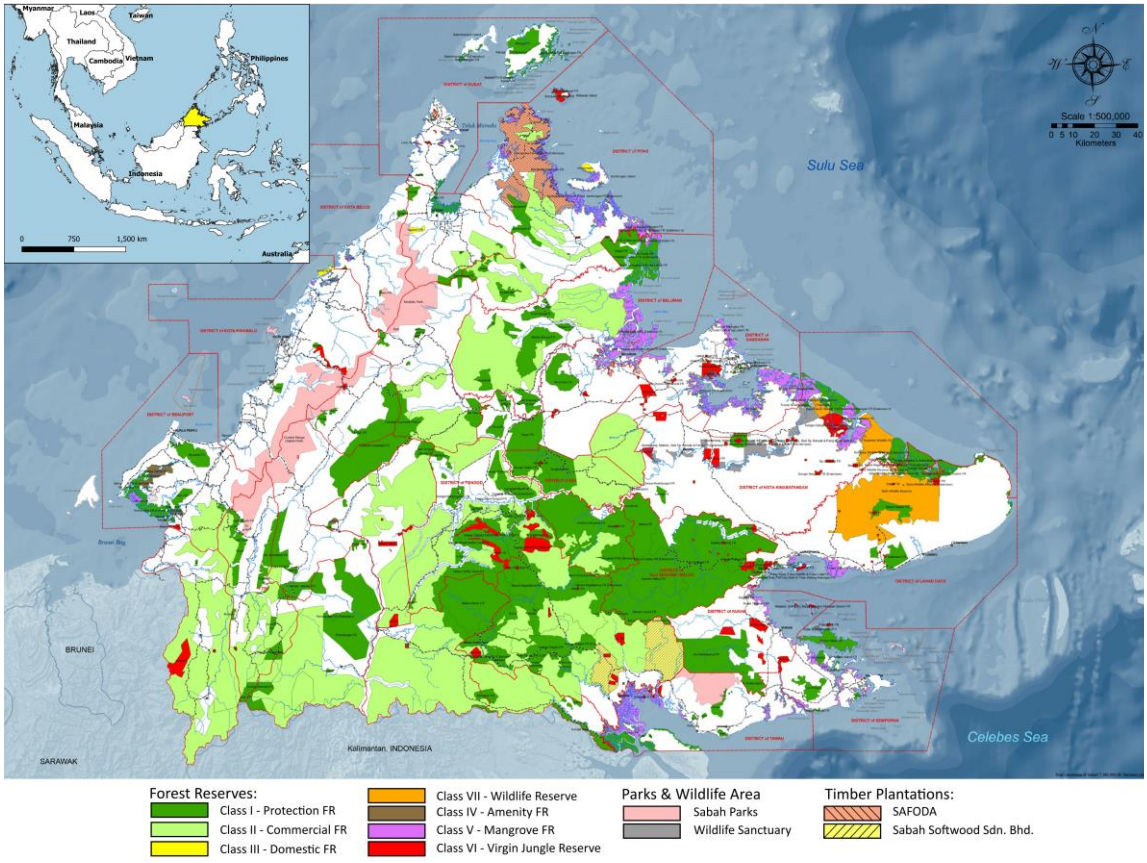


Figure 2.1 Map of the land within Sabah managed by the Sabah Forestry Department and Sabah Parks and Wildlife. Each of the seven forest classes, as well as Sabah Parks and Wildlife Sanctuaries, are indicated in the legend by colour. Publicly owned timber plantations, including those owned by Sabah Softwood Sdn Bhd (a subsidiary of Innoprise Corporation, the commercial wing of Yayasan Sabah) and SAFODA (a statutory body under the chief minister's department) are indicated in the legend by shading. FR = Forest Reserve. Modified from Sabah Forestry Department (2022), image reproduced with permission of the rights holder, Sabah Forestry Department, Sandakan.

The Dipterocarpaceae

Like many forests in Southeast Asia, the majority of forests in Sabah are dominated by a single family of tree species, the Dipterocarpaceae (often referred to as dipterocarps).

Within Southeast Asia, this family makes up around 20% of all trees by number (Slik et al., 2003), over 50% of the forest basal area, more than 60% of the standing volume (Sist & Saridan, 1999) and over 70% of the canopy biomass (Bruenig, 1996; Curran & Leighton, 2000). Dipterocarps are typically found below 1200 m above sea level (Whitmore, 1984) and are among the tallest trees in the tropics, with some growing to over 100 m in height (Shenkin et al., 2019). The Dipterocarpaceae are a pantropical family and originated, like many flowering plants, in Gondwana (i.e., what is now South America and Africa; Ashton et al. 2021). Despite their origin, they are now by far most common in Southeast Asia, which is inhabited by the subfamily Dipterocarpoideae, containing 13 genera and about 475 species (Appanah & Turnbull, 1998; Ashton et al., 2021). The other two subfamilies, Monotoideae and the Pakaraimoideae, occupy South America and Africa with far fewer genera and species (Fig. 2.2).

There are several features which make dipterocarps interesting to ecologists. They are generally fast-growing but are not pioneers (Banin et al., 2014), are mast fruiting trees (Ashton et al., 1988), have wind-dispersed and winged fruits (Smith et al., 2015), and form symbiotic ectomycorrhizal relationships (Brearley, 2012), all of which likely contribute to their dominance within the relatively consistent physical and climatic conditions of the lowland tropics of Southeast Asia.

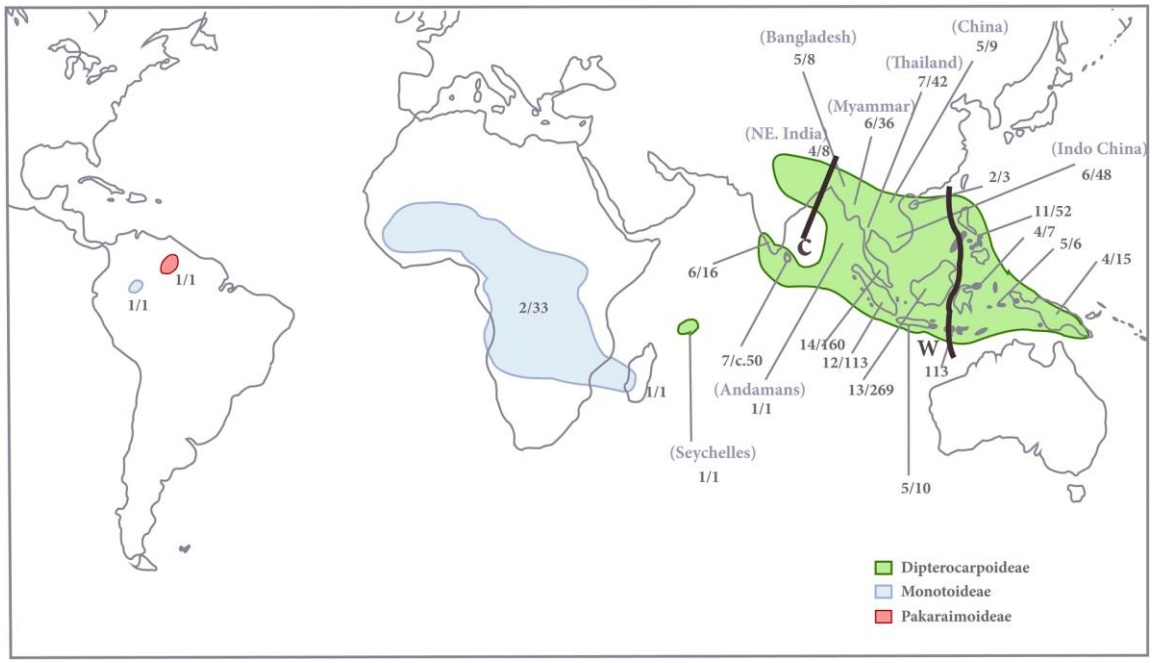


Figure 2.2 World distribution of the Dipterocarpaceae, by subfamily (Dipterocarpoideae, Monotoideae, and Pakaraimoideae). Numbers take the form *A*/*B*, where *A* represents genus richness and *B* represents species richness within that location. Letters **C** and **W** represent Chatterjee's Line and Wallace's Line, respectively. From Ashton et al. (2021), image reproduced with permission of the rights holder, the Board of Trustees of the Royal Botanic Gardens, Kew.

Drivers of forest degradation within Sabah

Tropical timber

Despite evidence that dipterocarp forests, the main forest type within Sabah, require approximately 60 years for aboveground biomass to reach pre-logging levels (Bryan et al., 2013; Philipson et al., 2020), 86% of Sabah's logged forest has been logged at least twice, 12% three times, and around 1% four or more times (Bryan et al., 2013). Each successive round of logging is likely to have cumulative negative impacts on ecosystem recovery

(Reynolds et al., 2011). This style of logging is very typical of the 'boom-and-bust' forest management within tropical forests (Shearman et al., 2012).

The timber industry has historical importance to Sabah, the Malaysian state with the highest poverty rate (Suffian et al., 2021). In its recent post-colonial form, the timber industry was utilised and exploited with the near-exclusive goal of socio-economic gain (Pang, 1989), and across the 1970s and 1980s over half of Sabah's state revenue came from the timber industry (Pang, 1989). In terms of volume, Sabah averaged nine million cubic metres of timber production per year from 1979 to 1988 (Dauvergne, 1997) and peaked at 13 million m^3 of timber production in 1978 (Reynolds et al., 2011). Since then, Sabah has experienced a steady decline in timber exports. As of 2022, only around 1.0 million m^3 of tropical timber was produced (Sabah Forestry Department, 2022). Plantation-sourced timber increased by 16% from 2021 to 2022, producing 0.28 million m^3, for a total timber production close to 1.3 million m^3 in 2022 (Sabah Forestry Department, 2022).

Within Sabah, there are several possible fates for logged dipterocarp forest, depending on the intention when logging takes place. Eventual re-logging has been the typical fate of forest reserves within Sabah. Alternatively, a forest reserve could be conserved and given some form of protection status (as either a Class I, VI, or VII forest) to avoid any large-scale deforestation in the future. However, a forest reserve could instead be designated as a future timber or palm-oil plantation and undergo successive rounds of more intensive logging, often referred to as 'salvage logging', before eventual conversion. The fate of a forest reserve may also be impacted by unplanned events such as forest fires, which effectively facilitate conversion to alternative land uses. Forest fires are also more likely to happen and cause more damage in heavily disturbed forests (Wilcove et al., 2013), making the probability of fire-facilitated conversion higher in logged than unlogged forests. The

variety of pathways that any one forest reserve could take over the past 50 years has resulted in a mosaic of land modifications across Sabah, ranging from pristine old-growth forest to once, twice, or repeatedly logged forest, all the way to homogeneous timber or oil palm plantations (Marsh et al., 2022).

Palm oil agricultural expansion

More recently, palm oil production has been a major driver of land conversion within Sabah. Palm oil demand has grown consistently for the past few decades, and global production has doubled every decade. From 1975 to 2000, oil palm coverage increased by nearly 1600%, from around 59,000 ha to over one million ha (Malaysian Palm Oil Board, 2022), and currently, there is over 1.5 million ha of palm oil plantation within Sabah, making up 20.5% of the state's total land area (Malaysian Palm Oil Board, 2022). Currently, oil palm accounts for 2.1% of the GDP of Malaysia (Malaysian Palm Oil Board, 2022). Within Malaysia, Sabah is the second largest palm oil-producing state, having only recently been surpassed by Sarawak (Malaysian Palm Oil Board, 2022).

Palm oil plantations themselves are regarded as a key component of Malaysia's 2012 'Bioeconomy Transformation Programme' (Bioeconomy Corporation Malaysia, 2016), which attempted to establish a sustainable bioeconomy driven by technological developments. The aim was to make use of natural resources and biomass, in combination with technology, to increase human capital and reduce poverty in rural areas of Malaysia. Palm oil production is viewed as a tool to achieve these aims, particularly in rural areas. Palm oil provides a reliable income source alongside infrastructure development and aids in the creation of highly skilled jobs as the industry becomes more technologically advanced. Consequently, palm oil production, similar to timber production in the 20th

century, should be viewed not only as an economic development tool but also as a key political project in socio-economic advancement on a national scale.

Recognising the potential issues relating to palm oil agricultural overexpansion, there have been commitments to limit total palm oil agricultural land in Malaysia to 6.5 million ha (Yusof, 2019). Within Sabah, steps have been taken to improve the sustainability and equitability of the national economy (Ng et al., 2022). These include voluntary participation in international certification standards (such as FSC for timber and RSPO for palm oil), which are more stringent than Malaysian legal requirements, and protecting more forests compared to national and international targets. However, criticisms persist around how often intention is followed up with action (Ng et al., 2022). As such, continued effort is required to not only identify the ecological drivers of ecosystem services within tropical forests but also to adequately communicate these requirements to key decision-makers.

The Sabah Biodiversity Experiment

Yayasan Sabah, the Malua Forest Reserve, and historical logging

The Sabah Biodiversity Experiment (http://www.sabahbiodiversityexperiment.org) is located in the southern section of the Malua Forest Reserve, Sabah, Malaysian Borneo, occupying 500 ha of the 33,969 ha (340 km^2) reserve.

The Malua Forest Reserve is part of the larger Yayasan Sabah Forest Management Area (YSF Management Area), a reserve approximately one million ha large which is publicly owned by Yayasan Sabah (The Sabah Foundation), which holds a 100-year forest concession for increasing socio-economic standards for the local Sabahan population (Fig. 2.3). The majority of the YSF Management Area was logged from the 1960s to the mid-

1990s, with Malua being logged in the 1980s. Although extraction records for this reserve during this period no longer exist, we know that the nearby Ulu Segama Forest Reserve (also within the YSF Management Area) had an average harvesting volume of 120 m^3 ha^{-1} of useable timber, with peaks nearing 170 m^3 ha^{-1} (Reynolds et al., 2011). These figures represent some of the highest harvesting densities on record for dipterocarp forests. We also know that the Malua Forest Reserve's landscape contains terrain which has generally more gentle slopes and deep alluvial soils, which would allow it to support greater biomass densities. As such, harvesting quantities likely exceeded even that of the Ulu Segama Forest Reserve. This timber was used almost exclusively to supply a timber mill in the nearby town of Lahad Datu (for a description of towns and cities within Sabah relevant to research in Sabah, see the supplementary text in Appendix A). The exploitation left the Malua reserve heavily degraded but with a significant quantity of less damaged forest, typically in regions away from skid tracks, high-lead yarding machinery and haulage roads (Marsh & Greer, 1992), creating a fragmented ecosystem with some patches of undisturbed forest remaining.

Under the original logging plan, logged forest regions were to be given 60 years for natural regeneration in between logging cycles. This period of natural recovery was shortened as a result of an agreement between China and Malaysia in 1998 to establish a pulp mill, which required 3060 km^2 of land within YSF Management Area to be converted to a fast-growing plantation. This region included the Malua Forest Reserve. Logging of the designated regions began in 1999, and although plans for the pulp mill were abandoned in 2001, logging contracts had already been issued. Consequently, Malua was logged for a second time between 2003 and 2007. This event acted as a catalyst for the early release of

other forest coupes, and the vast majority of the YSF Management Area was relogged by 2010.

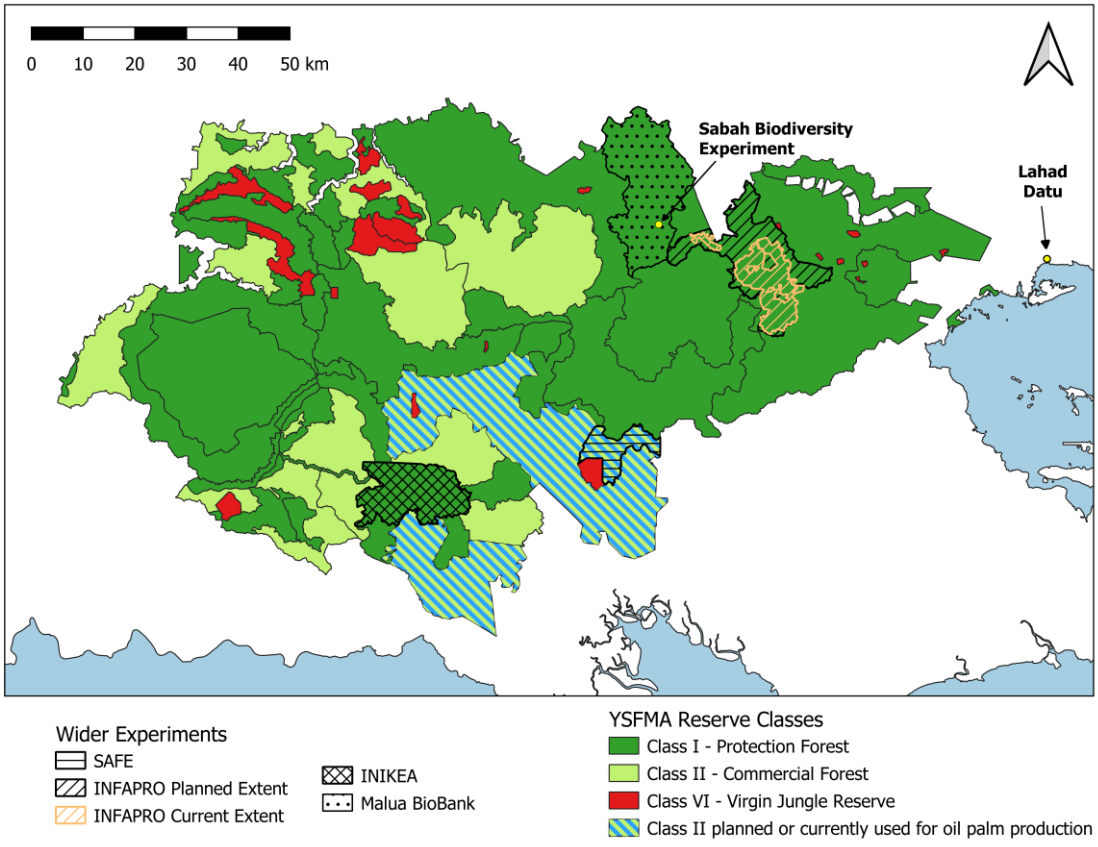


Figure 2.3 The Yayasan Sabah Forest Management Area. The Sabah Biodiversity Experiment location is indicated on the map. Other nearby experiments and restoration projects and forest classifications of each reserve within the management area are indicated in the legend by shading and colour.

The Ulu Segama Forest Reserve began to be logged in 1999, two years before plans were abandoned. At the time, the forest was expected to be converted after logging, and sustainable management practices were reduced as a result. For instance, the minimum diameter at breast height for trees eligible for logging was reduced from 60 cm to 40 cm, steeper slopes (greater than 25°) were permitted to be logged with the use of helicopter

yarding, and other non-dipterocarp trees were permitted to be harvested. Even with the reduced minimum diameter and increased maximum slope for harvesting average yield was still approximately 15 m^3 ha^{-1} because of the forest having had limited time for regeneration. An additional consequence was that previously undisturbed fragments within the logging reserve were targeted, reducing the amount of undisturbed forest and creating a more homogeneously damaged landscape overall. Malua Forest Reserve, on the other hand, was largely logged using reduced impact logging methodologies. These included pre-felling assessments, mapping of planned skid trails and haulage roads, and a maximum harvesting size to protect ancient trees.

Following the second round of mass-harvesting, the Malua and Ulu Segama reserves were merged with several other forest reserves into a single larger district, the Ulu Segama-Malua Forest Reserve (USM Forest Reserve; Fig. 2.4), sometimes also referred to as the Ulu Segama-Malua Sustainable Forest Management Project. The reserve was established with the goal of sustainable forest management, focused on forest restoration and the provision of ecosystem services. Several large-scale forest restoration projects operate within the USM Forest Reserve, and both Class I and Class VI (both Totally Protected Areas) are represented within the reserve's scope.

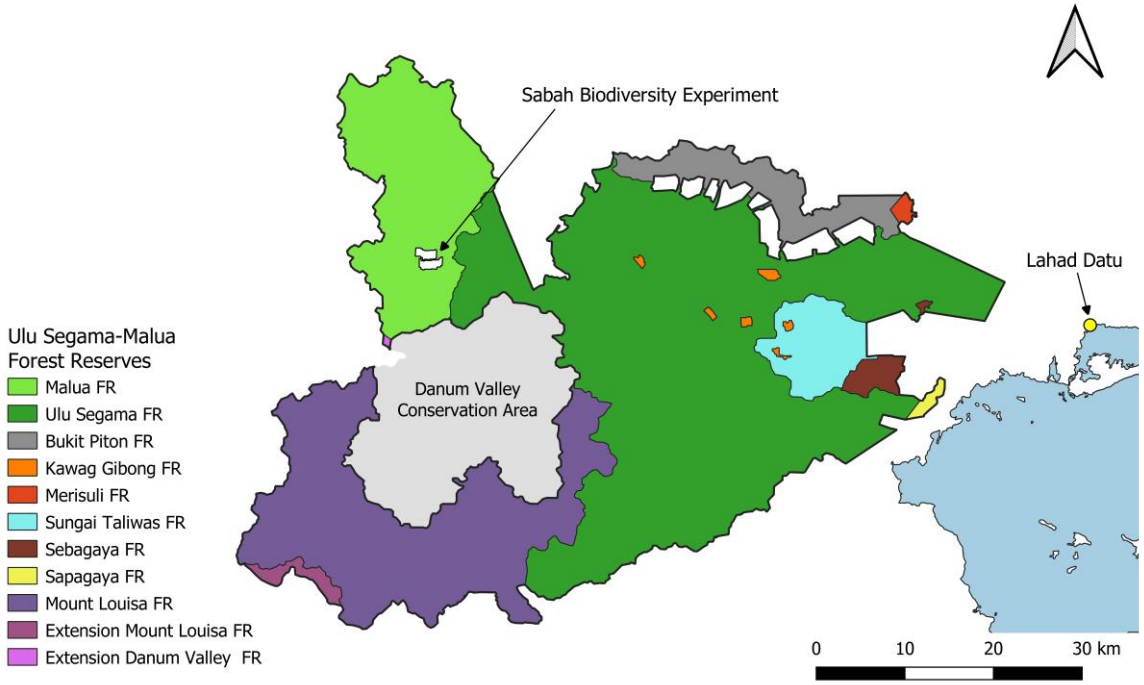


Figure 2.4 The Ulu Segama-Malua Forest Reserve and its component forest reserves. This region almost totally encircles the Danum Valley Conservation Area and includes the Sabah Biodiversity Experiment. FR = Forest Reserve.

The Sabah Biodiversity Experiment

In 2000, a suitable location for an experimental site was identified in the southern section of the Malua Forest Reserve (05°05'20" N, 117°38'32" E, 102 m above sea level), which had been logged in the 1980s. The pre-logging timber volume was around 193-221 m^3 ha^{-1}, with dipterocarps comprising the majority of this volume (180-216 m^3 ha^{-1}; Hector et al. (2011)). The soil is classified as orthic acrisol, which is acidic (pH between five and six), highly weathered, and generally low in both nutrient content (81% base saturation) and organic carbon content (at the experiment topsoil: 1.2%, and at one m depth: 0.6% ; Saner et al. (2009)).

The experimental design consists of 124 four-ha (200 m x 200 m) plots of secondary forest, grouped into two blocks separated by an old logging road, with 60 plots in the northern block and 64 plots in the southern block (Fig. 2.5). Twelve of these plots were left as naturally regenerating controls, with no treatment added. The remaining 112 plots underwent enrichment planting, where 20 parallel planting lines (running north to south) were established in each plot with 10 m spacing between each line. Planting lines themselves were kept clear of other seedlings, shrubs, and lianas at a width of two metres. A seedling was planted every three metres along each planting, giving 66 planted seedlings per planting line. To plant these seedlings, research assistants carried up to 40 kg of tree seedlings on their person in wire mesh backpacks and manually planted them along each line (Fig. 2.6).

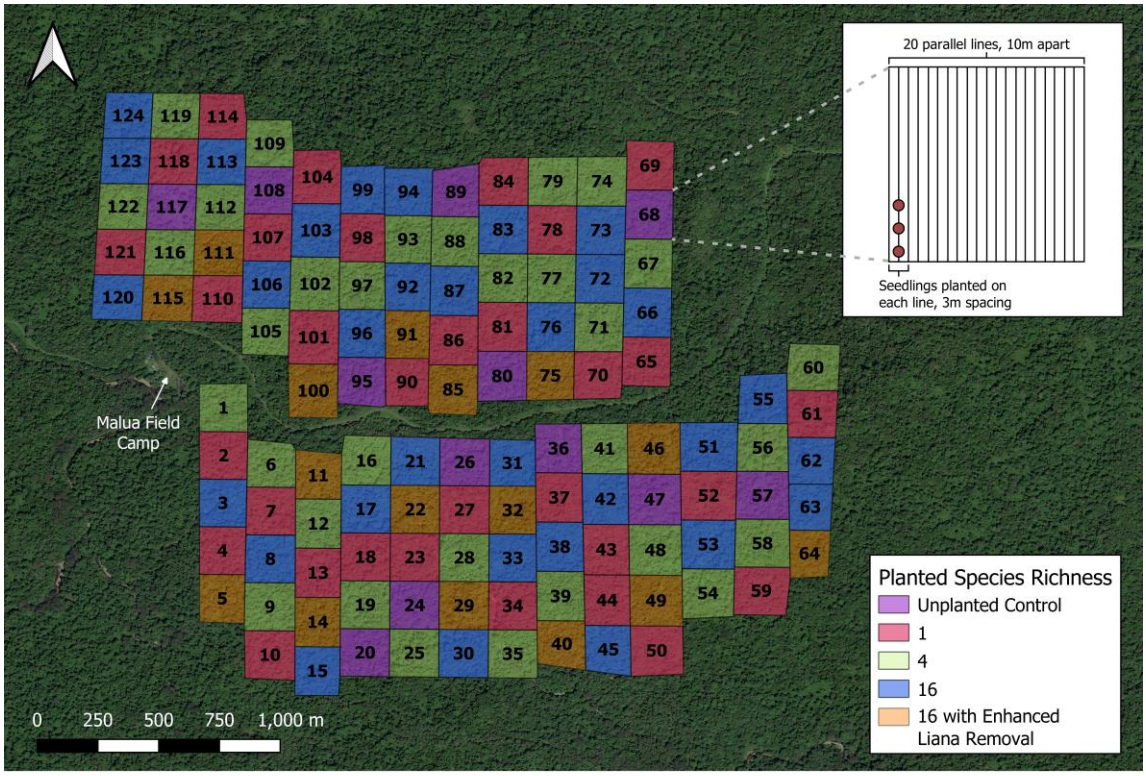


Figure 2.5 Design of the Sabah Biodiversity Experiment. The Sabah Biodiversity Experiment comprises 124 four-hectare plots, separated into blocks via a logging road. Each plot was assigned one of five major treatments: unplanted controls, plots enrichment planted using either one, four, or sixteen species, and plots enrichment planted with 16 species and underwent an additional liana removal treatment. Treatments are indicated in the legend by colour. The Malua Field Camp is located near the experiment, approximately 100 m west of plot one (labelled with a white arrow). (**Top right**) In each enrichment planted plot, dipterocarp seedlings were planted every three m along 20 parallel lines 10 m apart.

Figure 2.6 Seedling planting and monitoring at the Sabah Biodiversity Experiment. (**A**) A typical seedling at the time of first planting. (**B**) Two research assistants carry out growth and survival surveys of seedlings at the experiment.

Planted species richness

Of the 112 enrichment planted plots, each was randomly assigned one of three possible species richness diversities: one, four, or 16 species of planted dipterocarp. The design uses a set of 16 species that were available in the local seedling nursery in sufficient numbers. These 16 species were grown in single-species enrichment planting plots and also combined to form enrichment planting plots of four or 16 species (Veryard et al., 2023a). For plots with more than one species planted, an even number of each seedling was used. To help provide practical recommendations, the Sabah Biodiversity Experiment used INFAPRO enrichment planting techniques during replanting, and the initial cohort of

seedlings was supplied by the INFAPRO seedling nursery near Danum Valley Field Centre (see below).

Genus diversity and canopy structural complexity

The intermediate four-species diversity level is comprised of 16 different species compositions that produce two further treatments that are factorially crossed. These two treatments manipulate genus diversity (two levels) and predicted canopy structural complexity (two levels). The genus diversity treatment compares mixtures of four species comprising two or four dipterocarp genera. The canopy structural complexity treatment also features two levels that either combine species with similar predicted mature heights or with a wider range of these predicted heights. In total, this factorial manipulation of genus and canopy structural complexity comprises 32 plots (the 22 factorial combinations of the four treatments, each with four replicate species compositions, each replicated in the two blocks).

Liana removal

Sixteen plots of the most diverse (16-species) mixtures underwent two rounds of liana removal ('climber cutting') across the entire plot. These plots were compared with 32 enrichment planted plots with the same number of species which only had lianas removed within one metre on either side of each planting line. Due to practical constraints, these cuttings took place in two stages. In July 2011, 10 plots were cut in the southern block, and in June 2014 these 10 plots, as well as six plots in the northern block, underwent a full round of liana removal. During each cut, all lianas of at least 10 cm in height were cut at their base in line with standard Malaysian enrichment planting procedure (Veryard et al.,

2023a). For a complete list of plot-level treatments within the Sabah Biodiversity Experiment see Table A1 in Appendix A.

Planting and replanting

After the initial cohort of seedlings was planted (between January 2002 and September 2003), a second cohort was planted to replace initial mortalities. The second cohort was planted from September 2008 to August 2009 (Veryard et al., 2023a). During replanting, exact numbers of species which suffered mortality in the first cohort were replaced for each plot. In combination, the two planting cohorts enabled the surveying of nearly 100,000 dipterocarp seedlings (Veryard et al., 2023a). Further details of the Malua reserve and the Sabah Biodiversity Experiment can be found in previous publications (Hector et al., 2011; Tuck et al., 2016; Veryard et al., 2023a).

The Sabah Biodiversity Experiment was designed to be a field-scale project that could provide relevant insights into forestry and tropical forest conservation whilst applying the highest standard of experimental design. However, the size, location, and environmental conditions surrounding this experiment meant that some experimental design elements were not as practical or safe to carry out as they would be on a smaller scale. A review of these logistical challenges and constraints can be found in Chapter 6.

Malua Field Camp

Due to the location of the Sabah Biodiversity Experiment, a nearby field station was required. The Malua Field Camp is a satellite of the Danum Valley Field Centre and is located to the immediate west of the southern block of the experiment. This remote field station can support around a dozen field researchers and research assistants at a time. It is

also equipped with a power generator, Wi-Fi capacity, and a seedling nursery to help supply the Sabah Biodiversity Experiment and all satellite experiments with any required seedlings. Whilst 16 species of dipterocarp were enrichment planted as part of the Sabah Biodiversity Experiment, in total 32 tropical tree species have been used in the various satellite research projects conducted at Malua Field Camp (Table 2.3).

Due to the COVID-19 pandemic, the field site was closed from March 2020 to April 2023, during which the site fell into considerable disrepair. Most of the field camp's structures were damaged by elephants, reducing the capacity of the site to host large groups of researchers. In April 2023, access to the site was restored via the repair of the old logging road used for access, and field operations have now resumed at Malua Field Camp.

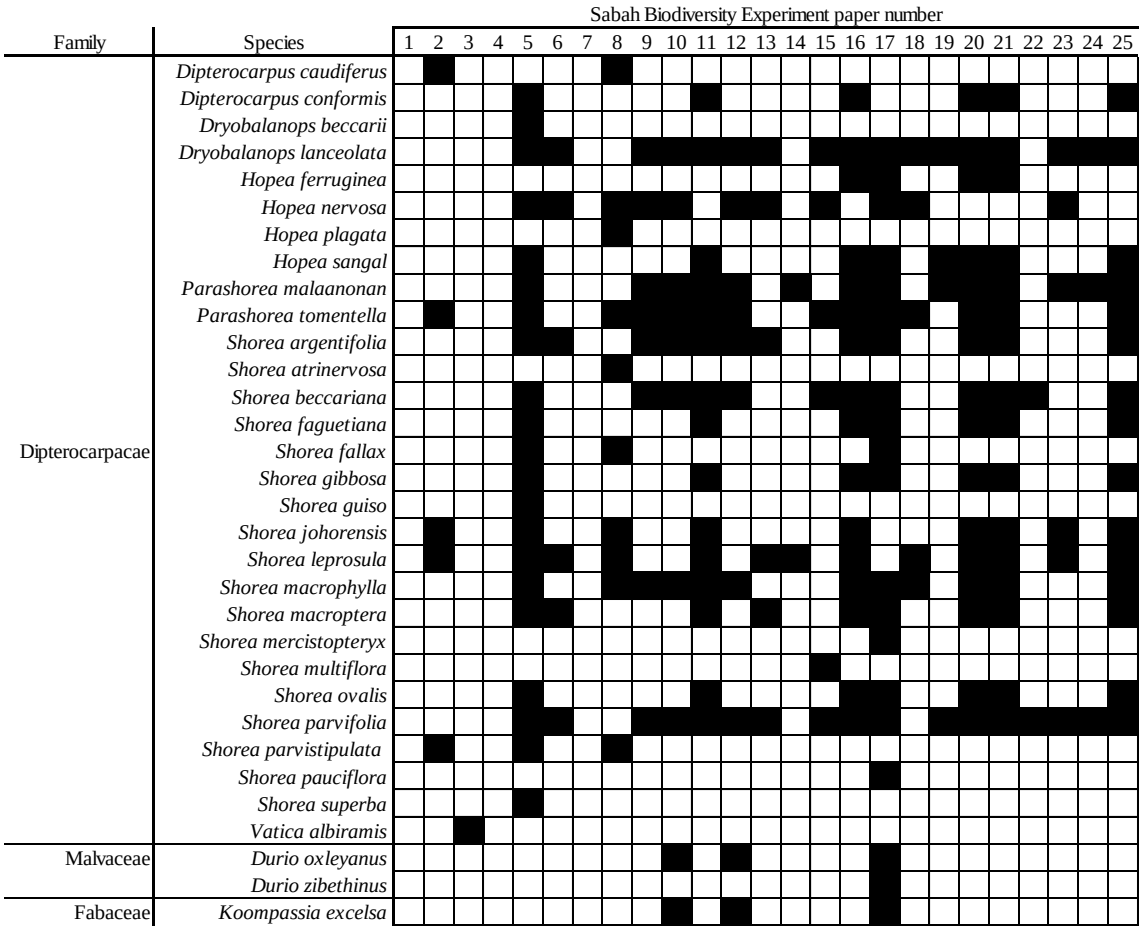
Survey frequency and intensive plots

Due to the size of this experiment, only two full censuses of the Sabah Biodiversity Experiment have taken place. The first (November 2003 to May 2005) was carried out before the planting of the second cohort, and the second census (November 2011 to September 2013) includes both cohorts. A third census began in late 2023. In each census, the diameter two centimetres above the base of each seedling and, if the seedling was large enough, the diameter at breast height (measured at 130 cm) was measured. The survival of the seedling was also recorded (i.e., if dead or alive).

Because of the size of the Sabah Biodiversity Experiment, a subset of plots were identified in the Southern block close to the Malua Field Camp that would be surveyed more regularly. These six plots (3, 5, 8, 11, 14, 17) are all 16-species polycultures, half of which (5, 11, and 14) have also received the liana removal treatment described above. These have

been much more frequently surveyed, with 10 total surveys to date ranging from 2004 to 2020. There was a pause in surveying due to the COVID-19 pandemic but seedling surveys resumed at the Sabah Biodiversity Experiment in late 2023. For a complete timeline of seedling planting, full censuses, intensive plot surveys, and other satellite experiments during the current lifetime of the Sabah Biodiversity Experiment, see Fig. 2.7.

Table 2.3 The 32 species used in each Sabah Biodiversity Experiment publication to date. Publication numbers are assigned to each publication from the Sabah Biodiversity Experiment and can be indexed in Table A2. Black boxes indicate that a species is explicitly used within that publication.



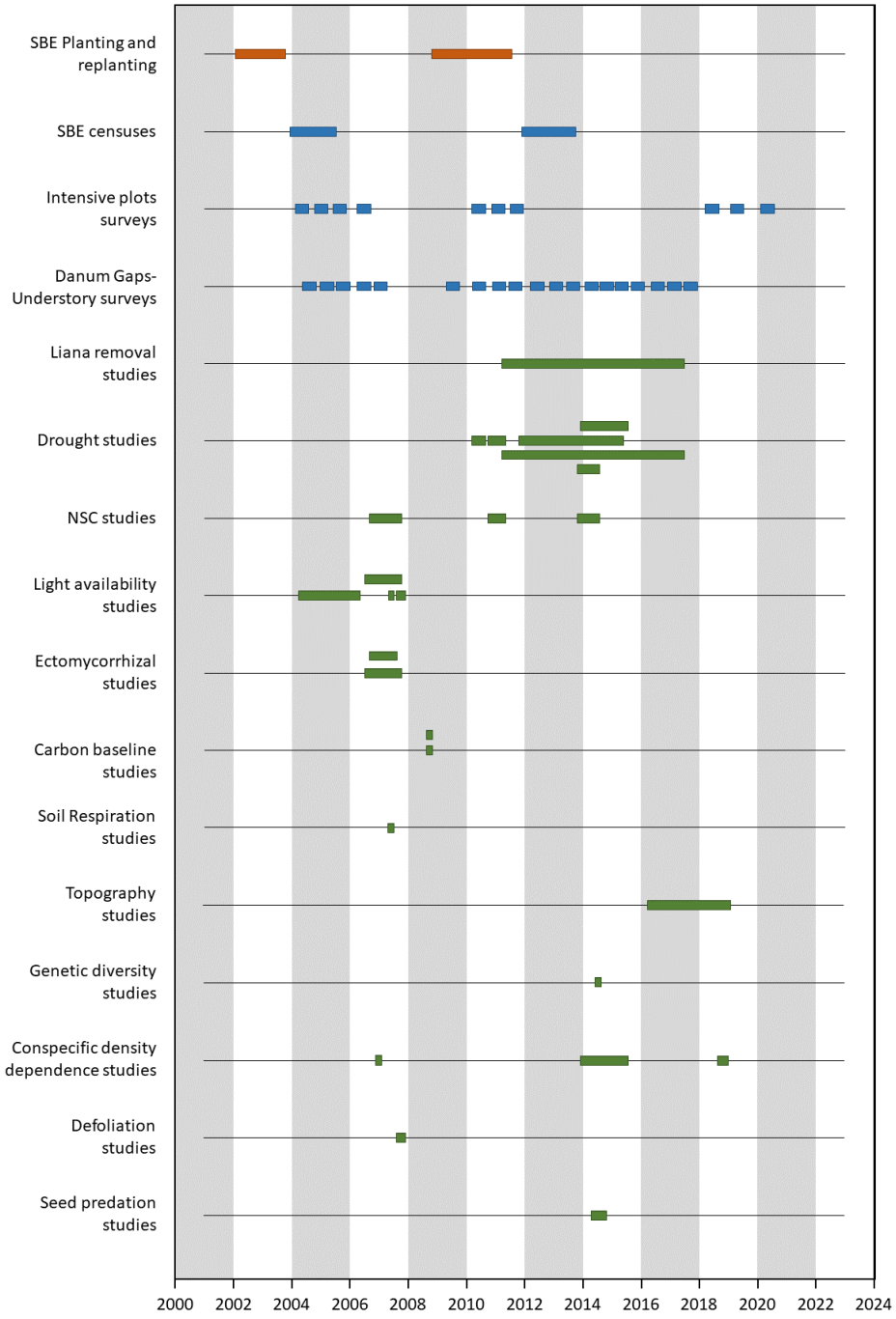


Figure 2.7 Surveys and studies carried out at the Sabah Biodiversity Experiment (SBE) since its inception. Red bars indicate planting at the SBE, blue bars indicate direct censuses of plots at the SBE, and green bars indicate times that other studies were carried out at the SBE or at the nearby Malua Field Camp. Studies are grouped by type and can appear in multiple groups if they contain multiple themes.

Wider Malua

Although the Sabah Biodiversity Experiment site was spared from a second round of logging due to the presence of the project, the remainder of the Malua Forest Reserve was logged between 2003 and 2007. The Sabah Biodiversity Experiment can be compared to the wider Malua Forest Reserve to estimate the amount of deforestation avoided by the creation of the experiment. Wu et al. (2020) showed that post-logging, vegetation cover of the Malua Forest Reserve declined by 3% on average and by 7% in the most severely logged regions, whilst the Sabah Biodiversity Experiment showed a 5% increase in vegetation cover. This study also estimated that the Malua Forest Reserve lost approximately 2.7 million Mg of biomass due to logging, which suggests that around 120,000 Mg of biomass was directly spared from logging within the Sabah Biodiversity Experiment (Wu et al., 2020). Assuming that the majority of this biomass was in the form of tree stems and that 47.4% of wood is carbon (Martin & Thomas, 2011)(Eggleston et al., 2006), approximately 57,000 Mg of carbon loss, or roughly 115 Mg C ha^{-1}, was directly avoided as a result of the creation of the Sabah Biodiversity Experiment. For a second estimate, Asner et al. (2018) used LIDAR and satellite imaging to show that, in April 2016, Malua Forest Reserve had an average aboveground carbon density of 101 Mg C ha^{-1} and the nearby old-growth Danum Valley Conservation Area had an average carbon density of 207 Mg C ha^{-1}. Philipson et al. (2020) showed that the naturally regenerating Ulu Segama Forest Reserve (adjacent to the Malua Forest Reserve) accumulates carbon at a rate of 2.9 Mg C ha^{-1} $year^{-1}$. This estimates the 2007 post-logging forest carbon density at 75 Mg C ha^{-1} and a direct carbon loss avoidance of 132 Mg ha^{-1}, similar to the estimate derived from Wu et al. (2020).

Danum Valley Conservation Area

Within the YSF Management Area, south of the Malua Forest Reserve and effectively encircled by the entire Ulu Segama-Malua Forest Reserve, is the Danum Valley Conservation Area, a 438 km^2 (43,800 ha) piece of primary forest, which has never been logged and potentially has no historical record of human presence or cultivation (Marsh & Greer, 1992). This region is within Yayasan Sabah's original forest concession but had been largely unexplored when the concession was first established. Besides gold prospecting in the 1880s-1890s (Fitch, 1955; Leong, 1974), the first real exploration came from geological surveys by Fitch (1955) and Leong (1974). In 1976 an expedition was jointly organised by the Sabah Parks Board and WWF Malaysia to explore the area, where they subsequently recommended the establishment of a national park encompassing the entire catchment area of the Danum River, with the southern boundary being defined by the Segama River. Despite initial work by Yayasan Sabah to achieve this via amendments to existing permits, some 20,000 ha of proposed protected area in the headwaters of Danum were licensed and logged (Marsh & Greer, 1992). In response, in 1980 the remaining area was retained by Yayasan Sabah (so that the land could not be licensed out) and classed as a special status zone for the protection of wildlife, which was later formalised in a Yayasan Sabah Management Plan (Sabah, 1984). Since being classed as a protected area, the Danum Valley Conservation Area has remained free from logging and has been strengthened by restoration projects within the USM Forest Reserve. This buffering was enhanced more recently through the subsequent reclassification of the USM Forest Reserve as a Totally Protected Area in 2012. Given that less than 700 km^2 of primary lowland dipterocarp forest remains in Sabah (Reynolds et al., 2011), this is arguably one of the most important regions for lowland dipterocarp protection.

Danum Valley Field Centre

The Danum Valley Field Centre was established in 1986 to provide facilities to support research into sustainable forest management techniques (Marsh & Greer, 1992). The field centre has continued to expand, and can now accommodate dozens of researchers, research assistants, tourists, and permanent staff. Danum Valley Field Centre is between two and three hours away from Malua Field Camp by car depending on road and weather conditions.

Danum Gaps-Understory Experiment

After the initial planting of the Sabah Biodiversity Experiment, many seedlings were still available at the INFAPRO nursery, as were several additional species. To make use of these remaining seedlings, a smaller experiment was established in 2004 by Chris Phillipson, Andy Hector, and colleagues to investigate the growth and survival of seedlings within naturally occurring canopy gaps and understory of a primary lowland dipterocarp forest. The forest surrounding Danum Valley Field Centre was selected as it is relatively near the Sabah Biodiversity Experiment and had nearby infrastructure which made establishment and monitoring less logistically challenging. This experiment is referred to as the Danum Gaps-Understory Experiment.

The difference in forest type (primary forest for the Danum Gaps-Understory Experiment and secondary forest for the Sabah Biodiversity Experiment) meant that elements of experimental design could not be conserved between both experiments for practical and regulatory reasons. For instance, clear-cutting lines and removing lianas would not be permissible in a Class I protected forest reserve, and planting almost 100,000 seedlings within the Danum Valley Conservation Area would not have been feasible. Though the two

experiments share many of the same planted species and contain seedlings which came from the same initial seedling stock, experimental design and analysis differ. For a more complete comparison between both experimental sites, see Table 5.1 in Chapter 5.

Danum Gap and Understory Plots

Extending from Danum Valley Field Centre are several walking trails, which were initially created for research but more recently have been used primarily for tourist walking trips. Along several of these trails are the plots used in the Danum Gap Understory experiment (Fig. 2.8). Specifically, these plots lie along the 'West Trail', 'Rhino Pool Trail', 'Tembeling Waterfall High Road' trail, and 'Tembeling Waterfall Low Road' trail.

Along these trails, 20 sites were identified with sufficiently large gaps in the canopy. At each location (subsequently defined as a plot), two identical subplots were established. Within each subplot, 25 seedlings, each from a unique species, were planted with 0.75 x 0.75 m spacing. For each plot under a canopy gap, a paired plot was established 30 m away at a random compass bearing, in a region of greater canopy cover, and within this plot two subplots were established with the same methodology as in each canopy gaps plot (Fig. 2.9). A total of 20 blocks were established, consisting of 40 paired plots and 80 total subplots. In total 2,000 seedlings were planted, using the same stock as the Sabah Biodiversity Experiment. Twenty-four planted species came from five genera of the Dipterocarpaceae family, and the final species was *Durio graveolens* from the Malvaceae family. For a complete list of species planted see Table A3. Of the 16 species used in the Sabah Biodiversity Experiment, 15 were also planted within the Danum Gaps-Understory experiment (*Shorea ferruginea* was not planted in the Danum Gaps-Understory Experiment due to limited seedling availability). The experimental setup was completed in November

2004, approximately one year after the completion of the first round of planting at the Sabah Biodiversity Experiment. Unlike the Sabah Biodiversity Experiment, no replanting was carried out for the Danum Gap-Understory Experiment.

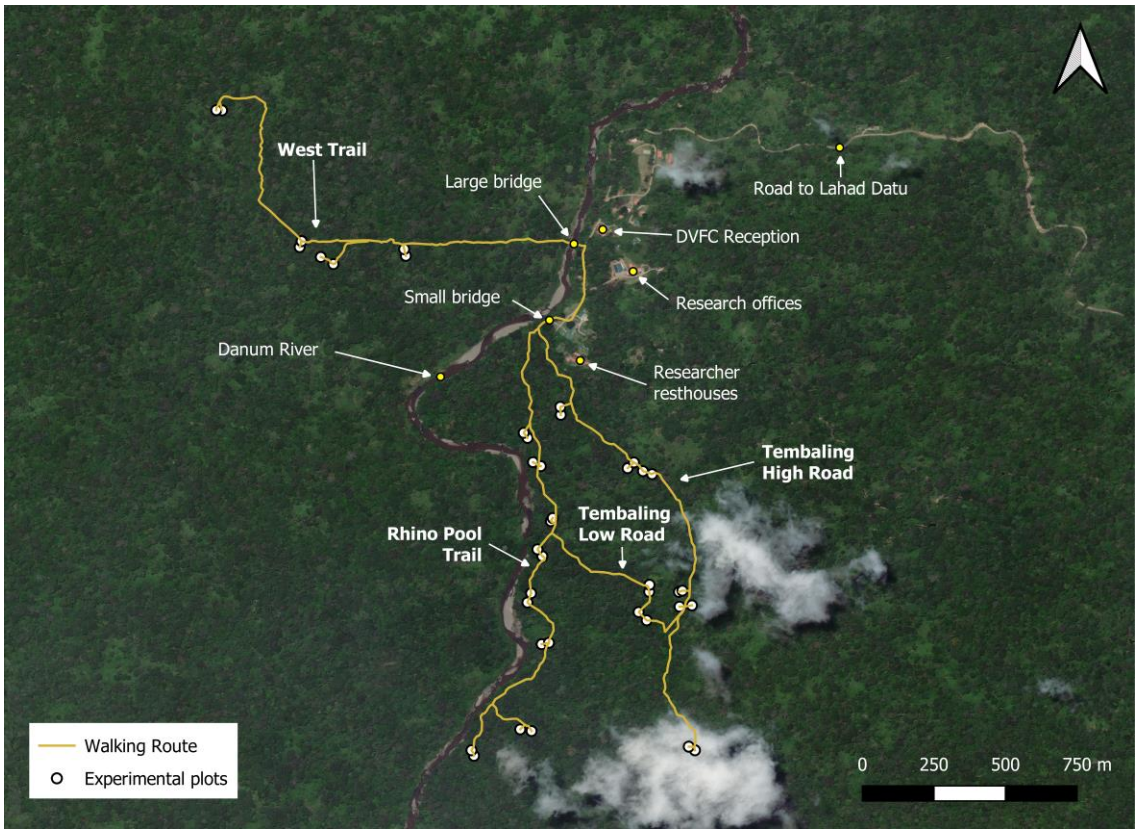


Figure 2.8 Planting location of the Danum Gaps-Understory Experiment. Individual plots marked as white points along each trail (shown as yellow lines) surrounding Danum Valley Field Centre. Trail names are indicated with bold text. Points of interest in and around Danum Valley Field Centre are indicated with yellow points and labelled.

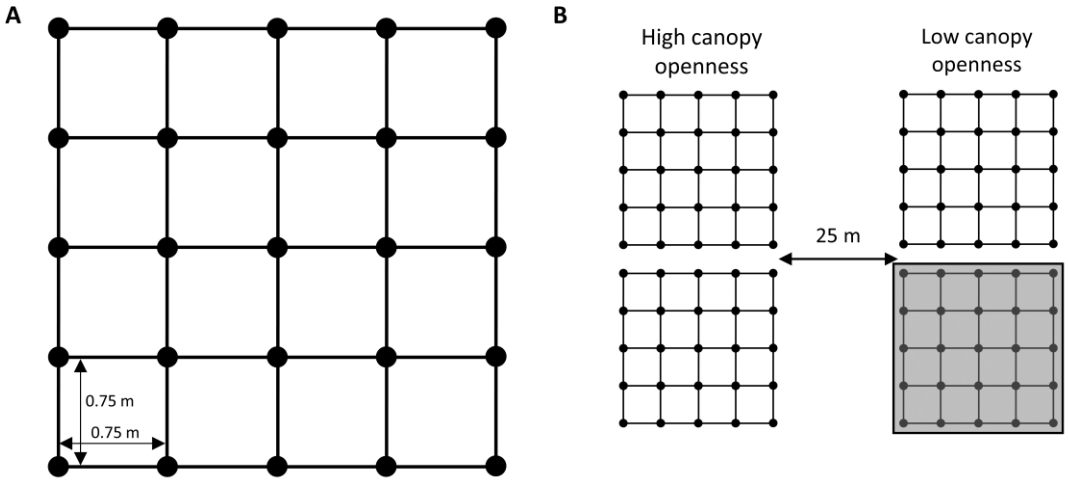


Figure 2.9 Experimental planting design for each subplot, plot, and block. (**A**) Twenty-five seedling species are planted in a grid with individual spacing 0.75 x 0.75 m to form one subplot. (**B**) Two subplots make up a plot in either a high or low canopy openness area, which are paired together and are no more than 25 m apart. Both plots (and all four subplots) make up a single block. Within 20 plots, one subplot had drought treatment later applied using a plastic sheeting (indicated by a grey box over one subplot). In 15 blocks this was applied to a high canopy openness plot and in five this was applied to a low canopy openness subplot.

Droughting treatment

As a sub-experiment, clear polyethylene plastic sheeting was applied over one subplot within 20 plots. In 15 of these cases, a gaps plot was used, and in another five an understory plot was used (Table A4; O'Brien et al. (2023)). This imbalance was due to the high mortality and slow growth in the understory subplots, which made applying the sheeting logistically difficult.

Survey frequency

As this is a smaller experiment than the Sabah Biodiversity Experiment and the experiment is located nearer the Danum Valley Field Centre, regular surveys are more feasible. Surveys were ongoing from 2004 until 2017, and 19 complete surveys have been completed to date. In 2023, additional surveys of the Danum Gaps plots began, and the plan is for regular surveying to resume. Between 2017 and 2023, it was reported that block 19, the block furthest along the West Trail (see Fig. 2.8), had been destroyed due to tree fall. The Danum Gaps-Understory Experiment now effectively consists of 19 blocks.

Recent advances of the tribe Shoreae

Of the 25 dipterocarp species planted in the Sabah Biodiversity Experiment and Danum Gaps-Understory Experiment, 18 belong to the genus *Shorea*. This genus has comprised the bulk of traded dipterocarp timber (Ashton & Heckenhauer, 2022) and so is a particularly important group within the Dipterocarpaceae. Since planting, a recent advance in the taxonomy of the tribe Shoreae (Dipterocarpaceae subfamily Dipterocarpoideae) has been made based on embryological and molecular evidence (Ashton & Heckenhauer, 2022), which has split species that were previously in the *Shorea* genus into seven genera (including those that remained in *Shorea*). For the purposes of consistency between publications coming from the Sabah Biodiversity Experiment and the Danum Gaps-Understory Experiment, this thesis will refer to the species as they were known at the time of planting, but for a list of species names at the time of planting and their updated nomenclature, see Table A5.

Other projects and locations of interest

Borneo Rainforest Lodge

The only other major settlement between Malua Field Station and Danum Valley Field Centre is Borneo Rainforest Lodge. This is a five-star eco-resort located near the northern boundary of Danum Valley Conservation Area with a capacity for 60 guests. It offers a range of experiences, including nature tours and access to Danum Valley's 300 m long, 26 m high canopy walkway. The road providing access to Borneo Rainforest Lodge lies approximately halfway along the road connecting Danum Valley Field Centre to Malua Field Camp, and Borneo Rainforest Lodge is the closest large, inhabited complex to Malua Field Camp in case of emergency (approximately 25 km, or 1-1.5 hours by car; Fig. 2.10). The road from Danum Valley Field Centre to Malua Field Camp is partially maintained by Borneo Rainforest Lodge, as tourists usually need to be driven to the lodge from Lahad Datu. Beyond Borneo Rainforest Lodge, the road is less actively maintained.

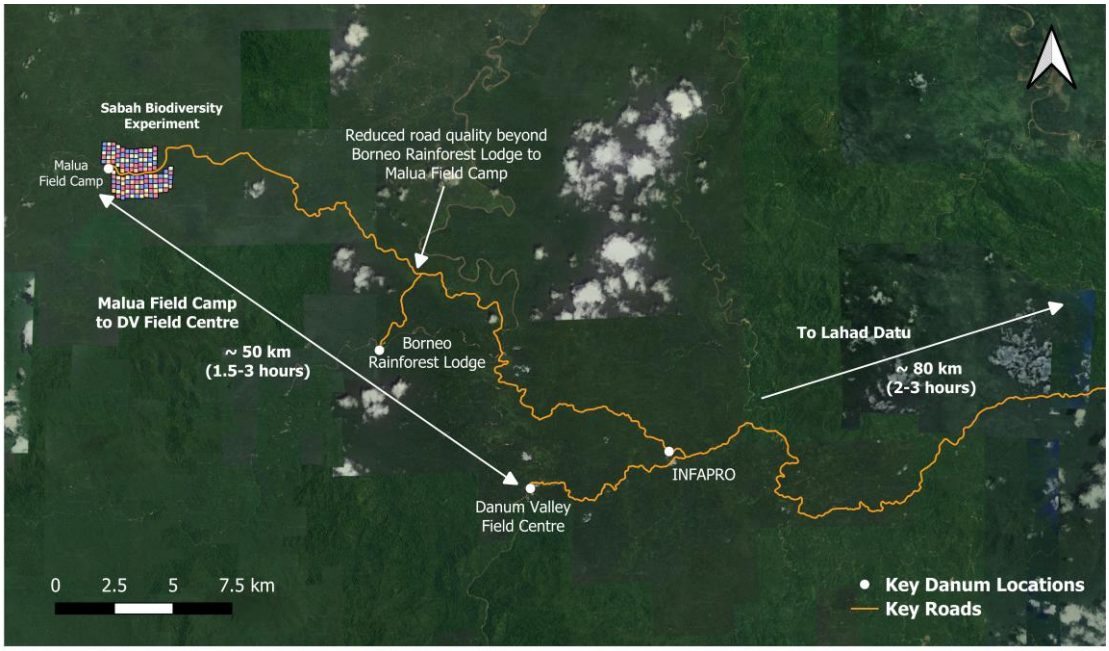


Figure 2.10 Map of key roads and locations between Malua Field Camp and Danum Valley Field Centre. Roads are highlighted in orange and key locations are represented by white points. It is approximately 80 km to Lahad Datu from Danum Valley Field Centre (2-3 hours depending on road conditions and weather), travelling on a road that passes the INFAPRO project. The journey from Danum Valley Field Centre to Malua Field Camp is around 50 km long and takes 1.5-3 hours depending on road conditions. Note that the road from Danum Valley Field Centre to Malua Field Camp is well maintained up to Borneo Rainforest Lodge, after which the road quality decreases and average vehicle speed decreases.

Malua Biobank

The Malua Forest Reserve section of the Ula Segama-Malua Forest Management Area was designated as a 'biobank' in 2008. The Malua BioBank (https://www.cbd.int/financial/offsets/malaysia-offsetmalua.pdf) is a joint venture between the Sabah State Government, Yayasan Sabah, and the Eco Product Fund, a private US fund

that invests in environmental markets (Wook et al., 2022). The BioBank aims to restore the logged Malua Forest Reserve and create a habitat that will help protect threatened wildlife within Sabah. This is done via the creation of 'voluntary biodiversity conservation certificates', each representing 100 square metres of rehabilitation and protection of the Malua Forest Reserve. Eco Product Fund pledged an investment of up to US $10 million to the Malua Trust in return for the right to market and sell these certificates to independent third parties at $10 per certificate. The certificates were marketed as a means for companies to achieve their biodiversity offsetting and wider environmental goals. They were initially marketed towards major oil palm companies within Malaysia before expanding internationally (Wook et al., 2022). The BioBank has struggled with the consistency of demand for biodiversity certificates, and without a legal framework for a 'no net loss' policy, consistent demand for such certificates will continue to be a challenge for the Malua BioBank's financial viability (Wook et al., 2022). In recent years, the Kota Kinabalu office for the Malua BioBank was closed, and the project is currently inactive. Despite these challenges, the creation of the BioBank is argued to have helped reclassify the Malua Reserve as a Class I fully protected forest in 2013 (Halley, 2015).

Innoprise-FACE Foundation Rainforest Rehabilitation Project (INFAPRO)

The Innoprise-FACE Foundation Rainforest Rehabilitation Project (INFAPRO; https://facethefuture.com/projects/sabah-maleisie-bosherstel-en-bescherming) is a large-scale rehabilitation and restoration project in the northeast corner of the Ulu Segama Forest Reserve, north of Danum Valley Conservation Area and east of Malua Reserve. INFAPRO was started in 1992 between Yayasan Sabah's commercial wing (Innoprise Corporation Sdn Bhd) and the FACE foundation, an environmental services company based in the Netherlands now known as Face the Future. To date, 12,000 ha have been restored using

their replanting methodologies across 24,000 ha of land managed by INFAPRO. Planted seedlings were mainly from the Dipterocarpaceae (52 dipterocarp species and five other canopy species), though they did plant 16 other species of native fruit trees to further enhance biodiversity (Philipson et al., 2020). Notably, the main INFAPRO seedling nursery is located near Danum Valley Field Centre and, before Ulu Segama was reclassified as a Class I reserve in 2012, the INFAPRO planting area was an important buffer on the western side of the Danum Valley Conservation Area.

The INFAPRO project lies approximately 10 km away from Danum Valley Field Centre (around 15-20 minutes by car) and lies along the road connecting Malua Field Camp with Danum Valley Field Centre. It takes approximately 1.5 hours to reach INFAPRO by driving from the Malua Field Camp. The seedling stock used to plant and replant the Sabah Biodiversity, as well as to plant the Danum Gaps-Understory Experiment, were sourced from INFAPRO, and the Sabah Biodiversity Experiment was planted following INFAPRO standards. The seedling stock used to plant has since been shown to have species-specific variation in genetic diversity, which the authors suggest is due to differing numbers of available parent trees during the mast fruiting event in 2001 (Ang et al., 2016).

Innoprise-IKEA project (INIKEA)

The Innoprise-IKEA (INIKEA) project (http://www.borneoforestheritage.org.my/inikea.htm), also known as the Sow-A-Seed project, is located in the central-south region of the YSF Management Area, southwest of both the Danum Valley Conservation Area and the Malua Forest Reserve. This was established in 1998 in response to selective logging from the 1970s and subsequent forest fires during the El Niño drought event in 1983-1984 that increased degradation and

hindered natural recovery (Engström, 2023). This project was jointly funded by Yayasan Sabah and the Sow-A-Seed Foundation of the Swedish company IKEA and has operated over multiple 'phases' (phase one: 1998-2003, phase two: 2003-2008, phase three: 2008-2013, phase four: 2013-2020). To date, around 14,000 ha of forest has been restored by INIKEA (Engström, 2023). Although there is currently no formal collaboration between the INIKEA project and the Sabah Biodiversity Experiment, the INIKEA project does provide a point of comparison for restoration success. One difference between both sites is that the INFAPRO project, rather than replanting with exclusively (or nearly exclusively) dipterocarps like the Sabah Biodiversity Experiment, instead used a mixture of 70% dipterocarp, 25% non-dipterocarp, and 5% wild fruit tree seedlings. A wider range of genera was chosen to provide a variety of food sources to different organisms (IKEA, 2021).

Additionally, whilst the Sabah Biodiversity Experiment uses exclusively line-planting techniques to plant seedlings, the INIKEA project makes use of multiple restoration strategies, including line-planting, gap-cluster planting, and liberation. Gap-cluster planting is done in areas that contain many large climax trees but are overall dominated by pioneer species such as *Macaranga spp*. Gap-cluster planting involves the removal of pioneer trees and the planting of a mixture of tree species within gap areas. Liberation techniques were employed in areas that were less heavily degraded and had an existing canopy layer. In this method, lianas were removed and in some cases, pioneer species were girdled (Engström, 2023). One challenge in comparing these treatments across the INIKEA project and the Sabah Biodiversity Experiment is that the first three phases of the INIKEA project had treatments assigned non-randomly. Sections of the INIKEA project's forest area were assessed and the most suitable treatment was selected. This is not the case for phase

four of the INIKEA project, where four treatments (line-planting, gap-cluster planting, liberation, and untreated controls) were applied randomly to subsections of the treatment area. Phase four was completed in 2020, and it will take several years of growth and recovery before direct comparisons with the Sabah Biodiversity Experiment can be made.

Stability of Altered Forest Ecosystems (SAFE) Project

The Stability of Altered Forest Ecosystems (SAFE) Project (https://safeproject.net/) is the world's largest dedicated forest fragmentation experiment, which directly aims to assess how biodiversity and ecosystem function change as forests are modified by human activities. This project is based on the highly successful Biological Dynamics of Forest Fragments Project (BDFFP) based in the Amazon rainforest in the 1970s. The BDFFP was used to help determine the minimum critical size of a forest fragment before it would fail to sustain itself as a tropical forest system (Laurance et al., 2018).

The SAFE Project is broken into three interconnected sub-projects. The first examines the ecological changes along multiple sites comprising a gradient of forest modifications. Old-growth forest sites exist within the Maliau Basin Conservation Area, and another site exists just outside this area in a region that was lightly logged in the 1970s and mid-1990s to provide timber for a field centre (Ewers et al., 2011). Sites were established within the Mount Louisa Forest Reserve (see Fig. 2.4) to represent twice-logged continuous forests. Six sites were established within an 8,000 ha experimental area of the intensively logged Kalabakan Forest Reserve (Fig. 2.3), which later underwent multiple rounds of salvage logging in preparation for conversion into oil palm plantation, excluding the experimental sites. Finally, sites were established within existing oil palm plantations to the west of the experimental area.

Whilst the SAFE Project is not an enrichment planting experiment like the Sabah Biodiversity Experiment, there is potential for collaboration and synergy between the two experiments. The Sabah Biodiversity Experiment is a forest site that was logged intensively once, which is a level of habitat modification not captured within the SAFE Project. Additionally, the enrichment planting of the Sabah Biodiversity Experiment provides another point of direct comparison with the SAFE Project.

Within the experimental area, there are a range of different-sized forest fragments which are planned to be maintained (1 ha, 10 ha, and 100 ha) in six replicate blocks following the conversion of the surrounding landscape to oil palm. An additional experimental design element explores the role of river margins in maintaining river water quality and aquatic diversity. This work is not directly relevant to the work at the Sabah Biodiversity Experiment. As of 2023, palm oil crops have yet to be planted at the SAFE experimental site, and this part of the Kalabakan Forest Reserve is naturally regenerating. This experimental site allows researchers to study the recovery of forests after intense periods of salvage logging, which were not experienced within the Malua Forest Reserve. Currently, access to the SAFE site has been disrupted by COVID-19-related inactivity, which caused its sole access road to be grown over and rendered unusable. Plans to continue research at SAFE are therefore dependent on the road being restored.

Chapter 3: Positive effects of tree diversity on tropical forest restoration in a field-scale experiment

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Data availability: All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. The data for this study have been deposited in the database Dryad and can be found at https://doi.org/10.5061/dryad.8w9ghx3rs.

Abstract

Experiments under controlled conditions have established that ecosystem functioning is generally positively related to levels of biodiversity, but it is unclear how widespread these effects are in real-world settings and whether they can be harnessed for ecosystem restoration. We used remote sensing data from the first decade of a long-term, field-scale tropical restoration experiment initiated in 2002 to test how the diversity of planted trees affected the recovery of a 500-ha area of selectively logged forest measured using multiple sources of satellite data. Replanting using species-rich mixtures of tree seedlings with higher phylogenetic and functional diversity accelerated restoration of remotely-sensed estimates of aboveground biomass, canopy cover and leaf area index. Our results are consistent with a positive relationship between biodiversity and ecosystem functioning in the lowland dipterocarp rainforests of SE Asia and demonstrate that using diverse mixtures of species can enhance their initial recovery after logging.

Introduction

A quarter century of ecological experimentation has demonstrated that when other factors are held constant, ecosystem functions like biomass production are generally positively related to levels of biodiversity (Cardinale et al., 2012; Isbell et al., 2017; Lefcheck et al., 2015; Tilman et al., 2014). However, for practical reasons, the first generation of biodiversity manipulation experiments was conducted with systems that are relatively quick to respond, particularly communities of grassland plants (Hector et al., 1999; Roscher et al., 2005; Tilman et al., 2001b; Van Ruijven & Berendse, 2005). More recent biodiversity experiments suggest that similar relationships between tree diversity and ecosystem functioning are present in many plantations and some forests (Feng et al., 2022), although there has been little research in tropical systems, particularly outside of the Americas (Forrester & Bauhus, 2016; Huang et al., 2018; Messier et al., 2021; Pelletier et al., 2018; Schnabel et al., 2019; Warner et al., 2022). It is also not clear to what degree the results of biodiversity experiments extend to more natural settings (Dee et al., 2023), nor whether they can be harnessed as a nature-based solution to forest restoration and carbon capture. Here, we report early results from a field-scale experiment that tests different approaches to the restoration of lowland tropical rainforests in SE Asia, focusing in particular on the role of the diversity of tree species used for replanting. Recent results from our lowland tropical forest study system in Sabah, Malaysian Borneo, show that active restoration, including enrichment tree planting, can accelerate recovery (Philipson et al., 2020). Here we go further in demonstrating that recovery (measured using remote sensing estimates of aboveground biomass, canopy cover and leaf area index) can be enhanced by replanting with ecologically diverse mixtures of tree species.

The Sabah Biodiversity Experiment (O'Brien et al., 2019; Saner et al., 2011; Tuck et al., 2016) is designed to simultaneously test the applied question of whether increasing tree diversity in replanting schemes enhances restoration and the ecological hypothesis of whether there is a positive relationship between tree diversity and ecosystem functioning in tropical forests. There is ongoing debate over the generality of the positive relationship between diversity and ecosystem functioning demonstrated by experiments for real-world ecosystems (Dee et al., 2023), including the importance of tree diversity for the functioning of tropical forests, with some predictions of no or small ecological differences among tree species in tropical forests. On the one hand, neutral theory and related ideas (Adler et al., 2007; Hubbell, 1997, 2001, 2006) hypothesize that tree species in tropical forests are ecologically identical (or near identical), and therefore predict a weak or absent link between diversity and functioning. In contrast, classical (Darwinian) niche theory predicts complementary differences among species coexisting within communities, leading to an ecological "division of labour" (Hector & Hooper, 2002) and therefore a positive, saturating relationship between diversity and function (Turnbull et al., 2016; Wang, 2022). The Sabah Biodiversity Experiment tests the hypothesis that increasing the diversity of tree species used to replant selectively logged forest enhances recovery rates. To address the underlying mechanisms, we tested the related hypothesis that enhanced recovery rates are associated with higher levels of functional (Petchey & Gaston, 2002), phylogenetic (Faith, 1992) and taxonomic (genus) diversity as predicted by niche theory (Turnbull et al., 2016; Wang, 2022). We also tested whether restoration rates were increased by the removal of the liana functional group, based on previous findings that lianas can reduce tree growth and survival (Clark & Clark, 1990; Schnitzer et al., 2000).

To be relevant to forestry and forest restoration, the Sabah Biodiversity Experiment was designed to be field scale and covers 500 ha of selectively logged tropical forest in the Malua Forest Reserve. The experimental treatments are applied to 4-ha plots and comprise different restoration approaches including liana removal ('climber cutting') and enrichment line planting where seedlings of the harvested native tree species are planted back into the resulting selectively logged vegetation (Fig. B1 in Appendix B). The seedlings used in the initial planting were collected throughout the Ulu Segama-Malua Forest Reserve with the exception of *Hopea ferruginea* (sourced from the INIKEA nursery at Lawasong) and *Dipterocarpus conformis* (sourced from the Tawau Hill area) Approximately 100,000 seedlings of 16 different species of the dominant dipterocarp trees (Table B1 in Appendix B) have been planted along lines cut into the residual background vegetation left after selective logging in the 1980s—a setting unique among tree diversity experiments. The treatments include unplanted controls, single-species plots enrichment planted with seedlings of one of sixteen different species of dipterocarp, enriched plots planted with mixtures of 4 or 16 of these species, enriched plots planted with sixteen species mixtures combined with liana removal, and plots to assess manipulations of genus diversity (the number of genera planted) and (predicted) canopy structural complexity (Table 3.1). Enriched plots had equal density of saplings (planted every 3 m on parallel lines 10 m apart) with species equally represented in mixtures. Following standard practice in the study system, we used an initial round of enrichment planting in 2002-2003 followed by replacement of seedlings that died. The site has subsequently been monitored periodically for survival and growth of the planted seedlings. To gain an overview of the effects of the experimental treatments on the whole 500 ha area of the experiment over the initial stage of restoration, we used multiple sources of satellite remote sensing data including

RapidEye estimates of vegetation cover, aboveground biomass and leaf area index in 2012 and longer-term estimates of changes in cover from Landsat from 1999 (prior to enrichment planting) to 2012 (Wu et al., 2020).

Table 3.1 Sabah Biodiversity Experiment treatments. Columns (left to right) indicate the number of species and genera of enrichment planted trees, predicted canopy complexity, whether lianas are removed and the number of replicate plots. * indicates no experimental manipulation.

Number of species	Number of genera	Canopy complexity	Liana removal	Number of replicate plots
0	0	*	No	12
1	1	Low	No	32
4	2	Low	No	8
4	2	High	No	8
4	4	Low	No	8
4	4	High	No	8
16	5	High	No	32
16	5	High	Yes	16

Results

Analysis of estimates of vegetation cover, aboveground biomass and leaf area index derived from RapidEye satellite data in 2012 revealed differences among the restoration treatments a decade after initial planting (Fig. 3.1, Table B2). Comparison of unplanted controls with enrichment planted plots revealed that, after a decade, active restoration increased levels of estimated aboveground biomass (mean [95% CI]: 182.7 [153.1 – 212.3] *vs* 226.0 [217.5 – 234.6] Mg ha^{-1}), cover (62.1 [56.6 – 67.5] *vs* 66.7 [61.7 – 71.7] %) and leaf area index (4.57 [3.89 – 5.26] *vs* 4.96 [4.40 – 5.53] $m^2 m^{-2}$). There were statistically significant differences for aboveground biomass (difference [95% CI]: 43.3 [13.3 – 73.2] Mg ha^{-1}) and cover (4.63 [1.08 – 8.07] %) but not leaf area index (0.39 [-0.18 – 0.95]; Fig. 3.1, Table B3).

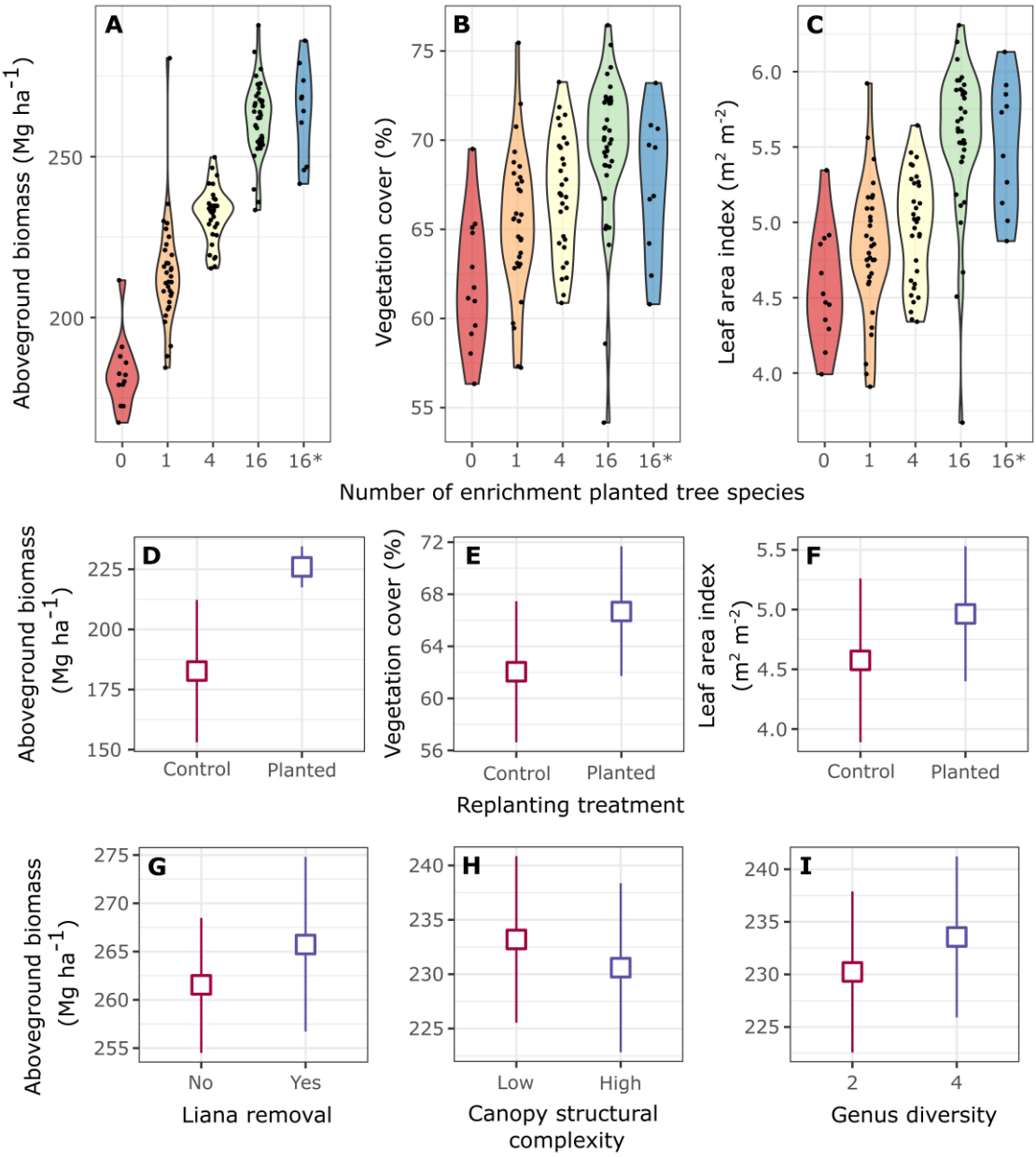
A
B
C
Aboveground biomass (Mg ha-1)
Vegetation cover (%)
Leaf area index (m2 m-2)
0
1
4
16
16*
Number of enrichment planted tree species
D
E
F
Control
Planted
Replanting treatment
G
H
I
No
Yes
Liana removal
Low
High
Canopy structural complexity
2
4
Genus diversity

Figure 3.1 RapidEye satellite remote sensing estimates as a function of restoration treatment a decade after initial planting. (**A** to **C**) Data points for individual plots overlaid on violin plots showing (left to right) aboveground biomass, percent vegetation cover and leaf area index in relation to enrichment planting with seedlings of 0, 1, 4, or 16 species of dipterocarp tree species (16*: enrichment planting with sixteen species plus liana cutting). (**D** to **F**) Treatment means (with 95% confidence intervals) for unplanted controls versus enrichment planted plots (panels as in top row). (**G** to **I**) Aboveground biomass as a function of (left to right) genus diversity of plots enrichment planted with four-species (2 genera vs 4 genera); canopy complexity (low vs high); and liana removal ('climber cutting').

While enrichment planting had a general positive effect on restoration, its effectiveness was positively related to the diversity of species used. The relationship was positive and approximately linear with the logarithm of the number of enrichment planted species: each doubling in tree species richness increased estimated aboveground biomass by 12.9 Mg ha^{-1} [10.3 – 15.1] (Fig. 3.2A), cover by 1.06 % [0.44 – 1.66] (Fig. B2), and leaf area index by 0.23 m^2 m^{-2} [0.16 – 0.30] (Fig. B3; Table B4).

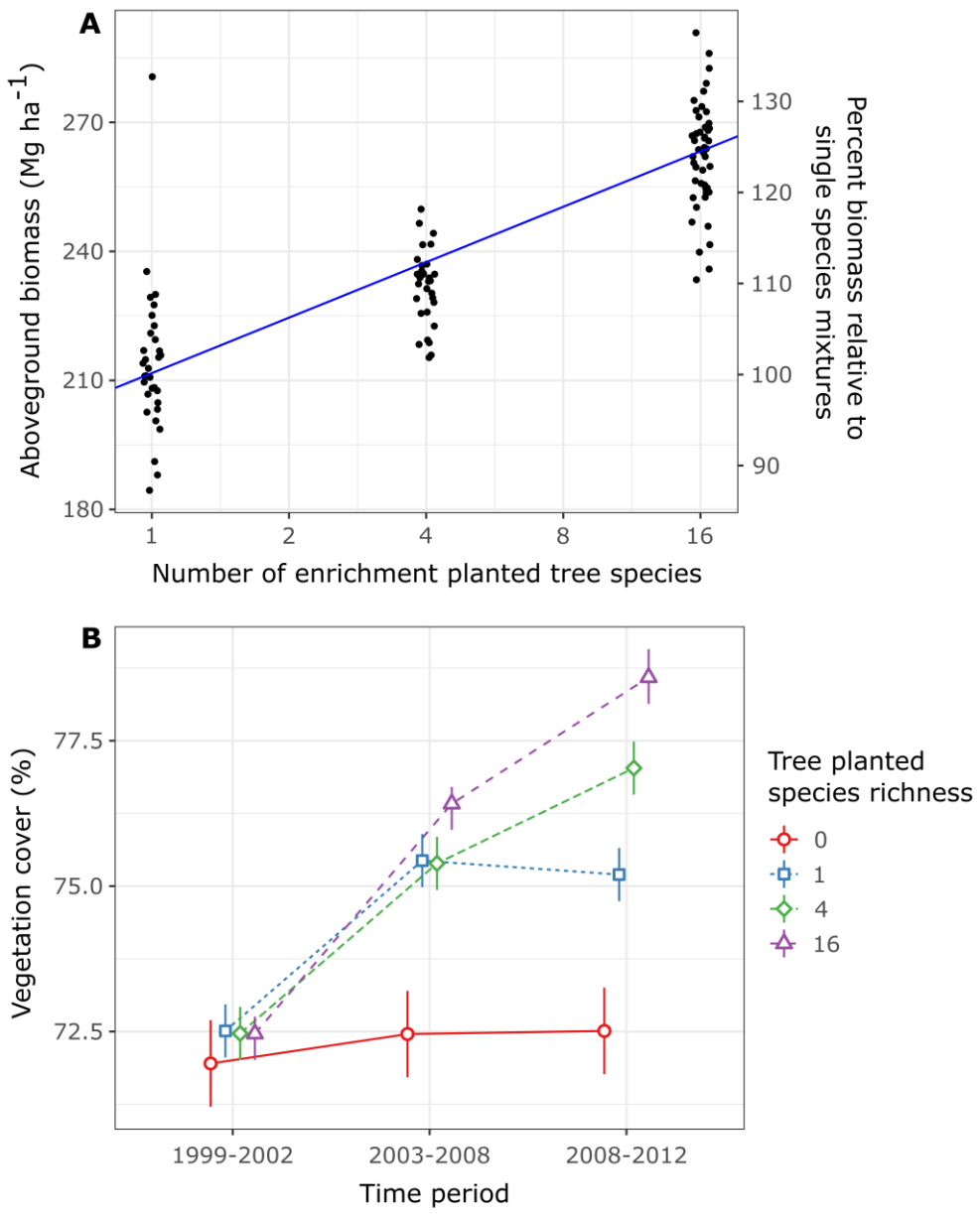
A
Aboveground biomass (Mg ha-1)
270
240
210
180
130
120
110
100
90
Percent biomass relative to single species mixtures
1
2
4
8
16
Number of enrichment planted tree species
B
Vegetation cover (%)
77.5
75.0
72.5
1999-2002
2003-2008
2008-2012
Time period
Tree planted species richness
0
1
4
16

Figure 3.2 Effects of the diversity of enrichment planted trees on aboveground biomass and vegetation cover. (**A**) Estimated aboveground biomass (RapidEye) as a function of the number of enrichment planted tree species a decade after initial planting. The line is the regression slope with the $\log_2$ number of tree species from the mixed-effects model analysis (points jittered to reduce overlap). The second y axis re-expresses aboveground biomass values as percentages of the single-species treatment average. (**B**) Changes in vegetation cover over time as a function of the number of enrichment planted tree species. Estimates of mean cover (with 95% confidence intervals) for the LANDSAT monitoring periods 1999-2002 (prior to planting), 2003-2008 and 2008-2012 for plots enrichment planted with seedlings of 0, 1, 4, or 16 species. Individual species richness mean values are jittered to avoid overlap.

These treatment differences in the RapidEye satellite data from 2012 were supported by estimates of changes in vegetation cover across three LANDSAT monitoring periods covering the preceding decade which show the absence of treatment differences prior to restoration (1999-2002), the emergence of positive effects of enrichment planting (2003-2008) and the subsequent divergence of treatments (2008-2012), with those planted with a greater diversity of tree species showing stronger recovery of vegetation cover (Fig. 3.2B; Table B5).

Our experimental design also contains a factorial manipulation of two other aspects of diversity within the four-species treatment level. Half of the four-species plots were enrichment planted with seedlings of four species from four different genera and half with four species from only two genera. This manipulation of genus diversity is crossed orthogonally with a canopy structural complexity treatment that compares mixtures of four species with a lower or higher diversity of predicted mature tree height that is

intended to produce canopies that are thinner and simpler or thicker and more complex (Table B6). During the initial phase of the experiment, both manipulations produced only slight changes in estimated mean aboveground biomass with enhanced genus diversity and canopy structural complexity (Fig. 3.1; Table B7) that were statistically indistinguishable between treatments (vegetation cover and leaf area index showed qualitatively similar results: Fig. B4, Table B7).

A subset of the plots planted with 16-species were also subjected to an additional treatment that reduced lianas in the tree canopy by stem cutting ('climber cutting'), another management practice often used in these forests (O'Brien et al., 2019). At the time of the RapidEye data snapshot in 2012, the liana removal treatment had only been applied to the southern block, and the treatment had no clear effects on the satellite remote sensing estimates of aboveground biomass (Fig. 3.1), cover, or leaf area index (Fig. B4, Table B8). Previous analysis of longer-term field data extending to 2017 (O'Brien et al., 2019) has demonstrated positive effects of liana removal on the growth and survival of trees, particularly seedlings and saplings in the understory, most likely due to increased light availability (although with potential increased seedling mortality if cutting is followed by drought; O'Brien et al. (2019)). A more complete test of the liana removal treatment will require a longer time series of more detailed field and remote sensing data that can distinguish lianas from dipterocarp tree canopies when monitoring changes in tree canopy cover.

To understand why the manipulation of diversity from 1-16 species had detectable impacts on multiple measures of restoration, while increasing genus diversity of the 4-species mixtures from 2 to 4 genera did not, we calculated quantitative estimates of functional and phylogenetic diversity (FD and PD) for our species mixtures. Levels of

aboveground biomass were positively related to levels of FD and PD across the full species richness gradient from 1 to 16 enrichment planted species but showed only small, statistically indistinguishable increases from the two to four genera treatments and in relation to the manipulation of canopy structural complexity (Fig. 3.3, Table B9). The explanation for the lack of effect of our manipulation of genus diversity probably involves both the small increase in diversity from two to four genera relative to the increase across the whole gradient from 1 to 16 species and the fact that dipterocarp taxonomy when the experiment was designed did not accurately reflect the underlying evolutionary relationships (the genus *Shorea* is now thought to be polyphyletic, although dipterocarp taxonomy remains in flux). The analyses of functional and phylogenetic diversity support this interpretation, showing much smaller increases in diversity within the subset of treatments applied to the four species mixtures than across the entire gradient from 1 to 16 species (Fig. 3.3). These results suggest that the benefits of low levels of diversification in enrichment planting can be increased by the use of seedling mixtures that are more species-rich.

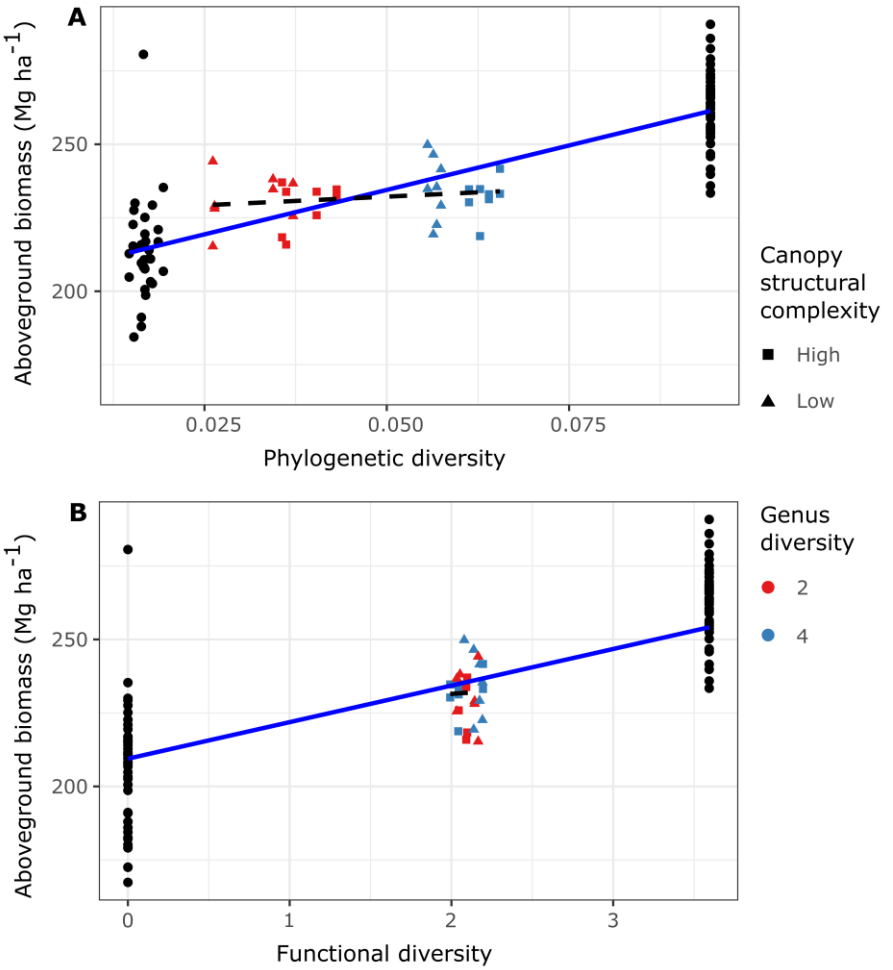

Figure 3.3 Estimated aboveground biomass as a function of phylogenetic and functional diversity. Measures of **(A)** phylogenetic diversity (PD) and (**B**) functional diversity (FD) increase across the full diversity gradient from 1 to 16 species but not in relation to the treatments applied to the subset of four-species plots that manipulate genus diversity (2 *vs* 4 genera: red vs. blue points) and canopy complexity (lower vs higher: squares *vs* triangles). Solid blue lines show the positive relationship between estimated aboveground biomass and PD and FD across the full gradient from 1 to 16 species and dashed lines show the weaker, non-significant relationships for the subset of plots enrichment planted with only four species.

Discussion

Our results suggest that the positive relationship between biodiversity and ecosystem functioning observed in experiments in other ecosystems, including some forests, also applies to the lowland tropical rainforests of SE Asia. While our remote sensing data has limitations (see *Materials and Methods*) the results reported here appear robust since the same qualitative patterns are evident in two different sources of satellite data one of which documents their progressive development over the first decade of the experiment. Comparing these satellite data with field data for a similar period (Tuck et al., 2016) suggests that during the first decade of the experiment, the effects of diversity do not come simply through increased survival or higher trunk-diameter growth rates. Instead, we hypothesize that the differences detected by satellite remote sensing are due to the development of different canopy architectures in monospecific and multi-species mixtures that are not captured by our standard measures of tree size (trunk-diameter at base and breast height). Although there is no effect of our limited manipulation of canopy structural complexity at this stage of our experiment, diversity-dependent growth forms have previously been shown to play a role in generating biodiversity effects in the Wageningen biodiversity experiment (Van Ruijven & Berendse, 2005), and evidence for complementarity among tree crowns has been observed for temperate-boreal species in another tree diversity experiment (Niklaus et al., 2017; Williams et al., 2017) and in a European network of permanent forest plots (Jucker et al., 2015). Testing this hypothesis, and whether differences in canopy responses subsequently feed back to improve survival and diameter and breast height growth in mixtures, will require continued long-term monitoring, ideally including a coordinated combination of field and remote sensing data to provide more detailed measurements of individual tree architecture and canopy structure.

Because biodiversity was manipulated through the enrichment planting of tree seedlings into selectively logged forest vegetation, the Sabah Biodiversity Experiment provides a unique combination of experimental control within a real-world context. Although consistent with the results of the majority of other biodiversity experiments (Loreau et al., 2022), the positive effects of biodiversity reported here (on estimates of forest biomass, cover and leaf area index) contrast with some studies that have failed to find similar relationships in non-experimental settings (Dee et al., 2023). Positive relationships between biodiversity and ecosystem processes like productivity are predicted when low levels of diversity are associated with vacant or under-utilized niches (Loreau & Hector, 2001), as is likely in the selectively logged forests of SE Asia where species of the dominant family of dipterocarp trees have been deliberately harvested. The satellite remote sensing data presented here has limited ability to examine the detailed underlying biological mechanisms. However, this niche packing (niche complementarity) mechanism is supported by the positive effects of functional and phylogenetic diversity seen in our results. In contrast, studies of real-world systems where diversity has not been reduced and where niches are occupied would not necessarily be expected to reveal a positive relationship between biodiversity and ecosystem functioning.

Recent analyses of secondary succession after deforestation provide a mixed picture of recovery rates. Some properties of forests at sites in the Americas and West Africa can recover old growth levels in as little as two decades so long as land-use intensity after deforestation is low (Poorter et al., 2021)**,** while other forests show longer-term reductions in biodiversity and carbon (Moreno-Mateos et al., 2017; Newbold et al., 2015). Our results demonstrate the potential for the recovery of lowland forests in

aseasonal SE Asia to be accelerated by active restoration through enrichment planting, especially with diverse mixtures of native tree species with complementary niches. Differences between our results from the forests of SE Asia and those from some other parts of the tropics may be due to characteristics of the Dipterocarpaceae that have the potential to slow the recovery of these forests, including the absence of a soil seed bank, intermittent mast fruiting and the low dispersal ability of many species (Banin et al., 2014, 2023; Ghazoul, 2016).

These initial results from our project suggest that the positive relationship between biodiversity and ecosystem functioning observed in many other experiments (Loreau et al., 2022) is also found in the lowland tropical rainforests of SE Asia. This emphasizes the need to conserve the diversity of tree species in these forests in order to maintain the ecosystem functions and services that they provide—a matter of urgency given the recent estimate that 70% of Bornean dipterocarp species are threatened with extinction (BGCI, 2021). Our results also suggest that replanting of these secondary forests with diverse mixtures of the native species previously removed by selective logging (Hector et al., 2011) may provide a nature-based solution for their accelerated restoration.

Materials & Methods

Study system

The Sabah Biodiversity Experiment (http://www.sabahbiodiversityexperiment.org/) occupies 500 ha in the southern part of the Malua Forest Reserve, in Sabah, Malaysian Borneo (Fig. B1). The Malua Forest Reserve is an area of approximately 35,000 ha of predominantly selectively logged forest that is publicly owned through Yayasan Sabah (The

Sabah Foundation), which holds a 100-year concession under its goal to increase socioeconomic standards in the state. Within the wider Yayasan Sabah logging concession is the Innoprise-FACE Foundation Rainforest Rehabilitation project (INFAPRO), a 25,000-ha area dedicated to promoting the rehabilitation of forests through large scale enrichment planting within logged areas. To help provide practical recommendations, the Sabah Biodiversity Experiment followed INFAPRO enrichment planting techniques. The region experiences an average temperature of 27°C and an annual rainfall of >3000 mm, distributed between two wet seasons (Lussetti et al., 2016; Marsh & Greer, 1992; Saner, 2009). The Malua Forest Reserve area has been logged twice, once in the 1980s and again in 2007. The 500-ha area of the Sabah Biodiversity Experiment itself was spared the second round of selective logging in 2007 due to the establishment of the experiment in 2002 and has therefore been recovering from the initial round of logging for nearly 40 years. Elevation at this site is under 250 m, with 0-20^{o} range in topography. The pre-logging timber volume of this region has been estimated at 193-221 m^3 ha^{-1}, of which dipterocarps account for the vast majority at 180-216 m^3 ha^{-1} (Hector et al., 2011).

Study species

The 16 species used in this experiment are native species belonging to the Dipterocarpaceae: *Dipterocarpus conformis* Slooten, *Dryobalanops lanceolata* Burck, *Hopea ferruginea* Parij, *Hopea sangal* Korth., *Parashorea malaanonan* (Blanco) Merr., *Parashorea tomentella* (Blanco) Merr., *Shorea argentifolia* Sym., *Shorea beccariana* Bruck, *Shorea faguetiana* Heim., *Shorea gibbosa* Brandis., *Shorea johorensis* Foxw., *Shorea leprosula* Miq., *Shorea macrophylla* Ashton, *Shorea macroptera* King, *Shorea ovalis* Korth., and *Shorea parvifolia* Dyer. Generally, dipterocarps in Sabah are emergent tree species, rarely found 1,200 m above sea level (Whitmore, 1984). They have an array

of characteristics which likely contribute to their dominance in SE Asian forests including their symbiotic ectomycorrhizal associations (Brearley et al., 2016a) and wind-dispersed winged fruits (Numata et al., 2013). Reproduction takes place largely through 'mast fruiting' events that occur between 2-10 years apart, where many or most of the dipterocarp species simultaneously produce fruit. Dipterocarps have recalcitrant seeds (Hautier et al., 2010) and no soil seed bank (Philipson et al., 2020). Instead, successful recruits form a seedling bank which often suffer from heavy herbivory (O'Brien et al., 2015). Dipterocarps dominate the lowland forests of SE Asia in terms of biomass but have been heavily selectively logged (Ashton, 1982).

Experimental design

The Sabah Biodiversity Experiment features several experimental treatments within its replicated, randomised block design. The experiment consists of 124 four-hectare (200 m x 200 m) plots, divided into two blocks separated by an old logging road (60 plots in the north block and 64 to the south). Each plot (apart from the unplanted controls) is enrichment planted with a mixture of seedlings with a controlled species number (richness) and composition. The design ensures at least one replicate plot for each species richness and composition treatment level in each of the two blocks. Each plot contains 20 parallel planting lines, separated by 10 m wide areas of remnant vegetation left after the prior selective logging. Within each line, seedlings were planted with three metres spacing, and planting lines were initially cleared of bamboo, lianas, and shrubs up to a maximum of one metre either side of the line of planted seedlings. The experiment was primarily designed to manipulate the diversity and composition of enrichment planted dipterocarps, but also investigates the forest management practice of liana removal ('climber cutting'). 112 of the plots make up a gradient in the diversity of enrichment planted tree species comprising

mixtures of 1, 4, or 16 species. The remaining 12 plots were left as naturally regenerating unplanted controls (six in each block). The design uses a set of 16 species that were available in the local seedling nursery in sufficient numbers. These 16 species were grown in single-species enrichment planting 'monocultures' and combined together to form enrichment planting 'polycultures' of 4 or 16 species (Table 3.1). The plots enrichment planted with only a single species of dipterocarp allow a comparison of individual species identity effects since each species has a replicate in each of the two blocks (a total of 32 single-species plots).

The intermediate four-species diversity level is comprised of 16 different species compositions that produce two further treatments that are factorially crossed. These two treatments manipulate genus diversity (two levels) and predicted canopy structural complexity (two levels). The genus diversity treatment compares mixtures of four species comprising two or four dipterocarp genera. The canopy structural complexity treatment also features two levels that either combine species with similar predicted mature heights or with a wider range of these predicted values. In total, this factorial manipulation of genus and canopy structural complexity comprises 32 plots (the 2^2 factorial combinations of the 4 treatments, each with 4 replicate species compositions, each replicated in the two blocks) (Table B6).

Sixteen plots of the most diverse (16-species) mixtures underwent two rounds of liana removal (‘climber cutting’), which were compared with 32 plots enrichment planted with the same number of species but without this local climber cutting restoration strategy (O’Brien et al., 2019). Due to practical constraints, these cuttings took place in two stages. In July 2011, 10 plots were cut in the southern block, and in June 2014 these 10 plots, as well as six plots in the northern block, underwent a full round of liana removal. Therefore,

at the time of the RapidEye satellite remote sensing in 2012, only the 10 plots in the southern block had been subjected to the liana removal treatment. Nevertheless, to avoid the risk of missing effects of this treatment, we included the liana removal treatment in our statistical analysis but only as implemented at the time of data collection (i.e., the six plots in the northern block are treated as 16-species plots without liana removal for the purposes of the analyses reported in this article, as opposed to longer-term assessments reported elsewhere that assess the liana removal treatment as applied to all plots (O'Brien et al., 2019)).

In line with standard enrichment planting procedure, after the initial cohort of seedlings were planted (between January 2002 and September 2003), a second cohort was planted to replace initial mortalities (cohort 2 planted September 2008 to August 2009). In combination, the two cohorts planted and surveyed a total of 96,369 dipterocarp seedlings. Further details of the Malua reserve and the Sabah Biodiversity Experiment can be found in previous publications (Hector et al., 2011; Saner et al., 2012; Tuck et al., 2016).

Remote sensing

Landsat Vegetation Continuous Fields (VCF) tree cover, RapidEye and MODIS imagery were selected to estimate variation in canopy structure based on the needs of data accuracy, the size of the study site and plots and the time period of the experiment (Table B10).

Landsat Vegetation Continuous Fields tree cover

The Landsat Continuous Fields tree cover (Landsat tree cover) estimates the percentage of horizontal ground per 30 m pixel which is covered with vegetation of at least 5 m vertical height (Sexton et al., 2013). In this study we refer to Landsat tree cover as Landsat

vegetation cover, as in Sabah virtually all vegetation detected by Landsat is higher than this minimum. The product is derived from all 7 bands of Landsat-5 Thematic Mapper (TM) and/or Landsat Enhanced Thematic Mapper Plus (ETM+). The partial resolution of the Landsat vegetation cover dataset is 30 m, which is appropriate for the Sabah Biodiversity Experiment's plot size of 200 m x 200 m, giving approximately 44 pixels per plot. This dataset contains three epochs, 2000, 2005, and 2010, each consisting of a composite of several years' worth of images in order to minimise the effects of cloud cover. The 2000 epoch consists of data from 1999 to 2002, our 2005 epoch contains years 2003 to 2008, and the 2010 epoch ranges 2008 to 2012.

MODIS MCD15A3H

MODIS MCD15A3H leaf area index is widely used in forest monitoring and exhibits very high accuracy (Brede et al., 2018; Li et al., 2018; Miller et al., 2019). However, the spatial resolution of 500 m means that each plot does not even have a single complete pixel. Instead, a comparison of the entire Sabah Biodiversity Experiment site with the surrounding re-logged area is reported elsewhere (Wu et al., 2020).

RapidEye imagery

This study used a RapidEye satellite image of the Sabah Biodiversity Experiment site for August 2012. RapidEye imagery uses a higher spatial resolution of five metres and a temporal resolution of 5.5 days (Jung-Rothenhäusler et al., 2007; Tyc et al., 2005). The multi-spectral scanner of the RapidEye satellites acquires data in five bands. The blue (0.44-0.51 μm), green (0.52-0.59 μm), red (0.63-0.68 μm), and near-infrared (0.76-0.85 μm) are very similar to that of the Landsat Spectral band equivalents, while also having an additional red-edge band (0.69-0.73 μm). This band allows RapidEye satellite images to

provide greater sensitivity to spatiotemporal changes in vegetation (Chander et al., 2013; Pfeifer et al., 2016).

Vegetation metrics inversion from RapidEye image

A FLAASH atmospheric correction model was applied to the RapidEye image, and vegetation cover, leaf area index, and aboveground biomass were calculated using empirical formulae develop in Pfeifer et al. (Pfeifer et al., 2016) (*Eqs. 1*, *2*, and *3*, respectively), which used RapidEye imagery of the nearby SAFE landscape. Although these equations were not derived for Malua (where the Sabah Biodiversity Experiment is located), the SAFE landscape is close by, and greatly more so than all other options. This provided us with high-resolution (5 m for RapidEye) estimates of leaf area index, vegetation cover and aboveground biomass using a method developed and validated for lowland dipterocarp forests in the same part of Sabah. Further details of the inversion methodology used can be found in the previous publication (Pfeifer et al., 2016).

Eq. 1.

$$\text{Vegetation cover} = 2.66 - 0.66 \cdot Red + 0.3 \cdot RedEdge - 0.08 \cdot NearIR - 0.17 \cdot DissB3 + 1.48 \cdot DissB4 - 0.42 \cdot DissB5$$

Eq. 2.

$$\text{Leaf area index} = 0.9 - 0.59 \cdot Red + 0.41 \cdot RedEdge - 0.11 \cdot NearIR - 0.53 \cdot DissB3 + 1.08 \cdot DissB4 - 0.36 \cdot DissB5$$

Eq. 3.

$$\text{Aboveground biomass} = 19.45 - \exp(MSAV12) - 2.39 \cdot Green + 1.08 \cdot RedEdge + 2.65 \cdot DissB2 - 0.28 \cdot DissB3 + 0.09 \cdot DissB4 - 0.13 \cdot DissB5$$

Where *MSAV12* is the Modified Soil-Adjusted Vegetation Index 2 (Qi et al., 1994). *Green*, *Red*, *RedEdge*, and *NearIR* all correspond to the RapidEye bands of the same name, and *DissB2*, *DissB3*, *DissB4*, and *DissB5* are the grey-level dissimilarities of green band, red band, near-infrared band, and red-edge band, respectively (Gallardo-Cruz et al., 2012). Satellite imagery was pre-processed using ArcGIS and overlaid with the Sabah Biodiversity Experiment plot layout based on GPS coordinates collected for the perimeter of each block.

Landsat and RapidEye cover comparison

While the Landsat and RapidEye estimates of vegetation cover show the same qualitative relationships with the Sabah Biodiversity Experiment treatments, they differ in the absolute value of the estimates. The two measures are positively correlated (Pearson product-moment correlation: 0.389, $P = 7 \times 10^{-6}$, $df = 122$) but the Landsat cover estimates are greater than RapidEye cover estimates (by 9.76 ± 0.371 %). There are at least three non-mutually

exclusive explanations for these differences. First, the spatial resolution of Landsat vegetation cover is much lower than that of RapidEye which means that less information can be extracted. However, it may be more difficult to extract information accurately from high spatial resolution data because more kinds of information can have an influence than with lower spatial resolution, such as topography. Second, the RapidEye data was collected from a single time point in 2012 while the Landsat cover estimates are calculated across a range of years ('epochs': for example, the 2010 epoch cover estimates come from the 2008-2012 period). Third, the calculation method of Landsat vegetation cover is developed for global coverage, while that of RapidEye is developed specifically for Borneo.

Phylogenetic and functional diversity

To investigate the effects of a broader range of aspects of diversity, we calculated measures of both phylogenetic and functional diversity. A phylogenetic tree was created using information specified in two papers detailing recent advancements in dipterocarp phylogeny (Cvetković et al., 2022; Heckenhauer et al., 2017). We calculated Faith's phylogenetic diversity (PD) (Faith, 1992), defined as the total branch length of the minimum spanning tree from each node to the tree root. We also calculated functional diversity (FD), a functional equivalent of Faith's PD, by the sum of branch lengths on a functional dendrogram (Petchey & Gaston, 2002). Out of 46 total trait measurements available we opted *a priori* to use leaf nitrogen, leaf phosphorus, leaf thickness, dry weight, wood density, and specific leaf area as these measurements have been used to estimate FD in the literature most widely (Barragán et al., 2011; Cosset & Edwards, 2017; Laliberté & Legendre, 2010), and there are current associations with the trade-off between rapid resource acquisition and faster growth and enhanced environmental tolerance and reduced growth (Chabot & Hicks, 1982; Wright et al., 2010). This also avoided using a large number

of partially correlated variables. Both PD and FD measurements are dependent on species richness, and so contain information of phylogenetic and functional diversity both among and within species richness levels.

Statistical analysis

We analysed the satellite remote sensing data using linear mixed-effects models that, after performing an initial overall test for the main experimental treatments, then implemented a series of *a priori* contrasts investigating the main comparisons of interest (Fig. B5), specifically:

1. Replanting (enrichment planted plots versus unplanted controls).
2. Species richness of enrichment planted trees (1, 4, or 16 species).
3. Genus diversity (1, 2, 4, or 5 genera across the whole species richness gradient and 2 vs 4 genera for the balanced comparison within the 4-species plots).
4. Predicted canopy structural complexity (mixtures of seedlings of species with similar predicted adult heights versus a greater diversity of adult tree heights).
5. Liana removal ('climber cutting'; 16-species plots with and without lianas removed).

The linear mixed-effects models were implemented using the lme4 (version 1.1-33) (Bates et al., 2015) and lmerTest (version 3.1-3) (Kuznetsova et al., 2017) packages for R (version 4.3.1) (R Core Team, 2023). As would be expected, the RapidEye estimates of vegetation cover, leaf area index, and aboveground biomass values were positively correlated with each other, so to reduce the number of statistical tests, we focused on aboveground biomass when available (RapidEye) and vegetation cover when not (Landsat). Our design contains a ‘nested’ series of comparisons (a two-factor factorial design is contained within the 4-

species enrichment planting treatment level for example), requiring a series of models to address all of the *a priori* contrasts contained within the overall design. We first fitted a model containing a single fixed factor with levels for the main treatments (five levels: unplanted; 1-species, 4-species, and 16-species enrichment planting; 16-species with liana removal) and used a sequential type I analysis of variance with Satterthwaite degrees of freedom to test for differences among treatment levels before proceeding to fit a series of more focused single degree of freedom contrasts to extract point estimates with confidence intervals for the comparisons contained within the overall design (enrichment planted vs. unenriched plots etc.) as specified below (models 1-6). Profile likelihood confidence intervals were generated using the 'confint' function within the 'stats' package (version 4.3.1) (R Core Team, 2023) and were used as they generally outperform standard asymptotic normal confidence intervals for nonlinear models (Royston, 2007). *R2m* and *R2c* values were created using the 'R.squaredGLMM' function within the 'MuMIn' package (version 1.47.5) (Barton, 2023). Note that post-hoc adjustments for multiple comparisons were unnecessary due to the shrinkage involved in the point estimates and predictions produced by the mixed-effects models (Gelman et al., 2012).

Model 3.1 – Initial overall test for differences among levels of the primary treatment:

$$y \sim Treatment + (1|block) + (1|Spp\_comp)$$

Where y is a continuous response variable (either aboveground biomass, vegetation cover or leaf area index), *Treatment* is a fixed factor with five levels (unplanted, 1-species, 4-species, 16-species, and 16-sepcies with climber cutting), *block* is a random factor with 2 levels (northern or southern block), *Spp_comp* is a random factor with 33 levels (16 1-

species compositions, 16 4-species compositions plus the full 16-species mixture), and (1|*Factor*) indicates random intercepts for levels of the factor in question.

Model 3.2 – Effect of planting (enrichment planted plots versus unenriched controls):

$$y \sim Planting + (1|Block) + (1|Spp\_comp)$$

Where y is as in *Model 3.1*, *Planting* is a fixed effect with two levels (enrichment planted vs unplanted). This model fits the *a priori* contrast that compares the unenriched controls with all of the enrichment planted treatment levels combined.

Model 3.3 – Linear (log_2 scale) contrast for the number of enrichment planted species:

$$y \sim \log_2(Spp\_richness) + \text{factor}(Spp\_richness) + Treatment + (1|block) + (1|Spp\_comp),$$
$$\text{subset} = \text{Spp\_richness} > 0$$

Where y is as in *Model 3.1*, log2(*Spp_richness*) is a continuous fixed response variable for the (log2-transformed) number of enrichment planted tree species (1, 4 or 16 species, excluding unplanted controls addressed by *Model 3.2*), species richness as a factor fitted sequentially after the continuous response variable captures deviations from log-linearity (Hector et al., 1999), and *Treatment* subsequently captures the effects of liana removal.

Model 3.4 – Effect of species richness for each of three Landsat time periods:

$$y \sim \text{factor}(Spp\_richness) * Year + (1|block) + (1|Spp\_comp) + (1|Plot)$$

Where y was Landsat estimated percent canopy cover (only), *Year* is a fixed factor with 3 levels and the asterisk (*) indicates an interaction between variables. Since there are three

repeated measures per plot, one for each Landsat time period, we also added a random factor with a level for each plot (124 levels).

Model 3.5 – Effect of climber cutting, genus diversity, and liana removal:

$$y \sim \text{factor}(Spp\_richness) + Gen\_div + Canopy\_type + Climber\_cutting + (1|block) + (1|Spp\_comp)$$

Where y is as in *Model 3.1*, *Spp_richness* is a factor with three levels (1, 4, 16), *Gen_div* is a fixed factor with 2 levels (2 vs. 4 genera), *Canopy_type* is a fixed factor with 2 levels (low vs high canopy structural complexity, and *Climber_cutting* is a fixed factor with 2 levels (liana removed vs. not),

Model 3.6 – Effect of phylogenetic/functional diversity

$$y \sim Diversity + (1|block) + (1|Spp\_comp)$$

Where *Diversity* is either phylogenetic or functional diversity, each fitted as a continuous response variable. To identify an effect within just the four-species plots, this model was run with all data initially, and then subsequently with a subset of only 4-species plots. As these measures of FD and PD were not controlled components of the original experimental manipulation, other fixed effects addressed in previous models have been omitted for simplicity (an approach which should be conservative as the variation explained by the omitted variables ends up in the error terms).

Acknowledgements

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Chapter 4: The impact of surrounding mature trees on dipterocarp seedling growth and survival

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This chapter has been written to the style requirements of *Ecology and Evolution* and will be submitted to this journal.

Authors' contributions: Conceptualisation: AH, CJM, ECT, and RV. Data curation: CJM and RV. Formal analysis: CJM and RV. Funding acquisition: AH, CJM, and RV. Investigation: JK, CJM, RM, MS, and RV. Project administration: MJOB, EG, AH, and MS. Supervision: EFMC, AH, and ECT. Visualisation: CJM and RV. Writing – original draft: RV. Writing – review & editing: All authors.

Abstract

Old-growth Southeast Asian forests are dominated by the Dipterocarpaceae, which are targeted by selective logging. Due to several traits (intermittent mast fruiting, limited dispersal, and recalcitrant seeds that form no seed bank), they can have poor natural regeneration rates in some selectively logged forests. Enrichment planting is commonly used to overcome recruitment limitations and increase restoration success. However, it is still unclear what factors influence the success rate of planted seedlings, including the surrounding tree matrix and local neighbourhood characteristics.

Here, we examine the growth and survival of 721 enrichment line-planted seedlings within 24 plots of the selectively-logged forest of the Sabah Biodiversity Experiment in Malaysian Borneo, in relation to their species identity and local neighbourhoods, including the traits of more than 5,000 surrounding trees. We mapped the spatial location, size, and species identity of surrounding matrix trees (> 10 cm diameter at breast height) within 10 m of focal planted seedlings in 2012 and 2015. We developed statistical models to determine levels of density-dependence (in terms of canopy openness and total basal area of surrounding matrix trees), asymmetric competition with naturally occurring trees (the proportion of total basal area within 10 m belonging to the largest tree), and confamilial density-dependence (the proportion of total basal area within 10 m belonging to dipterocarps) for each seedling.

We found that the survival and growth rates of enrichment planted seedlings were positively associated with canopy openness. We also observed that seedling survival was positively associated with the total basal area of the surrounding tree matrix, a counterintuitive result. No correlation between canopy openness and total surrounding

basal area was identified. These results were consistent between planting cohorts. This suggests that established trees may bring some benefits to planted seedlings, for example by reducing the risk of extreme temperatures and humidity, ultimately reducing drought-related mortality risk. However, other explanations exist, such as the benefits of established mycorrhizal networks or high levels of established tree biomass reflecting generally more favourable growing conditions. Forest management practice may increase planting success and cost-effectiveness through targeted planting in areas with moderate canopy openness. However, it remains to be seen whether higher seedling establishment results in eventual higher mature tree density.

Introduction

The tropical lowland forests of Southeast Asia are dominated by the Dipterocarpaceae (often referred to as dipterocarps), which make up over 50% of forest basal area and 60% of standing volume (Sist & Saridan, 1999). These regions are further regarded as carbon hotspots. For instance, undisturbed lowland forests of Borneo exhibit aboveground biomass values approximately 60% greater than the Amazon (457.1 Mg ha^{-1} vs 288.6 Mg ha^{-1}; Slik et al., 2010). Dipterocarp physical traits, specifically hardwood durability, straight and tall trunks, and attractive appearance, have resulted in the extensive extraction of mature dipterocarps across Southeast Asia (Estoque et al., 2019). Selective logging has been shown to remove between 55-66% of dipterocarp stock (individuals above 10 cm diameter at breast height (DBH); Saner et al., 2012), and this basal area is often initially replaced by fast-growing pioneer species that contribute substantially less to a forest's carbon stock (Saner et al., 2012).

The life history of the Dipterocarpaceae hinders the sustainability of these logging methods. These trees undergo irregular 'mast fruiting' events every two to 10 years (Ashton et al., 1988). Dipterocarp seeds are often relatively large and often have limited dispersal (despite usually being winged) and are also recalcitrant, forming a seedling bank instead of a soil seed bank (Umarani et al., 2015). Under ideal conditions, seeds germinate immediately but are known to suffer high mortality in open, dry, inundated, or otherwise disturbed areas (Appanah & Turnbull, 1998). Logging can cause extensive damage to seedling banks directly but may also indirectly harm seedling survival by reducing soil quality through compaction (Hattori et al., 2013; Nussbaum et al., 1995). The decline of aboveground biomass and changes in tree communities via disturbance can also negatively impact soil physiochemical composition, particularly in terms of soil carbon, nitrogen, and phosphorus

(Ngaba et al., 2020; Xu et al., 2018). Taken together, these characteristics may limit the ability of dipterocarps to recover following selective logging.

Regeneration of this high-value timber is environmentally and economically critical for countries with these resources. Reduced-impact logging is a set of common management techniques that aim to maintain the silvicultural value of forests by reducing the negative effects of harvesting (Putz et al., 2008). An associated technique aimed at accelerating recovery is the enrichment planting of the existing seedling bank with additional nursery-grown stock. This is commonly done by planting along cleared lines through a forest within the pre-existing matrix of seedlings and mature trees. It is an expensive process, costing between US $1500 and $2500 ha^{-1} in lowland Sabah (Philipson et al., 2020), and so it is important that this restoration method provides tangible benefits.

The effectiveness of such initiatives is based on the survival and growth of planted seedlings until they reach maturity. Therefore, predicting the outcome of enrichment planting is important for communities that depend on these forest products. Recent studies have investigated the response of dipterocarp seedling survival and growth to factors including water availability and frequency (O'Brien et al., 2013, 2015), light availability (Philipson et al., 2012), and ectomycorrhizal associations (Saner et al., 2011). Studies have also investigated more applied factors, such as the diversity of species used in enrichment planting (Tuck et al., 2016; Veryard et al., 2023) and the effect of liana removal (O'Brien et al., 2019). However, many studies have been conducted in easily controllable environments like shade houses (e.g., Ashton et al., 2006), which make experimental manipulations more feasible but exclude broader effects of the natural environment. Therefore, factors impacting seedling survival and growth need to be better understood within the context of the ecosystem where seedlings are planted.

Three key factors define the matrix surrounding planted seedlings: the number of surrounding trees, the size of these trees, and their species identity. These factors are a consequence of the logging history the forest has experienced. In relatively undisturbed areas, we might expect fewer yet larger trees, which indicates that mature canopy trees are dominant. Conversely, in an area of extensive selective logging, we might expect a greater number of small trees, mostly pioneer species, to undergo competitive release. We would also expect a higher proportion of non-dipterocarps due to the selective removal of commercially valuable dipterocarp species during logging and subsequent colonisation of pioneer non-dipterocarp species. Although some non-dipterocarp species are also highly valued and have experienced extraction in dipterocarp-dominated forests (Hayward et al., 2021), most timber harvesting within dipterocarp forests is driven by the extraction of the Dipterocarpaceae.

The extent and type of competition between planted seedlings and the surrounding matrix should be related to the number of surrounding trees, the size of these trees, and their species identity. Generally, increasing the surrounding basal area results in greater local competition and reduced seedling growth and survival (Kobe & Vriesendorp, 2011; Peters, 2003). Larger trees can compete strongly and asymmetrically with seedlings, often for light (Potvin & Dutilleul, 2009; Velázquez & Wiegand, 2020). In the tropics, this direct competition for resources may act alongside more indirect effects (Bachelot et al., 2020). Specifically, higher conspecific density can increase mortality levels, as species-specific pests and pathogens can more easily find appropriate hosts (Connell, 1971; Janzen, 1970; Oshima et al., 2015). There is some evidence that density-dependent mortality, if present, is most substantial in the tropics up to 10 m from adult trees (Murphy et al., 2017).

In contrast, positive density-dependent effects can arise through facilitation, where larger trees create more suitable microclimates (Bruno et al., 2003). For instance, an established canopy can reduce extreme variations in temperature and humidity, reducing the vapour-pressure deficit seedlings experience and potentially resulting in reduced water stress and drought-related mortality in seedlings (Adams et al., 2017). Young and recently enrichment planted seedlings are expected to benefit most from such canopy-related water stress mitigation, as they are smaller and less resistant to environmental perturbations (Turner, 2001). An increased proportion of conspecifics could also reduce local mortality through predator satiation (Iku et al., 2017), especially given that up to 92% of dipterocarp species have been observed masting fruit simultaneously (Curran & Leighton, 2000). However, due to the irregular fruiting times in dipterocarp forests, identifying a clear case of predator satiation can be challenging (Curran & Leighton, 2000).

To further complicate analyses, the type of competition observed between enrichment planted seedlings and the surrounding matrix may depend on interactions between these main factors. For a given extent of asymmetric competition or confamilial density-dependence, an increase in the total basal area of the surrounding matrix may increase competition non-linearly. For instance, if relatively few trees are nearby due to intensive logging, a few larger trees may create a more favourable local climate. In contrast, at high relative densities, benefits from an additional increase in the total matrix basal area could be overshadowed by increased competition. Similarly, predator satiation may only occur beyond a critical density of surrounding dipterocarps, so positive confamilial density-dependence may occur up to a threshold, after which increasing competition leads to increased negative interactions. Indeed, the existing literature is not clear on the effects of any one factor in isolation (e.g., Kobe & Vriesendorp, 2011; Lebrija-Trejos et al., 2014;

Lieberman et al., 1985; Peters, 2003; Pretzsch & Biber, 2010; Rozendaal et al., 2020). The underlying causes of tree mortality in the tropics are still widely debated (McDowell et al., 2018), and determining if the existing matrix influences the growth and survival of enrichment planted seedlings is difficult to infer if not tested directly and experimentally.

This study investigated how the survival and growth of 721 enrichment planted seedlings from 16 dipterocarp species were affected by the surrounding tree matrix in Sabah, Malaysian Borneo. We mapped the tree size, identity, and spatial location of 5,068 surrounding matrix trees with DBH > 10 cm within 10 m of each planted seedling. We then developed models to estimate the effects of light availability, the degree of local competition from the matrix (the basal area of the surrounding tree matrix), asymmetric competition (the proportion of basal area belonging to the largest tree, hereafter referred to as *proportion largest surrounding tree*), and confamilial density-dependence (the proportion of basal area belonging to dipterocarps, hereafter referred to as *proportion dipterocarps*) that was experienced by each enrichment planted seedling. We investigated potential relationships between the growth and survival of enrichment planted seedlings and these measures of local competition, including possible interactions between the basal area of the surrounding matrix and the proportion largest surrounding tree and the proportion dipterocarps.

Materials and methods

Study site

The Sabah Biodiversity Experiment (Hector et al., 2011; Tuck et al., 2016; Veryard et al., 2023a) occupies an area of 500 hectares within the southern section of the 35,000 ha Malua Forest Reserve in Sabah, Malaysian Borneo (Fig. 4.1). This selectively logged forest is

publicly owned and managed through Yayasan Sabah (The Sabah Foundation), which holds a 100-year concession with the aim to increase socioeconomic standards within Sabah. Initial logging occurred between 1984 and 1986 and yielded an estimated pre-logging timber volume between 193-221 $m^3 ha^{-1}$, predominantly composed of dipterocarps at 180-216 $m^3 ha^{-1}$ (Saner et al., 2012). Total timber production in Sabah has decreased since 1978, from a peak of 13 million m^3 (Reynolds et al., 2011) to, most recently, 1.02 million m^3 in 2022 (Sabah Forestry Department, 2022). The mean annual rainfall, recorded in the nearby Danum Valley from 1986 to 2010, averaged 2848.5 (± 94.0 *se*) mm, with monthly means fluctuating between 119.5 mm (April) and 302 mm (January and October).

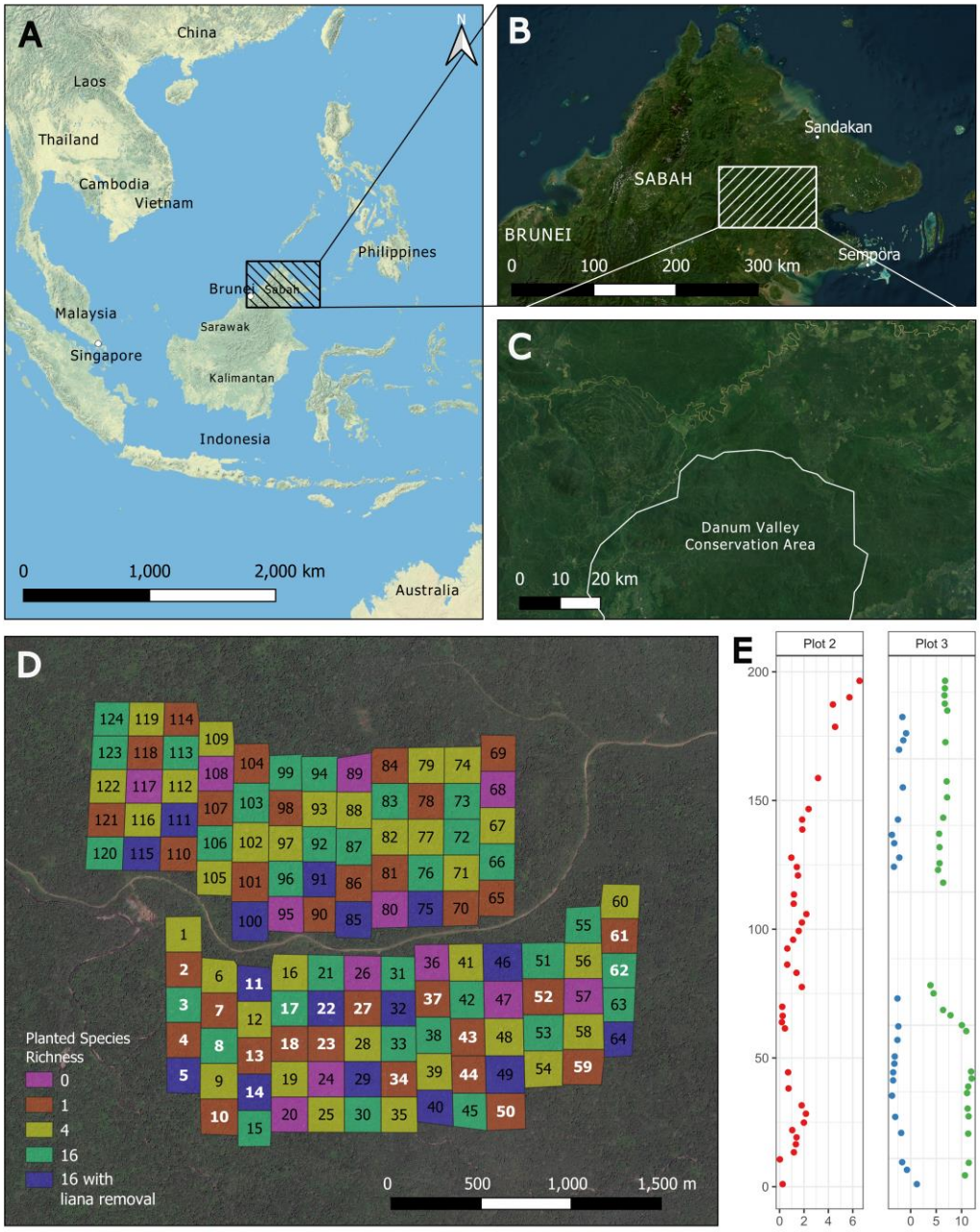
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Figure 4.1 Location and design of the Sabah Biodiversity Experiment. (**A**) The Sabah Biodiversity Experiment is located within Sabah, Malaysian Borneo. (**B** to **C**) The experimental site exists within the Malua Forest Reserve, just north of the Danum Valley Conservation Area and approximately 70 km west of the town of Lahad Datu. (**D**) The Sabah Biodiversity Experiment consists of 124 four-hectare plots split into two blocks separated by a logging road. Each plot has one of five possible treatments applied – unplanted controls (*0*), sites planted with either one, four, or 16 species (*1*, *4*, and *16*, respectively), and 16-species plots which have also undergone an additional treatment of liana removal (*16 with liana removal*). Plot treatment is indicated in the legend by colour. Plots with bold white labels are included in this analysis. (**E**) From each plot, either one (for single-species plots) or two (for 16-species plots) planting lines were selected for mapping. Plots show the relative locations of each tree along each planting line for a representative single-species (plot 2) and 16-species plot (plot 3). Points indicate the locations of planted seedlings along the planting lines, and axes provide relative distance (m) within each plot.

Study species

A total of 16 species from the Dipterocarpaceae were included in this experiment (Table C1 in Appendix C). These species were chosen because they represent those found in the surrounding forest, cover a range of traits and ecological strategies, and were available in sufficient quantities at the time of planting (Tuck et al., 2016).

Experimental design

The Sabah Biodiversity Experiment has a randomised block design in which individual seedlings are positioned along planting lines cleared within plots (for comparison with

unplanted controls). The experiment encompasses 124 plots (Fig. 4.1D), each measuring four hectares (200 × 200 m). Plots are grouped into two blocks, north and south of an old logging road (60 plots in the northern and 64 in the southern blocks). One hundred and twelve of these plots were randomly assigned to one of four treatments: single-species mixtures with one dipterocarp tree species planted (n = 32), four-species mixtures (n = 32), 16-species mixtures (n = 36), and 16-species mixtures which have also undergone enhanced climber cutting (n = 12), where all lianas were removed from the plot. The remaining 12 plots were left as unplanted, naturally regenerating controls.

Within each non-control plot, 20 parallel planting lines were cleared at 10 m intervals. In enrichment planted plots, seedlings were planted with three metres of separation along each planting line. After establishment, vegetation was cleared occasionally one metre on either side of each line in the years following. In line with standard enrichment planting procedures, a first cohort of seedlings was planted (between July 2002 and September 2003), followed by monitoring and planting of a second cohort to replace mortality that had occurred (second cohort planting carried out from September 2008 to August 2009. For example, within a subset of plots (3, 5, 8, 11, 14, and 17), approximately 44% of planting positions were replanted with a replacement seedling.

The large size (500 ha) of the Sabah Biodiversity Experiment made it necessary to sample a subsection of the experiment. Here, we examined 24 plots, consisting of 16 plots that were enrichment planted with a single species (one plot for each species planted in the Sabah Biodiversity Experiment) and eight 16-species plots. One planting line was mapped for single-species plots, and two adjacent lines were mapped for 16-species plots to allow sufficient measurements from seedlings of each of the 16 species given the lower densities

for each species in the higher diversity plots. In total, 853 enrichment planted seedlings were sampled across all planting lines.

Mapping of seedlings and matrix trees

For each planting line surveyed, the location and size all surviving enrichment planted seedlings were spatially mapped along with all naturally occurring trees (> 10 cm DBH) within a 10 m radius. Basal area was measured for all enrichment planted seedlings and DBH was measured for naturally occurring trees. The choice of a 10 m radius aligns with the methodologies of comparable studies (e.g., Fortunel et al., 2016). The mapping process was carried out using a ground-based laser Field-Map system (Institute of Forest Ecosystem Research (IFER), Ltd., Jílové u Prahy, Czech Republic; Hédl et al., 2009) to obtain relative x, y, and z coordinates for each tree. The FieldMap system combines an Impulse 200 Standard laser rangefinder (equipped with a tilt sensor for vertical angle measurements), a MapStar Module II electronic compass (both from Laser Technology Inc., Colorado, USA), and the specialised mapping software Field-Map v.11 (IFER, Czech Republic). Two initial rounds of mapping were undertaken in December 2012 and May 2015. Percentage canopy openness was recorded above each seedling using a canopy densiometer (Lemmon, 1956) in four cardinal directions from January 2013 to January 2014.

Vegetation matrix variable calculations

For each planted seedling, we quantified four qualities of the surrounding vegetation matrix, defined as the naturally occurring (i.e., unplanted) trees within 10 m of each seedling, that could impact seedling survival and growth. First, we quantified light availability, measured as the level of canopy openness above each seedling. Second, the

degree of local competition on enrichment planted seedlings was calculated as the total basal area of all surrounding matrix trees. Third, confamilial density-dependence was calculated as the proportion of the total basal area that belonged to dipterocarps surrounding each seedling. Finally, we calculated the proportion of the total surrounding basal area that belonged to the single largest tree within 10 m of a planted seedling as a measure of asymmetric competition.

Statistical analysis

We used generalised linear mixed-effects modelling to assess the impact of the estimated matrix parameters and their potential interactions on the growth and survival of planted seedlings between the 2012 and 2015 sampling periods. Of the 853 enrichment planted seedlings sampled, those with incomplete data across variables were excluded (n = 132) to yield 721 seedlings for analysis. Growth was calculated as relative growth rate (RGR), defined as the difference in log-transformed basal diameter (mm) over time (years). Canopy openness and total basal area were log-transformed, and the latter was centred (each value of total surrounding basal area had the mean total surrounding basal area subtracted from it, effectively making the new mean total surrounding basal area value zero). This was done to facilitate model fitting. Our initial model formulae (Wilkinson & Rogers, 1973) for survival (*Model 4.1*) and growth (*Model 4.2*) were:

Model 4.1 – Initial model of survival with a binomial variance function

$$cohort + richness + openness + p\_dip + p\_ba\_max + ba\_total +$$
$$ba\_total{:}p\_dip + ba\_total{:}p\_ba\_max +$$
$$(1|plot) + (1|species)$$

Where *cohort* is a fixed factor of two levels (cohorts 1 or 2), *richness* is a factor with two levels (single-species or 16-species mixtures), and o*penness* (canopy openness), *p_dip* (proportion dipterocarps), *p_ba_max* (proportion largest surrounding tree), and *ba_total* (total basal area of all trees) are covariates. Two variables joined with a colon indicate an interaction (e.g., *ba_total:p_dip*), and (1|*Factor*) indicates random intercepts for levels of the factor specified.

Model 4.2 – Initial model of growth with Gaussian variance function

$$cohort + richness + openness + p\_dip + p\_ba\_max + ba\_total +$$
$$ba\_total{:}p\_dip + ba\_total{:}p\_ba\_max +$$
$$(1|plot) + (1|species)$$

Where variables are the same as for *Model 4.1*, only individuals alive as of the 2015 census were retained for the growth modelling steps as only they had values for their basal diameters in 2015 and could have RGR estimates calculated.

Seedling cohort (1 or 2) was included in the analysis of both survival and growth to assess whether the cohorts behaved similarly or differently and to account for this aspect of our experimental design. Seedling plot identity (*plot*) and *species* were fitted with random intercepts to account for the experimental design. Because we only measured one single-species plot for each species (which gives reduced information on individual species responses), and earlier work on the same 16 species identified no species-specific responses to survival and growth (Philipson et al., 2014), we decided to treat species identity as a random (rather than fixed) effect. Initial interactions between the total basal area and both the proportion largest surrounding tree and proportion dipterocarps were fitted to investigate if the impacts of confamilial density-dependence and asymmetric competition,

respectively, on planted seedling growth or survival were dependent on the total basal area of surrounding matrix trees (local competition).

We might have expected nonlinear relationships for some of our covariates, such as canopy openness. However, for the range of values we explored, preliminary plots suggested relationships were approximately linear. We used Pearson's product-moment correlation coefficients to measure the correlation between combinations of canopy openness (*openness)*, total surrounding matrix area (*ba_total*), proportion largest surrounding tree (*p_ba_max*), and proportion dipterocarps (*p_dip*), and also to detect potential multicollinearity. Confidence intervals were estimated using bootstrapping, and we used the Bayesian information criterion (BIC) for model comparison (Schwarz, 1978). All data analysis was done in R (version 4.3.1; R Core Team, 2023) using the 'lme4' package (version 1.1-34; Bates et al., 2015).

Results

Surrounding matrix trees

In 2012, a total of 5,068 trees from the selectively logged matrix were measured. Of these, 733 were identified as dipterocarps (14.5%), and the remaining 4,335 were classified as non-dipterocarps. Among naturally occurring trees, dipterocarps were generally larger (median DBH = 20.5 cm; mean = 30.3 cm; maximum = 224.0 cm; Fig. 4.2A) compared to non-dipterocarps (median DBH = 16.5 cm; mean = 22.4 cm; maximum = 152.5 cm; Fig. 4.2B). The surrounding Dipterocarpaceae included some large trees that likely evaded logging but at lower densities than non-dipterocarps. The total area surveyed around planted seedlings was 12.4 ha, which resulted in an estimated basal area of 7.06 m^2 ha^{-1} for dipterocarps and 20.3 m^2 ha^{-1} for non-dipterocarps. These values are consistent with other

estimations made at the Sabah Biodiversity Experiment (Saner et al., 2012). Generally, naturally occurring dipterocarps were larger (median DBH = 16.5 cm; mean = 22.4 cm; range = 10.0 to 152.5 cm; Fig. 4.2E) than the enrichment planted dipterocarp seedlings (median basal diameter = 0.9 cm; mean = 1.5 cm; range = 0.2 to 15.4 cm; Fig. 4.2F).

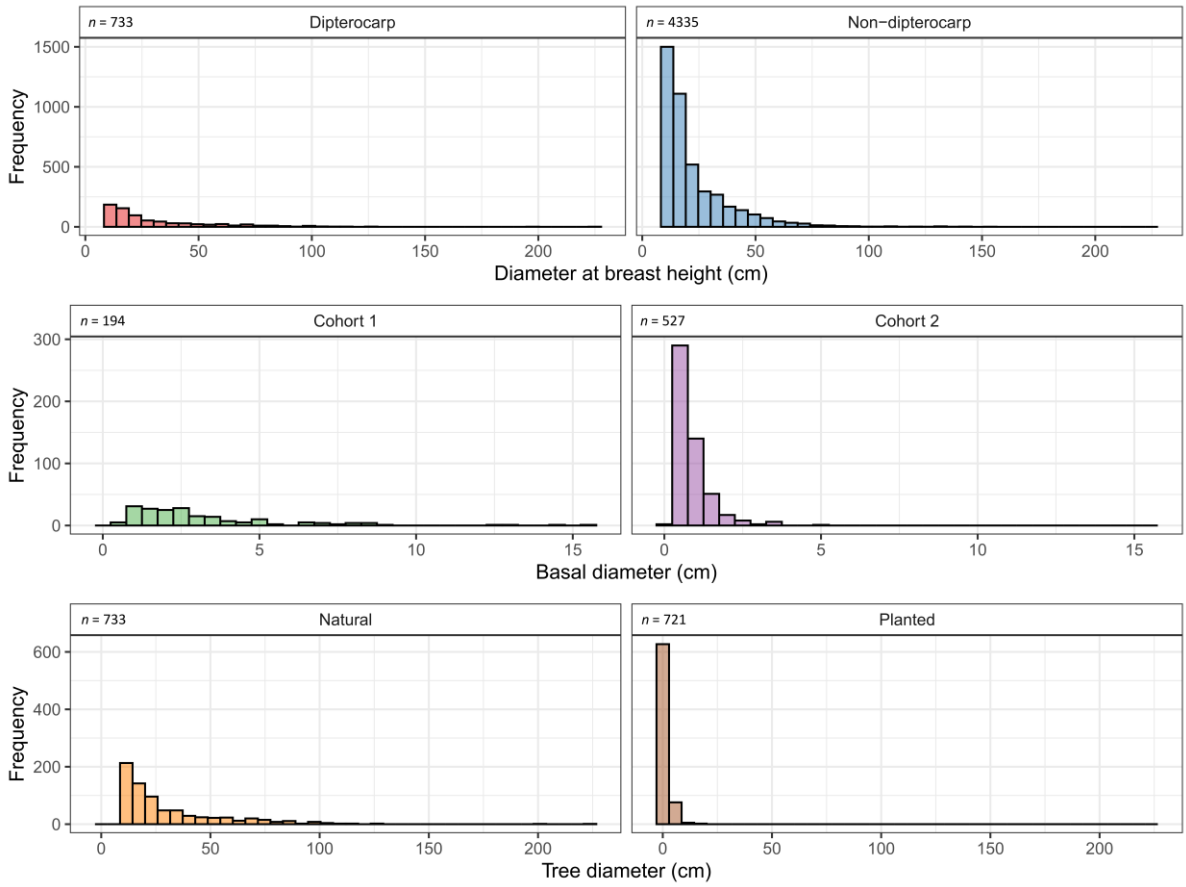

Figure 4.2 Comparisons of the surrounding dipterocarp and non-dipterocarp tree matrix, planted cohorts, and planted and naturally occurring dipterocarp tree diameters. Number of individuals that make up each plot (*n*) is indicated in the top-left corner of each plot. Top: Naturally occurring (**A**) dipterocarp and (**B**) non-dipterocarp trees within a 10 m radius of all planted seedlings, categorised by their DBH (cm). Middle: Planted seedlings from (**C**) cohort 1 and (**D**) cohort 2, categorised by their basal diameter (cm). Bottom: (**E**) Naturally occurring and (**F**) enrichment planted dipterocarps, categorised by DBH (cm) and basal area (cm) for naturally occurring and enrichment planted dipterocarps, respectively. Fig. 4.2E is equivalent to Fig. 4.2A, and Fig. 4.2F is the sum of Figs 4.2C and 4.2D. Note that naturally occurring trees (>10 cm DBH) were surveyed at breast height, whilst enrichment planted trees were surveyed at the base (basal diameter).

A range of values for each covariate was observed (Table C2). Notably, canopy openness values were generally low (median canopy openness = 6.75%, 1st quartile (Q1) = 5.50%, 3rd quartile (Q3) = 8.75%) as were values for the proportion of surrounding basal area belonging to dipterocarps (median proportion = 0.11, Q1 = 0.007, Q3 = 0.42), and median surrounding basal area within 10 m of each enrichment planted seedling was approximately 0.940 m^2 (Q1 = 0.596 m^2, Q3 = 1.31 m^2).

Of variables included in the initial model for survival (*Model 4.1*), cohort, canopy openness, and total surrounding matrix basal area were retained whilst proportion dipterocarps (estimated change in log-odds of survival per unit increase = -0.00049, 95% CI = -0.0078 to 0.0068) and proportion largest surrounding tree (0.732, 95% CI = -0.499 to 1.962) were excluded. Of the variables included in our initial growth model (*Model 4.2*), cohort and canopy openness were retained and total basal area (estimated slope = 0.0088, 95% CI = -0.0082 to 0.026), proportion dipterocarps (-0.00034, 95% CI = -0.00072 to 0.000039), and proportion largest surrounding tree (0.0322, 95% CI = -0.030 to 0.094) were excluded. Whilst random effects were retained across both models, variance components were small compared to the residual error.

Size and survival of planted cohorts

In total, from the 721 seedlings present in 2012, 544 seedlings (75.5%) survived while 177 (24.5%) died within the period to 2015. Cohort 1 experienced a higher (2012-15) survival rate than cohort 2: 194 seedlings from cohort 1 were surveyed and experienced an 87.1% survival rate (169 seedlings), whilst cohort 2 had a lower overall survival rate 71.2% (375 seedlings) of the total 527 seedlings surveyed. As anticipated, the older first cohort seedlings (planted 2002-03) generally exhibited larger sizes (median = 24.5 mm; mean =

31.6 mm; range = 3-154 mm; Fig. 4.2C) compared to the younger (planted 2009-10) second cohort seedlings (median = 7.0 mm; mean = 8.7 mm; range = 2-48 mm; Fig. 4.2D), although there were several instances of overlap. Some first cohort seedlings had attained large basal diameters (maximum = 168 mm), although the majority remained smaller.

Summary statistics of the raw data showed that surviving seedlings exhibited slightly larger average sizes in 2012 compared to those that subsequently died by 2015 (Fig. 4.3), both for cohort 1 (2012 mean basal diameter ± *SEM* for survived vs died: 32.5 ± 2.01 mm survived vs 25.6 ± 3.59 mm died) and cohort 2 (9.3 ± 0.31 mm survived vs 7.3 ± 0.44 mm died). Growth rates between 2012 and 2015 were highly variable across both cohorts but were slightly higher in cohort 2 (median RGR between 2012 and 2015 = 0.097 mm mm^{-1} $year^{-1}$, mean = 0.11 mm mm^{-1} $year^{-1}$, range = -0.28 to 0.51 mm mm^{-1} $year^{-1}$) than in cohort 1 (median = 0.077 mm mm^{-1} $year^{-1}$, mean = 0.084 mm mm^{-1} $year^{-1}$, range = -0.42 to 0.74 mm mm^{-1} $year^{-1}$; Fig. C1 in Appendix C).

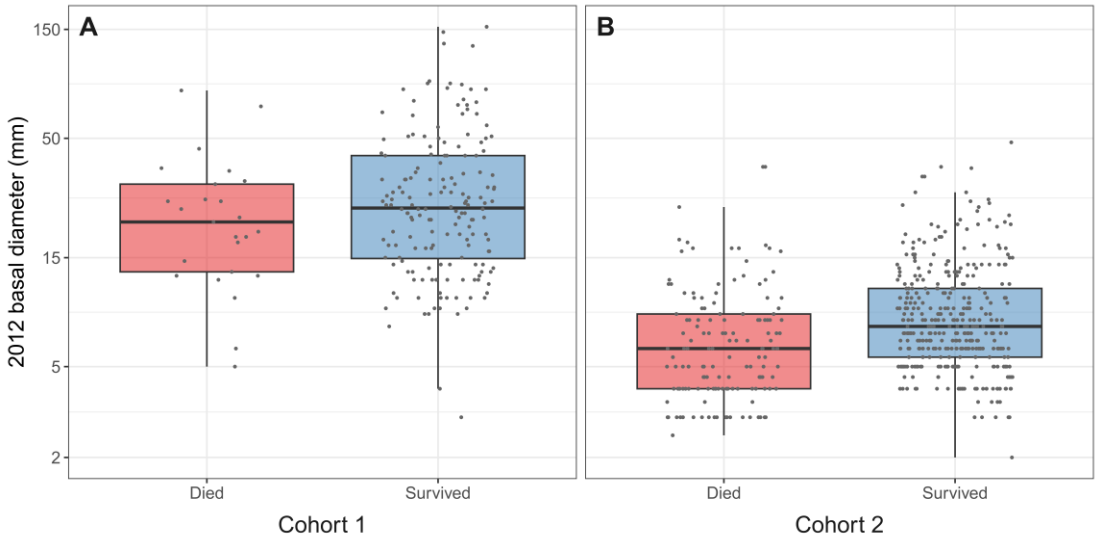

Figure 4.3 Seedling survival in 2015 as a function of size in 2012 (basal diameter, mm) for cohorts 1 (**A**) and 2 (**B**). The basal diameter (mm) of planted seedlings in 2012 belonging to the 1st and 2nd cohort seedlings that survived or died between the 2012 and 2015 measurements. Points represent individual seedling values; whiskers extend 1.5 times the interquartile range (boxes). Thick horizontal lines indicate median values. Note that basal diameter is plotted on a log axis.

Effect of light availability, local competition, confamilial density-dependence and asymmetric competition

Models estimated that older seedlings from cohort 1 exhibited higher survival rates compared to younger seedlings from cohort 2 (mean survival rate with 95% CI at mean openness and total basal area values: cohort 1 = 0.87, 0.82-0.92; cohort 2 = 0.72, 0.68-0.77). Conversely, seedlings from cohort 2 demonstrated higher growth rates (mean RGR and 95% CI at mean openness value: cohort 1 = 0.076 mm mm^{-1} $year^{-1}$, 0.047-0.100; cohort 2 = 0.117 mm mm^{-1} $year^{-1}$, 0.099-0.135).

Light availability, as measured through canopy openness, positively affected survival (Fig. 4.4A) and growth (Fig. 4.4B). Across our observed range of canopy openness scores, predicted survival and RGR increased from approximately 0.46 to 0.74 and 0.022 to 0.236 mm mm^{-1} $year^{-1}$, respectively. Local competition, the basal area of surrounding matrix trees, had a positive log-linear effect on the survival of planted seedlings (Fig. 4.5), with predicted survival increasing from 0.42 to 0.85 over the observed range of total surrounding basal area values. No effect of basal area was identified for seedling RGR. No relationship was identified between either seedling survival or growth and the proportion of the surrounding matrix belonging to either dipterocarps (confamilial competition) or the largest individual tree (asymmetric density-dependence). Further, no interaction between the total matrix basal area and the proportion dipterocarps, proportion largest surrounding tree, and canopy openness were identified for the survival or RGR of planted trees. Overall, our models explained a relatively small amount of total variance, with marginal R squared estimates of 0.079 and 0.085 for our final survival and growth models, respectively.

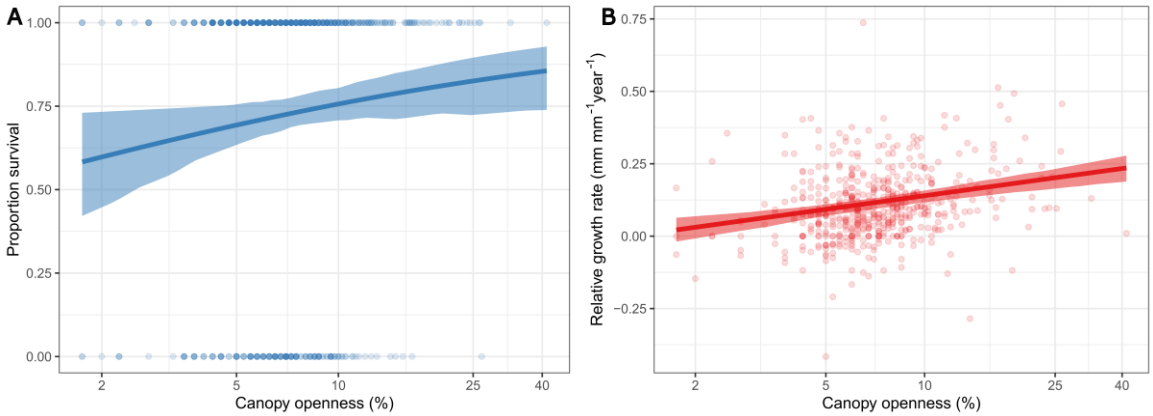

Figure 4.4 Estimated (**A**) survival and (**B**) RGR of dipterocarp seedlings in relation to canopy openness. Both predictions are made for cohort 2 seedlings, as they represent 527 of our 721 total seedlings and the observed relationship is conserved between cohorts (Fig. C2). All other covariates are held at their mean values. Coloured polygons represent the 95% confidence interval obtained through bootstrapping, and points depict the observed survival and RGR for individual enrichment planted seedlings. For both plots, n = 527.

Correlation between covariates

Across each covariate within our initial models, the correlation between the proportion largest surrounding tree and proportion dipterocarps was statistically significant ($r_{(719)}$ = 0.390, 95% CI = 0.327 to 0.451; Fig. C3; Table C3), as was the correlation between the proportion of trees belonging to dipterocarps and the surrounding total basal area ($r_{(719)}$ = 0.110, 95% CI = 0.037 to 0.181).

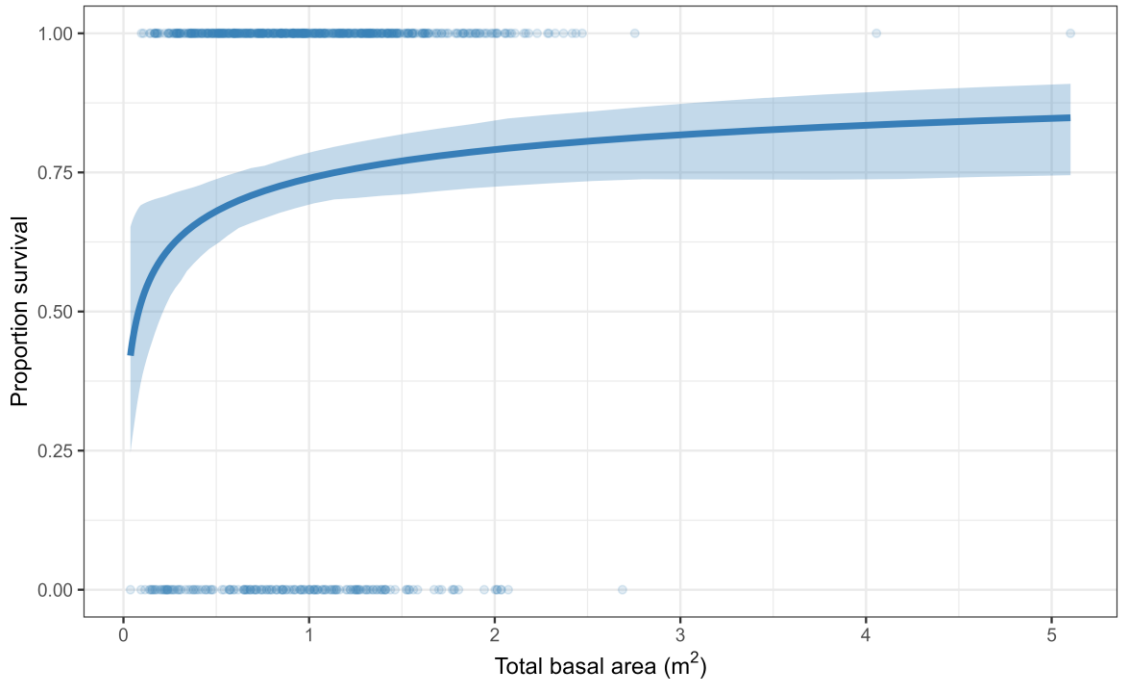

Figure 4.5 Predicted survival of dipterocarp seedlings in relation to the total basal area of matrix trees within a 10 m radius. Predictions are for cohort 2 seedlings, as they represent 527 of our 721 total seedlings and the observed relationship is conserved between cohorts (Fig. C4), and canopy openness is held at its mean value. The blue polygon represents the 95% CI obtained through bootstrapping, and individual points depict the observed survival of planted seedlings. *n* = 527.

Discussion

We investigated whether the survival and growth of planted seedlings were associated with key factors relating to surrounding matrix trees in an enrichment planting experiment. We first found that seedlings planted earlier (i.e., cohort 1) had greater survival but slower growth rates than younger seedlings (in cohort 2). We then found that light availability, measured as canopy openness, increased both seedling survival (Fig. 4.4A) and growth (Fig. 4.4B). We additionally observed a positive effect of the surrounding matrix total basal

area on the survival of seedlings, but no such effect was identified for seedling growth. Similarly, we identified no effect of the proportion largest surrounding tree and proportion dipterocarps, nor of any interactions between parameters.

We observed a wide range of growth and survival rates across species and cohorts. This variation may result in a more resilient forest if varying growth rates and survival trends reflect responses to different environmental conditions (Gunderson, 2010). Restoration interventions in Sabah can enhance adult tree diversity, particularly of rare species, decades post-intervention (Keller et al., 2023b). Studies in Sabah show that increased species diversity also promotes increased ecosystem functioning and resilience (Veryard et al., 2023a; Wu et al., 2020) due to variations in growth patterns and life history of planted trees (Hector et al., 2011). As well as this inter-species heterogeneity, environmentally influenced intra-species heterogeneity could in theory also contribute to ecosystem resilience. For instance, O'Brien & Escudero (2022) showed that dipterocarp seedling growth rates were greater further away from a river edge, but that seedlings from parent trees located on ridges were more resistant to drought and more tolerant of increased neighbour abundances. A patch in which some enrichment planted seedlings are slower-growing than other seedlings of the same species due to environmental variability, such as canopy openness or the degree of local competition, would enable these seedlings to remain as part of the seedling bank, enhancing forest resilience.

The effect of cohort

We found that seedlings from Cohort 1 (planted January 2002 to September 2003) had a higher survival rate from December 2012 to May 2015 than seedlings from Cohort 2 (planted September 2008 to August 2009). This is expected, as Cohort 1 seedlings were

planted six years earlier than Cohort 2 and had already suffered a high level of mortality before this study's monitoring period (Tuck et al., 2016), so the surviving seedlings would be the healthiest from Cohort 1's initial stock. In contrast, the higher mortality in cohort 2 reflects their shorter time since planting, more recent shock from transplantation (Close et al., 2005), restricted early root growth, and ultimately greater vulnerability to drought (Gilbert et al., 2001). We also anticipated a greater relative growth rate for Cohort 2 seedlings than for Cohort 1. Since plant growth rate is known to be size-dependent (Philipson et al., 2012; Turnbull et al., 2012), larger seedlings should have lower relative growth rate values, all else being equal. Cohort 1 seedlings were generally larger than cohort 2 (Figs 4.3c-d) and had correspondingly lower relative growth rates. This increased size can be attributed to their longer time growing in the experiment.

We found no difference in the growth or survival response to local competition, asymmetric competition and confamilial density between cohorts (i.e., no cohort by covariate interactions). Our lack of difference between cohorts provides additional robustness to our results. However, we may have expected the surrounding matrix's effects to be more pronounced in Cohort 2, as its increased sensitivity to perturbation could produce more pronounced differences in survival across the range of basal area densities observed across our experimental planting lines.

The effect of light availability

Within the range examined in this study (min. = 1.75% canopy openness; max. = 41.25% canopy openness), increased canopy openness positively influenced enrichment planted dipterocarp survival and growth. At the Sabah Biodiversity Experiment, there is evidence that enrichment planted seedlings grow better with greater light availability (Philipson et

al., 2012, 2014), so this result is consistent with these earlier findings. This is most likely linked to the surrounding vegetation mitigating extreme temperatures, low humidity, and intense radiation in more open environments, which may be particularly problematic for seedlings in the early stages of their establishment. However, we found no correlation between canopy openness and the total surrounding matrix basal area. This is likely because areas with high vegetation cover, dominated by pioneers or other plants, were not included in the measurement of the total basal area since they had a DBH of less than 10 cm. Consequently, it is difficult to isolate the specific effects of light availability from other factors associated with the surrounding vegetation. We have not investigated canopy openness levels over approximately 40% in this study, where we expect the positive relationship to change. Further increases in light availability would be expected to increase drought-related mortality or hinder the growth of shade-tolerant species (Adams et al., 2017; O'Brien et al., 2013). We anticipate that, as canopy openness decreases, competition for light becomes more important, outweighing any ameliorating effects.

Species-specific effects

Although our survival modelling revealed no significant species-specific effects on seedling survival (the random effect of *species* explained near-zero variation within the model; Fig. C5), there is evidence in the wider literature of species-specific relationships between canopy cover and mortality. Qie et al. (2019) showed species-specific responses to varying levels of degradation of naturally regenerating seedlings within Borneo. These results are similar to other evidence on the capacity of certain species to adapt to environmental conditions in recently logged forests (Clearwater et al., 1999), of which light availability is a primary driver. There have also been reports that seedlings do not show species-specific survival and growth rate responses to varying light conditions at the Sabah

Biodiversity Experiment (Philipson et al., 2014). The observed lack of species-specific light response to survival and growth rates could be because the species selected for inclusion at the Sabah Biodiversity Experiment generally comprise shade-tolerant species with potentially limited functional diversity. Further, in recent years there has been uncertainty surrounding the taxonomy of the Dipterocarpaceae (Ashton & Heckenhauer, 2022; Heckenhauer et al., 2017), which could blur the effect of species richness as our species mix is different than originally planned (Veryard et al., 2023a). Additionally, the relatively homogeneous area of the Sabah Biodiversity Experiment, relative to the wider Malua Forest Reserve and more so at the within-plot level (4 ha), may limit the capacity for species to fully exploit their partitioned niches. Together, this suggests a lack of certainty about the phylogenetic diversity of the species initially planted at the Sabah Biodiversity Experiment.

The effect of local competition

The positive relationship between the survival of planted seedlings and total matrix basal area was surprising as, in general, this relationship is negative (Peters, 2003) with some variation across species (Murphy et al., 2017). However, for a similar site in Southeast Asia, the relationship was positive if only heterospecifics were considered (Peters, 2003), encapsulated as the 'species herd protection hypothesis' (Wills & Green, 1995). This extension of the Janzen-Connell hypothesis explicitly considers the implications of biotic interactions mediated by heterospecific neighbours (Peters, 2003). It predicts that, for a given conspecific density, increased heterospecific density should reduce the frequency of encounters between hosts and pathogens. Our observed lack of effect between growth or survival of enrichment planted seedlings and the proportion of the surrounding matrix belonging to dipterocarps contradicts this idea, but as our site has undergone extensive

removal of dipterocarps (Saner et al., 2012) many seedlings were surrounded by no (24.5 % of all seedlings) or only a few dipterocarps (median proportion of basal area composed of dipterocarps = 0.11). Therefore, most interactions between planted dipterocarp seedlings and the surrounding matrix trees are predominantly with non-dipterocarps. At greater densities of matrix trees and proportions of dipterocarps, this result could change and would be valuable to identify for forest management. Other results supporting the species herd protection hypothesis can be found in Vietnam (Nguyen et al., 2016) and China (L. Chen et al., 2010; Lan et al., 2012), but interestingly Peters (2003) found no similar pattern in a neotropical site. Therefore, one potential direction for future research may be to investigate whether these patterns are unique to the dipterocarp-dominated forests of Southeast and East Asia and why.

Despite these theories, there are alternative explanations for our results. A correlation between total basal area and survival could reflect generally more favourable living conditions for trees locally in which fertile areas support higher densities of both naturally-occurring dipterocarps and non-dipterocarps, as well as providing favourable conditions for the enrichment planted seedlings. Clark & Clark (2000) showed that stem size, stand density, and spatial heterogeneity of stems were influenced by both soil type and topography in the Atlantic lowlands of Costa Rica, and Gourlet-Fleury et al. (2011) more recently showed that soil texture, depth, and hydromorphy constrained the amount of biomass stored in tropical moist forests. As well as these local differences, post-logging sites may have legacy soil conditions due to vehicle or log landing-related soil compaction (Hattori et al., 2013). An area with a greater current total basal area could have been less intensively logged previously, resulting in a more favourable environment for both naturally occurring and experimentally planted trees. One site may have more or a greater

diversity of ectomycorrhizal fungi, which are known to impact the growth of dipterocarp trees (Saner et al., 2011; Turjaman et al., 2005) and has been shown to be impacted by land use intensity in the Ulu Segama-Malua Forest Reserve (Kerfahi et al., 2014). There are many other possible mechanisms driving the relationship between seedling survival and total surrounding matrix basal area, and more detailed work on the effects of spatial variation in patch quality on the size and density distribution of naturally occurring and enrichment planted seedlings will be needed to identify a causal mechanism.

Implications for enrichment planting

Our findings indicate that the survival and growth rates of enrichment planted seedlings are positively associated with the amount of canopy openness each seedling experiences. In regions like Southeast Asia, where enrichment planting is commonly employed to facilitate post-logging regeneration, targeting areas with moderate canopy openness (but below 40%) could enhance the success of such efforts by increasing survival rates by up to 25%. Moreover, areas of forest with moderate canopy openness may more generally require enrichment planting compared to areas with greater canopy cover to facilitate their recovery. As enrichment planting is a relatively expensive process, targeted restoration can therefore offer multiple financial and ecological benefits.

The homogeneous response to survival and growth across species contrasts with other work carried out at the Sabah Biodiversity Experiment and beyond. We suggest that additional research be carried out on species-specific responses to spatial variation in logged forests before dipterocarp-wide management decisions are made. For monitoring, we suggest that seedlings across cohorts be monitored at the same relative age since planting, to account for the effects of transplanting and of size-dependent growth and mortality patterns.

Acknowledgements

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Chapter 5: Survival and growth of enrichment planted tree seedlings in old-growth and selectively logged lowland dipterocarp rainforests

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This chapter has been written to the style requirements of *Ecology and Evolution* and will be submitted to this journal.

Authors' contributions: Conceptualisation: AH, CP, and RV. Data curation: MJOB and RV. Formal analysis: MLS, MT, and RV. Funding acquisition: AH and RV. Investigation: MJOB, CP, and RV. Project administration: MJOB, EG, AH, and CP. Supervision: EFMC, AH, ER. Visualisation: RV. Writing – original draft: RV. Writing – review & editing: All authors.

Abstract

Degraded forests in Southeast Asia that are at risk of agricultural conversion are good candidates for restoration. Estimating growth and survival rates in selectively logged forests relative to old-growth forests provides important information for tropical ecology and planning tree-planting initiatives by comparing actively-restored seedlings to naturally occurring seedlings to understand the long-term ecological impacts of commercial logging. Here, we examine how the basal diameter growth and survival of 2868 enrichment planted dipterocarp seedlings from 15 species differ between selectively logged and old-growth forests over 15 years. Our results found that most species showed similar rates of seedling survival and growth in old-growth and selectively logged forests, although some species did show reduced survival and either greater or reduced growth rates in the selectively logged forest type. We identified a positive correlation ($r_{(13)} = 0.52$) between species-level growth rates in the two forest types. Survival and growth of enrichment planted seedlings were generally similar in our old growth and secondary forest study sites, but some species may be more sensitive to the impacts of selective logging than others.

Introduction

Tropical forests are often noted for their value to biodiversity and the global carbon cycle (Mitchard, 2018) and the threats they face (FAO & UNEP, 2020; Ometto et al., 2022). Drastic forest degradation and loss have resulted in secondary forests now accounting for greater total land cover than primary forests (FAO, 2020; FAO and UNEP, 2020), and so policy interventions have focused on the potential of forest restoration to promote biodiversity and mitigate the impact of global climate change (Griscom et al., 2020).

Selectively logged tropical forests can still generally support a wide range of ecosystem functions and services. A meta-analysis by Putz et al. (2012) showed that 76% of carbon is retained in once-logged forests, as well as 85-100% of mammal, bird, invertebrate and plant species. Within Sabah, Edwards et al. (2011) found over 75% of bird and dung beetle species were retained within twice-logged forests. Given the strong link between biodiversity and ecosystem functioning (Isbell et al., 2018), including in these forests (Veryard et al., 2023a), and that tropical forests host over 50% of global terrestrial species (Pennington et al., 2015), these forests can still carry out a range of ecosystem processes including carbon sequestration and hydrological regulation (Berry et al., 2010; Dinerstein et al., 2019; Keller et al., 2023a; Rozak et al., 2018). Heinrich et al. (2023) showed that regrowing degraded and secondary forests accumulated 107 Tg C $year^{-1}$ from 1984 and 2018, offsetting 26% of carbon emissions from humid tropical forest loss over the same period. More widely, local communities which depend on forest ecosystem services consistently rank clean water, clean air, and the regulation of temperature, flood, and erosion as the services most valued (Boul Lefeuvre et al., 2022), which Edwards et al. (2014) showed are generally conserved across logged forests. Together, degraded forests

can improve carbon sequestration whilst maintaining wider ecosystem functioning and protecting biodiversity.

There is a growing body of evidence that suggests that biodiversity is a strong predictor of ecosystem functioning in the tropics (Huang et al., 2018; Veryard et al., 2023a). The proposed mechanisms driving this biodiversity-ecosystem functioning relationship are based on species-specific responses to environmental conditions (Tuck et al., 2016) and it is a critical assumption of life-history theory that, due to a limitation in resource availability, not all traits can be invested in maximally and simultaneously (Grafen, 2006). These traits, including wood density, specific leaf area, and seed mass (Meira-Neto et al., 2019), are generally considered to underlie differences in species-specific life history, specifically the growth-survival trade-off classically observed across plant species (Wright et al., 2010) and argued to be driven by adaptation to a varying light environment (Philipson et al., 2012, 2014). The exact mechanisms that underlie these trends are still actively debated (Philipson et al., 2020).

Within Sabah, Malaysian Borneo, degraded forest landscapes at risk of conversion are prime candidates for restoration. As Malaysia's poorest state (Huda et al., 2022), Sabah's economy has historically relied upon the forestry sector (Reynolds et al., 2011) and more recently forests have faced pressure for conversion into oil palm plantations. Like most Southeast Asian countries, tropical forests in Sabah are characterised by the dominance of a single family of trees, the Dipterocarpaceae, whose life history hinders natural regeneration post-logging. Dipterocarps fruit irregularly, undergoing collective 'mast fruiting' events every two to 10 years (Ashton et al., 1988). These seeds have low dispersal ranges and are recalcitrant, producing no seed bank. Instead, seeds germinate immediately to produce a standing bank of living seedlings (Umarani et al., 2015). This seedling bank

is at a high risk of damage through tree felling, soil disturbance and compaction consistent with selective logging.

One restoration method used for dipterocarp forests is enrichment planting, where the naturally-regenerating seedlings are supplemented with additional seedling planting (Safa et al., 2004). These seedlings are typically of commercial interest with the aim to increase the long-term timber yield of the forest as well as for forest restoration purposes (Banin et al., 2023). Enrichment planting lowland dipterocarp forests is relatively expensive, costing between US \$1500 ha^{-1} and \$2500 ha^{-1} in lowland Sabah (Philipson et al., 2020). The level of management in active restoration also varies widely, from exclusively seedling planting to ongoing maintenance with weed and climber cutting, watering, protection from herbivores, and fertilisation (Banin et al., 2023). Given the high cost of active restoration, these practices must provide tangible benefits via increased future timber yields if slated for future logging and should allow for current assets to generate income including through carbon markets, non-timber forest products, and ecotourism.

Because of the expense of active restoration, there is a growing debate concerning its cost-effectiveness relative to natural regeneration (Crouzeilles et al., 2017; Philipson et al., 2020). As a result, many assessments of tropical forest recovery have compared actively restored forest to naturally regenerating controls. Global assessments have shown ecological success can sometimes be higher in naturally regenerating sites (Crouzeilles et al., 2017), but studies specific to Southeast Asia generally agree that active restoration does increase the growth and survival rate of seedlings (Banin et al., 2023), which is attributed to the ecological characteristics of the Dipterocarpaceae that make natural regeneration particularly challenging (Reynolds et al., 2011).

One underutilised point of comparison for enrichment planted dipterocarps is the growth and survival rates of similarly sized seedlings within old-growth forests. Selective logging may transform a forest environment, including through changes to the microclimate (Blonder et al., 2018) and species assemblages (Wright et al., 2015) such that establishment and growth of seedlings is negatively affected, slowing recovery. As land use changes can severely impact an ecosystem, there have been observations of ecosystems passing a threshold level of degradation whereby they enter an 'alternative stable state' (Hirota et al., 2011). These shifts can occur on multiple scales, from altering population size to complete changes in community composition (Folke et al., 2004). Alternative stable states and community shifts are relatively well studied in temperate and coastal environments (Bellwood et al., 2004) but have received little attention in the tropics. Engsröm (2023) found that a naturally regenerating forest at the INIKEA forest restoration project, Kalabakan Forest Reserve, Sabah, showed very little succession 40 years post-logging, but succession rates were faster for an adjacent actively restored fragment. Whilst analysis of growth rates of enrichment planted seedlings relative to naturally regenerating seedlings is valuable in quantifying the increase in carbon stock post-intervention, comparison with old-growth forest could provide target growth rates and comparative baselines and determine the degree to which selective logging has altered the growth environment for seedlings.

Taking a species-specific comparative approach to restoration may also allow us to identify specific species with increased or reduced resilience to logging effects. Evidence of a growth-survival trade-off in selectively logged forests has previously been identified by Philipson et al. (2014) and Tuck et al. (2016). As the growth-survival trade-off is argued to be an important element of life-history variation which allows dipterocarps to exploit

variation within their environment (Wright et al., 2010), it is of interest to see how this trade-off differs in undisturbed forest conditions and how, if at all, the relationship changes in response to logging-induced perturbation.

This study compares the growth and survival of enrichment planted dipterocarp seedlings within the selectively logged Malua Forest Reserve and the neighbouring old-growth primary forest at Danum Valley Field Centre in Sabah, Malaysian Borneo from 2004 to 2020. We also tested for a correlation between species-level growth rates between primary and secondary forests and between species-level survival rates across forest types. Finally, we tested for a growth-survival trade-off by identifying a correlation between species-level growth and survival rates for each forest type.

Materials and methods

Study sites

The study was conducted with two sites in Sabah, Malaysian Borneo (Fig. 5.1A), the Sabah Biodiversity Experiment and the Danum Gaps-Understory Experiment, within the Yayasan Sabah Forest Management Area, an approximately one million-ha piece of land managed publicly by Yayasan Sabah (The Sabah Foundation), designed to increase socioeconomic standards within the state. The mean annual rainfall of both study sites from 1986-2010 averaged 2848.5 (± 94.0 *se*) mm $year^{-1}$, with monthly means varying from 119.5 mm in April to 302 mm in January and October. This region had a pre-logging timber volume of 193-221 m^3 ha^{-1}, of which dipterocarps comprised the majority at 180-216 m^3 ha^{-1} (Saner et al., 2012). Sabah has been historically dependent on timber production for economic development. Production peaked at over 13 million m^3 of timber in 1978 (Reynolds et al.,

2011), and current production rates are around one million m^3 $year^{-1}$ (Sabah Forestry Department, 2022).

The Sabah Biodiversity Experiment

The Sabah Biodiversity Experiment (http://www.sabahbiodiversityexperiment.org) is a large field-scale biodiversity experiment established in 2001 (Hector et al., 2011). The experiment occupies 500 ha of the southern section of the wider Malua Forest Reserve (05°05'20'' N, 117°38'32'' E, 102 m above sea level). The Malua Forest Reserve is approximately 35,000 ha in size and was selectively logged once in the 1980s followed by a second time between 2003 and 2007. The Sabah Biodiversity Experiment site was protected from this second round of logging by the presence of the experiment and has only been logged once.

The Sabah Biodiversity Experiment encompasses several experimental treatments within a replicated and randomised blocked design. The experiment contains 124 four-hectare (200 m x 200 m) experimental plots separated into two blocks by a logging load that runs roughly east-west (64 blocks in the southern and 60 in the northern blocks; Fig. 5.1B). Of these 124 plots, 12 were left as naturally regenerating controls, and the remaining 112 plots were enrichment planted with varying numbers of dipterocarp species. In detail, the 112 enrichment planted plots were randomly assigned one of three species richness treatments: single-species mixtures where one species of dipterocarp was planted (n = 32: 16 species x 2 replicates), four-species mixtures (n = 32: 16 mixtures x 2 replicates), and sixteen-species mixtures (n = 48: 32 replicates equally divided between the two blocks plus 16 with an additional liana removal treatment applied - see below). In total, 16 species of dipterocarp were planted across the Sabah Biodiversity Experiment (Table D1 in Appendix

D). The species selected represent the species found in the surrounding forest, cover a wide range of traits and ecological strategies, and were available in sufficient quantities at local seeding nurseries when planting (Tuck et al., 2016).

This experiment planted almost 100,000 seedlings and so complete censuses take a long time to complete. There have been two complete censuses of the seedlings, with a third full census underway in late 2023. To complement this monitoring, six 16-species enrichment planted plots in the southern block were selected for more intensive monitoring. Intensively monitored plots have had their enrichment planted seedlings censused 10 times between January 2004 and March 2020 and are the plots used in this study. During each census, the basal diameter and survival of each seedling are measured, as well as the diameter at breast height (DBH) if the seedling is sufficiently large. In total, 7036 eligible seedlings from the Sabah Biodiversity Experiment were included in this analysis.

The Danum Gaps-Understory Experiment

After the initial planting at the Sabah Biodiversity Experiment, seedlings of 15 dipterocarp species remained, the exception being *Hopea ferruginea* which had insufficient stocks after planting, plus an additional 10 species with insufficient stocks to have been used in the main Sabah Biodiversity Experiment (Table D1). A second experiment was established in 2004 using these species to compare their growth and survival within the naturally occurring canopy gaps and understory of the nearby primary forest at Danum Valley (Fig. 5.1C).

The Danum Valley Field Centre (04°57'36"N 117°48'00"E; 180 m above sea level) sits within the Danum Valley Conservation Area, a 43,800 ha (438 km^2) Class I (fully

protected) primary lowland dipterocarp rainforest which has never been commercially logged. The forest surrounding Danum Valley Field Centre was selected for planting, and along the main walking trails 20 locations (blocks) were identified with suitably large gaps in the canopy (12-400 m^2). Within each block, two replicate plots were established (Fig. 5.1D). Each plot contained two replicate subplots, each containing a 5 x 5 grid of 25 seedlings, one from each of the study species with 0.75 m spacing. For each plot, a paired plot was established 30 m away at a random compass bearing in a forest area with a closed canopy. Both plots, each containing two subplots, make up each of the 20 blocks, which were placed across a range of topographies found in Danum Valley. In total, 80 subplots and 2,000 seedlings were planted. Planting was carried out and completed in November 2004.

Species were planted randomly within each subplot, each with a unique planting pattern. To date, 19 full censuses of these 20 blocks have been conducted between November 2004 and November 2017, and partial censuses have been completed as recently as May 2023. In each census, each seedling's basal diameter and survival was recorded, and DBH was also measured if the seedling was large enough. Of the 80 subplots, 20 had clear polyethene plastic sheeting applied over the understory between 2013 and 2014 to add a drought treatment. These subplots were excluded from this analysis to improve comparability with the Sabah Biodiversity Experiment which had not had a rainfall reduction treatment applied. In total, 910 eligible seedlings from the Danum Gaps-Understory Experiment were included in this analysis.

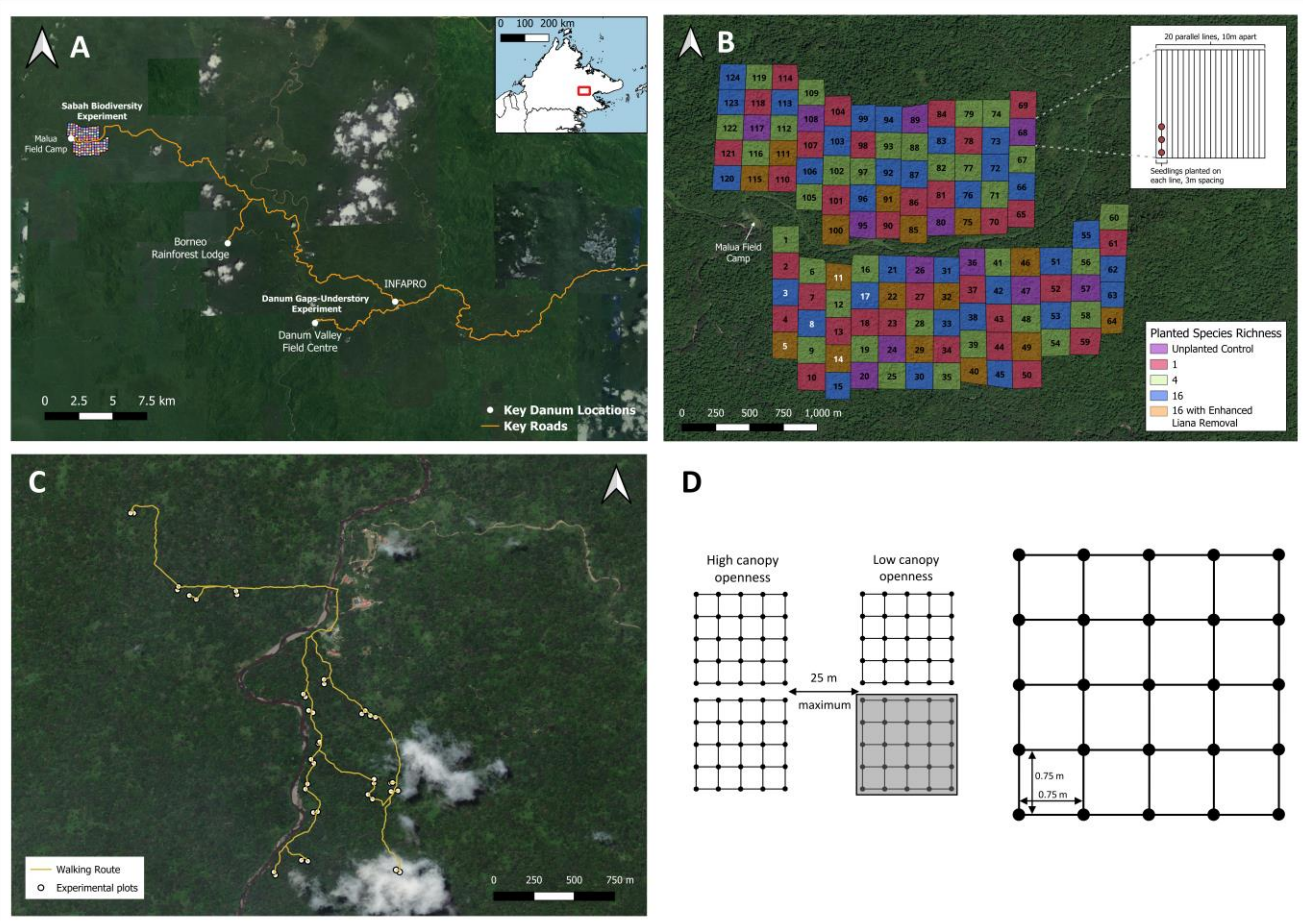
A
0 100 200 km
Sabah Biodiversity Experiment
Malua Field Camp
Borneo Rainforest Lodge
INFAPRO
Danum Gaps-Understory Experiment
Danum Valley Field Centre
0 2.5 5 7.5 km
Key Danum Locations
Key Roads
B
20 parallel lines, 10m apart
Seedlings planted on each line, 3m spacing
Malua Field Camp
0 250 500 750 1,000 m
Planted Species Richness
Unplanted Control
1
4
16
16 with Enhanced Liana Removal
C
Walking Route
Experimental plots
0 250 500 750 m
D
High canopy openness
Low canopy openness
25 m
maximum
0.75 m
0.75 m

Figure 5.1 Locations and experimental designs of the Sabah Biodiversity Experiment and the Danum Gaps-Understory Experiment. **(A)** Both experiments are within the Yayasan Sabah Forest Management Area, approximately 20 km apart. **(B)** The Sabah Biodiversity Experiment consists of 124 four-ha plots, separated by a logging road used for access. Each plot was assigned one of four treatments: unplanted controls, plots enrichment planted using either single-, four-, or 16-species mixtures, and plots enrichment planted with 16-species mixtures with additional liana removal. In each enrichment planted plot, seedlings were line-planted every three m in cleared lines with 10 m spacing. Plots in this analysis are labelled in white, and plots not used here are labelled in black. **(C)** The Danum Gaps-Understory experiment is distributed across 20 blocks along the main walking trails around the Danum Valley Field Centre. **(D)** Within each block, two plots are established in regions of high and low canopy openness. Within each plot are two replicate subplots in which 25 seedlings are planted into a 5 x 5 grid with 0.75 m individual spacing. In 20 of 80 subplots, an additional treatment of droughting was applied, indicated by a grey shading on one subplot.

Comparison of experimental designs

The experimental sites are approximately 20 km apart, share similar pre-logging site characteristics (Table D2; Saner et al. (2012)), and are long-term studies of planted seedling growth and survival. These two sites also share a common seedling stock – of the 16 species used in the Sabah Biodiversity Experiment and the 25 in the Danum Gaps-Understory Experiment, 15 are shared (the exception being *Hopea ferruginea*), and the seedling stocks were sourced from the same INFAPRO nursery. They therefore offer an opportunity to compare growth across primary and secondary forest types. However, these experiments do have some differences in their design. For instance, it is not desirable or legal to carry out line planting within the protected Danum Valley Conservation Area, which requires clearing forest understory. This means that the seedling planting density and arrangement of the two projects differs substantially. The Danum Gaps-Understory Experiment seedlings are planted in a square grid with 0.75 m spacing while Sabah Biodiversity Experiment seedlings are planted in parallel lines 10 m apart with 3 m spacing along the lines. However, it is important to note that these densities of the enrichment planted seedlings ignore the background vegetation. Generally, the Danum Gap-Understory Experiment plots have no other trees rooted within the grid. The Sabah Biodiversity Experiment lines are roughly 1-2 m wide with the intervening several metres consisting of background vegetation. Within 10 m of each seedling, the mean basal area of preexisting trees in the forest matrix is approximately 1 m^2. For a more complete comparison between both experimental sites, see Table 5.1.

Table 5.1 Comparison of the Sabah Biodiversity Experiment and the Danum Gaps-Understory Experiment.

Comparison point	Sabah Biodiversity Experiment	Danum Gaps-Understory Experiment
Location	Malua Forest Reserve.	Danum Valley Conservation Area.
Forest type	Secondary forest.	Primary forest.
Size	500 ha.	0.1 ha.
Plot-level design	124 plots split into two blocks.	80 subplots, divided into 40 plots, divided across 20 blocks.
Planting design	Seedlings are planted every three metre along planting lines. Adjacent planting lines separated by 10 m.	Five-by-five grid of seedlings, adjacent seedlings given 0.75 m spacing.
Planting density	One seedling per 30 square metres.	One seedling per 0.56 square metres.
Second planting	A second planting was carried out between September 2002-August 2003.	No second round of planting.
Experimental manipulations	Combination of unplanted and single-species, four-species, 16-species enrichment planted, and 16-species enrichment planted plots with additional liana removal.	Half of the subplots were planted within canopy gaps, other half was planted near areas of increased canopy cover. Twenty plots underwent additional drought treatment.
Liana removal	All non-control plots had lianas cleared within one m of planting lines. Twelve plots had all lianas at least 10 cm in height removed from within the plot.	No liana removal.
Species used	All members of the Dipterocarpaceae.	Twenty-four species from the Dipterocarpaceae, one from the Malvaceae (*Durio graveolens*).
Survey frequency	Two full censuses to date. Ten censuses of six plots which were more frequently censused.	Nineteen complete censuses to date.
Survey range	January 2004 – March 2020	November 2004 – November 2017
Seedling stock	Sourced from INFAPRO nursery stock.	Sourced from INFAPRO nursery stock.

Study species

Although the taxonomy of the Dipterocarpaceae, specifically the tribe Shoreae, has recently been updated (Ashton & Heckenhauer, 2022), we will use the species names used when the Sabah Biodiversity Experiment was first established (Hector et al., 2011) for consistency across publications.

Statistical analysis

Growth modelling

We modelled the log-transformed mean basal diameter (mm) change in response to the years since the first survey. To aid model convergence, species were analysed individually. Due to high variation in growth patterns within and between species, we compared a range of different approaches to modelling size over time. Three approaches were considered: a linear mixed-effects model with a second-degree (quadratic) polynomial of the time dimension, a nonlinear mixed-effects regression model with an asymptotic functional form, and a generalised additive mixed-effects model (GAMM) with a thin plate regression spline. Each model was constructed to estimate a difference in growth rate between forest types and initially included the same random effects of individual tree IDs and plots.

Each model's population-level predictions for the growth of each species in each forest type were compared to observed changes in diameter over time to identify and discard models that produced estimates outside the observed data range or notably underestimated observed values. All nonlinear mixed-effects regression models with asymptotic functional forms were also discarded at this stage as many individual seedlings died at an early stage and therefore lacked enough observations for analysis, meaning that our growth analysis and interpretations would consequently be restricted to only the healthiest seedlings. The

remaining models were compared by their residual standard error to select the best-fitting model to continue with. Generalised additive mixed-effects models were selected as the most effective model with a general form (Wilkinson & Rogers, 1973) of:

Model 5.1 – Initial model of growth with a generalised additive model and thin plate spline

$$s(years\_since, by = type) +$$
$$type +$$
$$s(tree\_id, bs = "re")$$

Where *years_since* is a covariate representing the number of years since the first survey point for an individual tree, *type* is a factor of two levels (primary or secondary forest), and *tree_id* is a factor with one level for each enrichment planted seedling. The term 's(*years_since*, by = *type*)' indicates a smoother term to be fitted, with the addition of 'by = *type*' specifying that a separate smoother will be estimated for each level of the factor type. The term 's(*tree_id*, bs = "re")' represents a smooth random effect for the factor *tree_id.* Note that it was not possible to survey seedlings at the Sabah Biodiversity Experiment at the time of planting to prioritise planting the entire experiment in as short a time span as possible, and so instead a round of surveying took place once planting was complete.

Our comparison of growth in the two forest types using GAMMs differs from other commonly used alternatives. Comparisons amongst species using relative growth rates (change in log-transformed size over time) has the disadvantage of potentially mis-interpreting the general slowing of growth with increasing size with the effects of differences in traits between species (i.e., comparing smaller individuals of one species

with larger individuals of another and attributing the lower growth rate to differences between the species rather than the universal effects of increasing size) (Paine et al., 2012b; Turnbull et al., 2012). One alternative is to estimate a size-standardized growth rate at a common size (Philipson et al., 2014; Turnbull et al., 2012) but this usually requires a common growth form and is limited to a commonly shared size, if one exists. No single functional growth form was suitable for modelling the growth of all of our species in the two forest types. Instead, our use of a regression spline GAMM allows a more flexible approach that permits more complex growth curves. The drawback of this method is the lack of a simple coefficient from the GAMM that can be compared across species as with the RGR and SGR approaches. Instead, GAMMs tend to be interpreted by displaying the curves with a confidence interval. This has the advantage of comparing growth over a period of time rather than at a single point. However, to take into account differences in initial size, time was expressed as the number of years after a species achieves the minimum common size predicted between forest types. To identify if growth rates varied between forest types, models were fitted with and without separate smoothers for each forest type, and both models were directly compared using the Bayesian information criterion to identify the best-fitting model (Schwarz, 1978). This information criterion was selected as we wanted to prioritise choosing simpler models closer to the true data distribution, rather than more complex models used for prediction where AIC is often preferred. Generally, Bayesian information criterion scores within two units are equivalent when models are of equal complexity (otherwise the simpler model is preferred; Schwarz, 1978).

Mortality data analysis

We quantified mortality or survival of individual seedlings as a binary response variable that classified the survival of planted seedlings as alive or dead at the final census date (primary forest: 26 November 2017; secondary forest: 13 April 2018). Since censuses of

the primary forest site began 10 months after the secondary forest site, the latter sites' final census was 13 months later than the primary forest.

Our initial model for survival (*Model 5.2*) was:

Model 5.2 – Initial model of survival with a binomial variance function

$$survival \sim species * type + (1|plot)$$

Where *survival* is the binary response variable (1 indicating a living seedling, 0 a dead one), *species* is a factor with 15 levels (for each species), *type* is a factor with two levels (primary and secondary forest types), and *plot* is a factor with 26 levels for each Sabah Biodiversity Experiment plot or Danum Gaps-Understory Experiment plot. (1|F*actor*) indicates random intercepts for levels of the specified random factor. An asterisk between two variables indicates the fitting of each factor's main effects and an interaction between them. Confidence intervals were estimated using bootstrapping, and we used Bayesian information criterion for model comparison.

Our final dataset contained 910 trees from the primary forest and 7036 trees from the secondary forest experiment, of which 908 trees from the primary and 1922 trees from the secondary forests were alive at their first survey. There was variation in the number of surviving planted seedlings of each species present within a forest type at their first census (primary forest: minimum number of individual seedlings = 39 [*P. malaanonan*], maximum = 83 [*P. tomentella*]; secondary forest: minimum = 47 [*S. argentifolia*], maximum = 202 [*S. ovalis*]; Table D3). Of the initial 2868 living trees in 2004, 726 survived until our experimental period's end. Of these, 272 were from primary forest plots, and 454 were in

the secondary forest. There was again variation within each forest type at the species level (primary forest: minimum number of individual seedlings = 4 [*S. leprosula*], maximum = 43 [*H. sangal*] = 39; secondary forest: minimum = 1 [*S. argentifolia*], maximum = 66 [*H. sangal*]; Table D3).

We identified a large amount of mortality (approximately 75% of all seedlings) in the Sabah Biodiversity Experiment at the first census of plots (around 700 days after planting on average). This is approximately triple the two-year mortality rate reported in a meta-analysis by Banin et al. (2023) for tropical and subtropical Asia. An El Niño drought coincided with the establishment of the Sabah Biodiversity Experiment and is thought to have contributed towards the high initial mortality period. This mortality rate is also higher than that observed for seedlings replanted to replace the dead seedlings (Fig. D1 in Appendix D), suggesting that this increased mortality rate was cohort-specific and not entirely attributed to the environmental conditions at the Sabah Biodiversity Experiment. Further, the Danum Gaps-Understory Experiment was planted after the El Niño drought event, and so a comparison between forest types was restricted to events outside El Niño droughts. All seedlings reported dead at the first survey were discarded to retain only those which were alive at the first point of surveying to account for initial mortality prior to censuses and minimise the risk of the El Niño drought obscuring ecological differences between both forest types. Consequently, this limits our results to only the healthiest of planted seedlings.

Correlation between survival and growth estimates

To test for a correlation between growth and survival, a single value representing species-specific growth and survival rates were required for direct comparison, and to aid

comparability with previous studies at the Sabah Biodiversity Experiment which identified a growth-survival trade-off (Philipson et al., 2014; Tuck et al., 2016). Single values representing species-specific survival rates were obtained from *Model 5.2*, but growth data was remodelled as relative growth rate, defined as the difference in log-transformed basal diameter (mm) over time (years) between the first and last measurement of the basal diameter of each enrichment planted seedling. The model for relative growth rate (*Model 5.3*) was:

Model 5.3 – initial model of relative growth rate with a Gaussian variance function

*Species * type +(1|plot)*

Where all terms are as described in *Model 5.2*, predicted values were subsequently extracted from this model, and four Pearson's product-moment correlation coefficients were calculated: predicted relative growth rates across both forest types, predicted survival proportions across both forest types, and predicted relative growth rate and survival proportions across both forest types. All data analysis was undertaken in R (version 4.3.1; R Core Team (2023)).

Results

Growth

After size-standardisation, considerable variation in growth rates can be seen for each species within each forest type (Fig. 5.2).With the exclusion of *S. argentifolia* due to its small sample size, the fastest species estimated were *S. parvifolia* and *S. macrophylla,* which reached basal areas of 68.1 mm (95% CI = 57.7 – 80.5 mm) and 62.8 mm (54.5 – 72.4 mm), respectively, whilst *P. tomentella* and *D. conformis* attained the smallest

estimated sizes of 28.3 mm (25.7 – 31.1 mm) and 29.8 mm (27.7 – 32.0 mm), respectively. Within primary forests, *S. argentifolia* and *S. macrophylla* grew the most to basal areas of 79.1 mm (63.7 - 98.2 mm) and 54.6 mm (45.3 – 65.9 mm), respectively, and *P. malaanonan*, and *D. conformis* grew the least amount to 12.7 mm (10.9 – 14.7 mm) and 14.5 mm (12.9 – 16.4 mm), respectively, over the studied time period.

Bayesian information criterion model selection identified six species which had an improved model fit after the inclusion of separate smoothers for each forest type, indicating different growth rates between forest types (Fig. 5.3; Table D4). The remaining nine species showed an increase in Bayesian information criterion scores after separate smoothers were included supporting a common pattern of growth over time in both forest types.

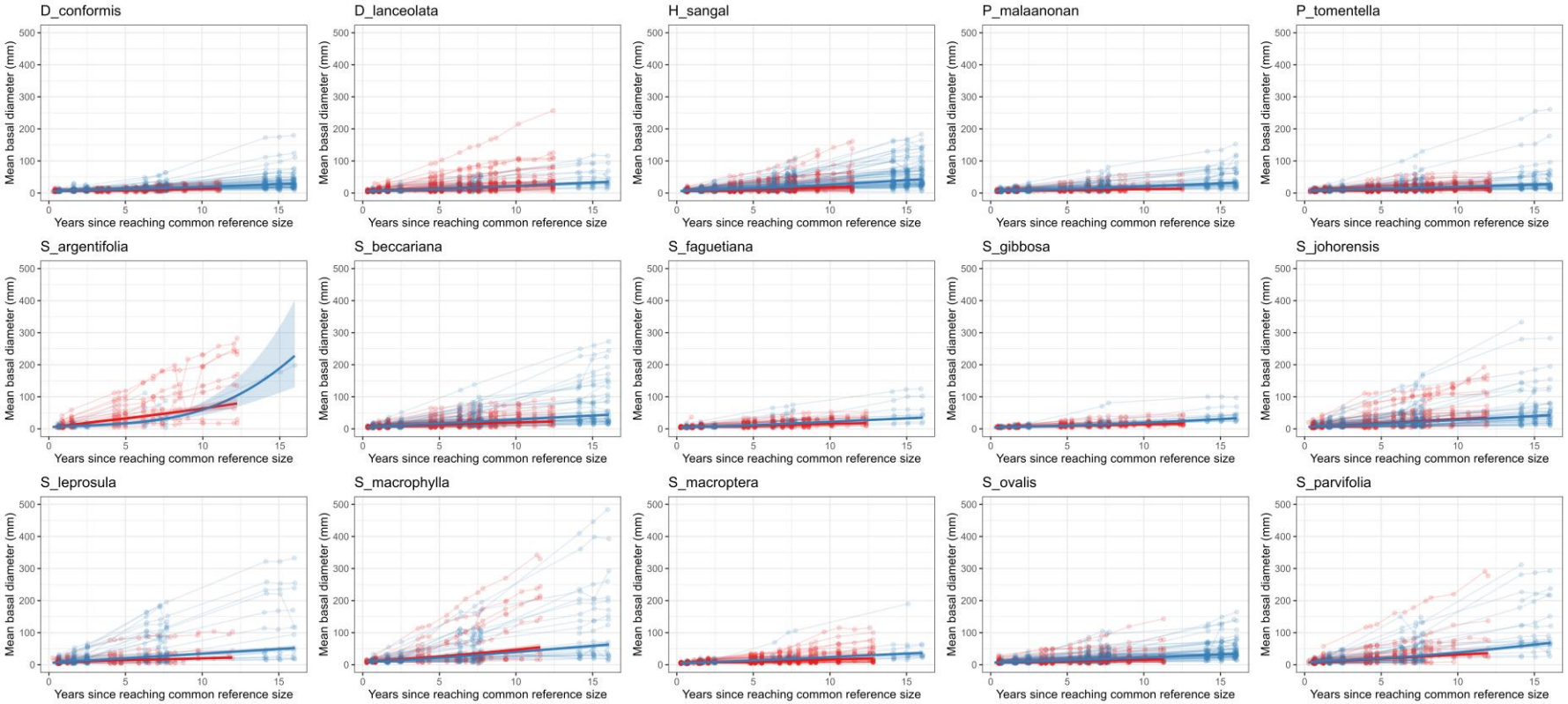

Figure 5.2 GAMM estimates of growth (since reaching a common minimum size) of 15 dipterocarp species in primary (red) and secondary (blue) forest types. Predicted growth curves for each species in each forest type are plotted as thicker coloured lines, with a 95% confidence interval (shaded regions). Observed sizes of individual seedlings are plotted as smaller coloured dots, connected with a coloured line. Comparison of Bayesian information criterion scores (see Fig. 5.3) suggests that *P. malaanonan*, *S. argentifolia*, *S. gibbosa*, *S. johorensis*, *S. macrophylla*, and *S. macroptera* demonstrate different growth rates between forest types while growth rates for the other nine species were indistinguishable in primary and secondary forest.

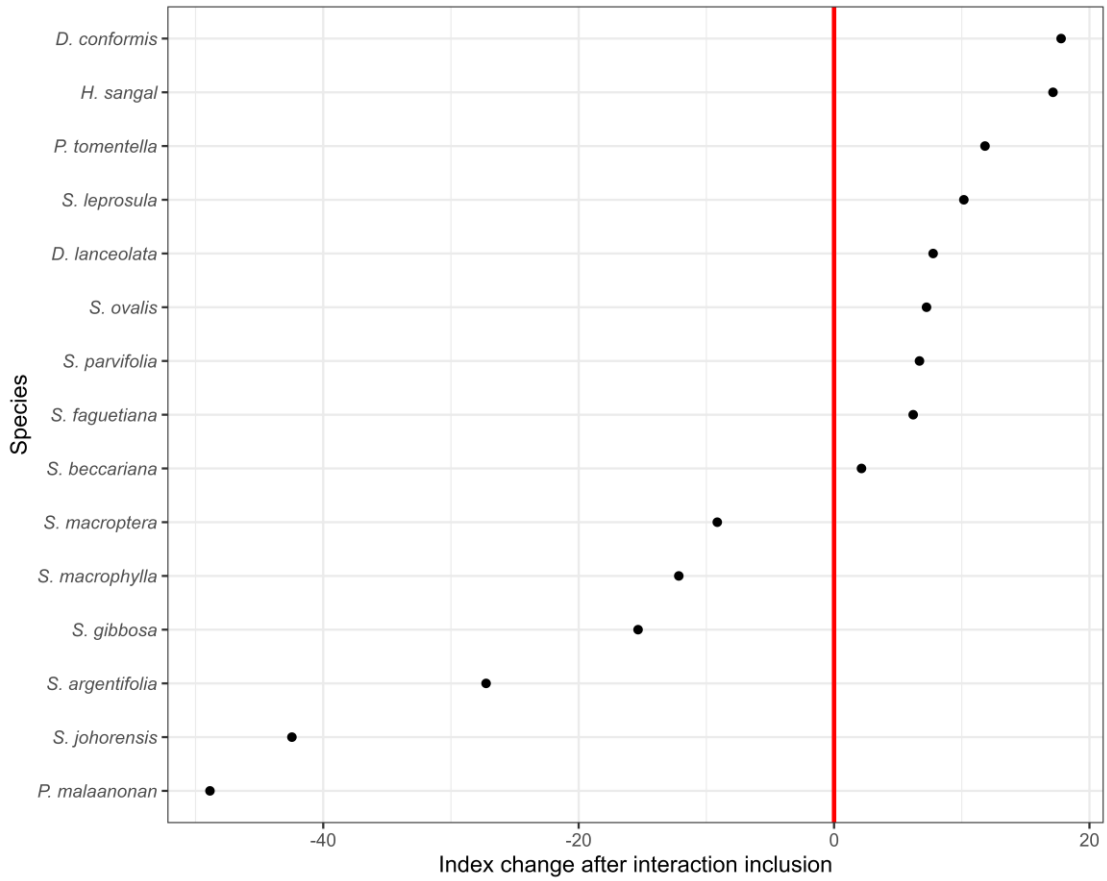

Figure 5.3 Change in Bayesian information criterion estimates after fitting separate smoothers for each forest type. Negative values (left of the red vertical line) indicate species which produce a lower Bayesian information criterion score when individual smoothers are fitted for each forest type across time. Positive values indicate where allowing the smooth terms to vary between forest types leads to worse Bayesian information criterion scores and negative values indicate improved scores.

Survival estimates

Of the seedlings that were reported alive at first census, a mean survival rate of 0.236 was observed in the secondary forest and 0.302 in the primary forest type. Model results showed species-specific differences in survival. Within the secondary forest, *H. sangal* and *D. conformis* had the highest estimated survival rates of 0.374 (95% CI = 0.282 – 0.477) and 0.333 (0.244 – 0.436), respectively, and *S. argentifolia* and *S. faguetiana* had the lowest

estimated survival rates at 0.022 (0.0003-0.137) and 0.083 (0.016 – 0.144), respectively. Within the primary forest site, *H. sangal* and *D. lanceolata* gave the highest survival rates of 0.710 (0.576 – 0.815) and 0.556 (0.420 – 0.684), respectively, whilst *S. leprosula* and *S. parvifolia* had the lowest survival rates at 0.050 (0.016 – 0.144) and 0.0865 (0.038 – 0.172), respectively.

Our model could not identify any difference in the proportion of trees surviving between forest types for 11 of the 15 investigated species. Four species (*D. lanceolata*, *H. sangal*, *S. faguetiana*, and *S. macroptera*) showed higher survival rates in the old-growth forest in the secondary forest (Fig. 5.4; Fig. D2; Table D5).

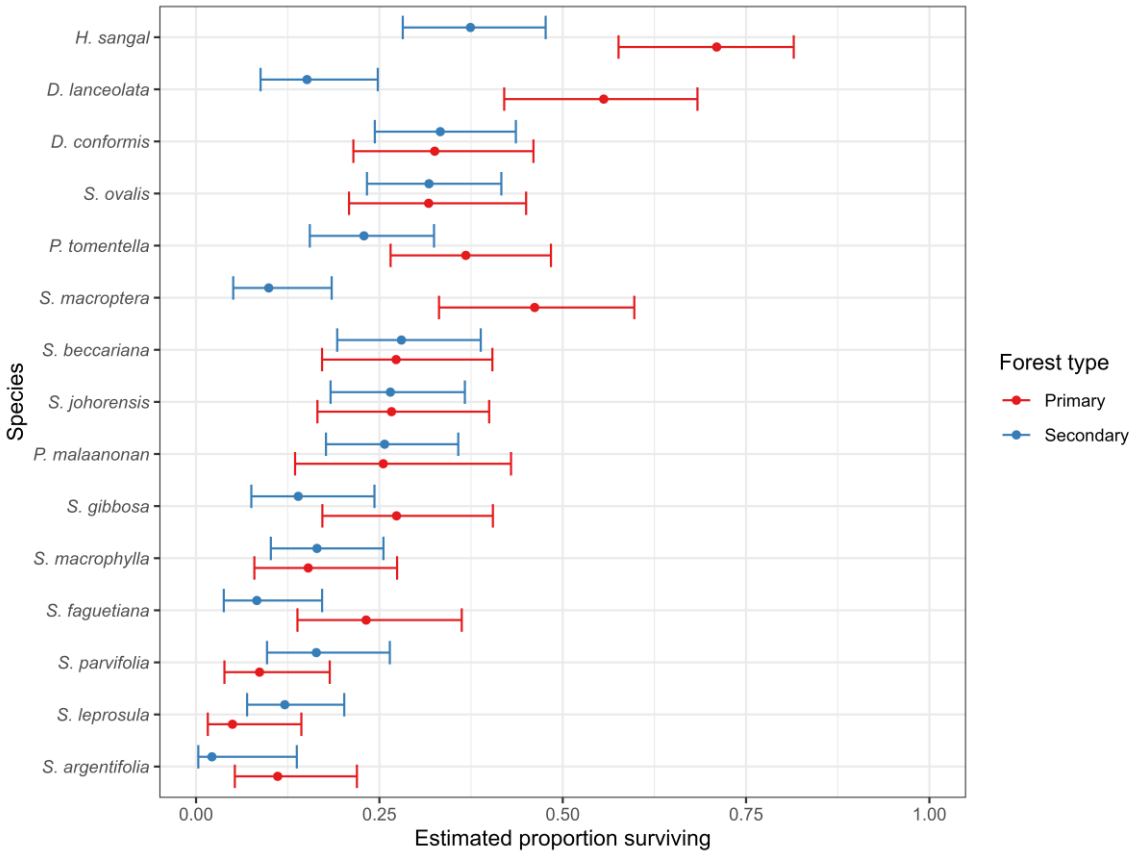

Figure 5.4 Estimated proportion of species surviving between 2004 and 2018. 95% confidence intervals are represented with horizontal lines. Forest type is indicated by colour in the legend.

Correlation between forest type and survival and growth

A marginally insignificant positive correlation between species-level survival between forest types was identified (survival proportions: $r_{(13)} = 0.47$, 95% CI = -0.059 to 0.79; Fig. 5.5A) and a statistically significant positive correlation was identified for relative growth rates between forest types ($r_{(13)} = 0.52$, 95% CI = 0.008 to 0.81; Fig. 5.5B).

A correlation was also identified across both forest types between the survival proportions and relative growth rates of each species (primary forest: $r_{(13)} = -0.79$, 95% CI = -0.93 to -0.46, Fig. 5.5C; secondary forest: $r_{(13)} = -0.94$, 95% CI = -0.98 to -0.82, Fig. 5.5D),

indicating that species with higher relative growth rates also have lower overall survival rates throughout this study period.

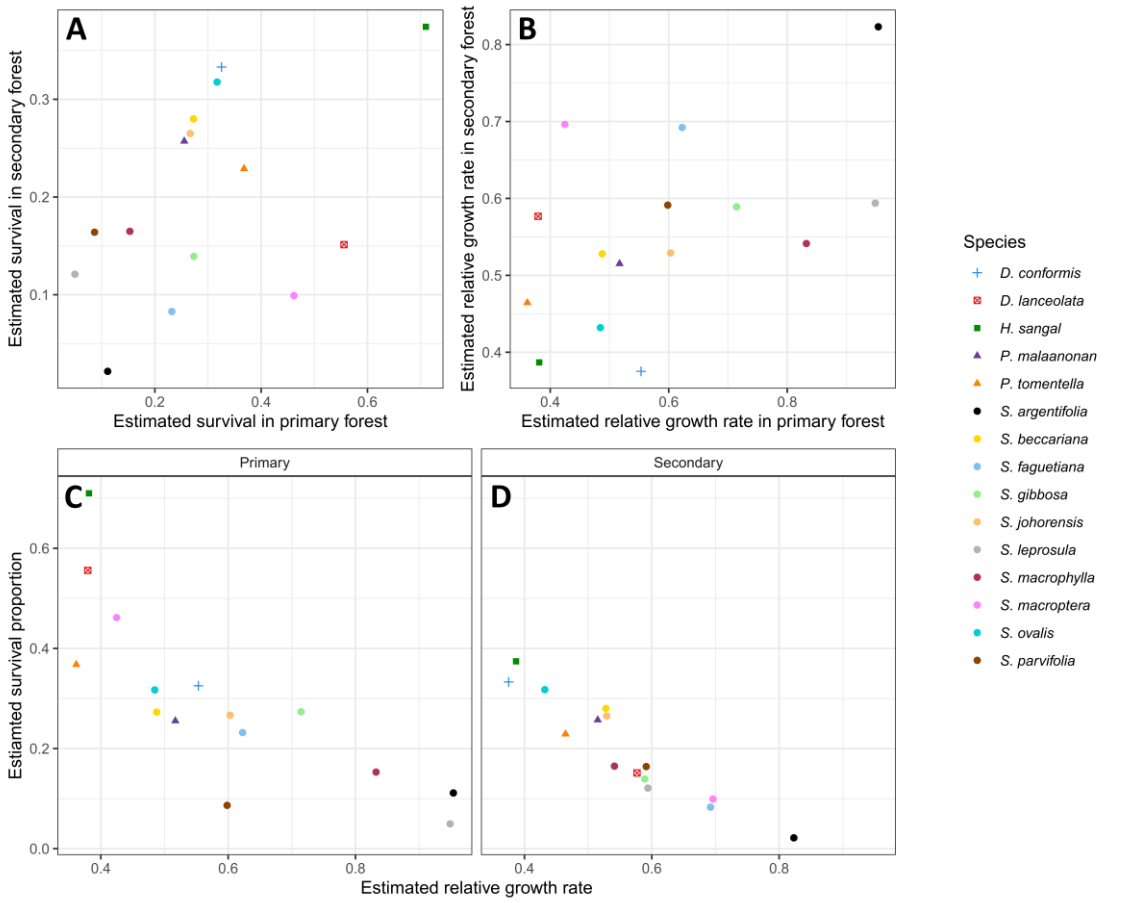

Figure 5.5 Correlations between measures of survival and growth in the primary and selectively logged forest. **(A)** Correlation between survival probability estimates in primary and secondary forest sites for each species, $r_{(13)}$ = 0.47, 95% CI = -0.059 to 0.79. **(B)** Correlation between estimated relative growth rate (mm mm^{-1} year^{-1}) between primary and secondary forest sites, $r_{(13)}$ = 0.52, 95% CI = 0.008 to 0.81. **(C)** Correlation between estimated growth and survival in primary forest. $r_{(13)}$ = -0.79, 95% CI = -0.93 to -0.46. **(D)** Correlation between estimated growth and survival in secondary forest. $r_{(13)}$ = -0.94, 95% CI = -0.98 to -0.82. Across all plots, species is indicated by point colour and genus is indicated by point shape in the legend.

Discussion

We investigated how the survival and growth of 15 enrichment planted dipterocarp species varied across two forest types. We first identified that six species showed differences in growth rates of planted seedlings between forest types, although considerable within-species and across forest type variation was observed. Four species showed increased survival rates in the old-growth forest site compared to the selectively logged forest, and the remaining 11 showed no clear difference across forest type. Only a single species (*S. macroptera*) showed differences in both growth and survival rates across forest type. A positive correlation between species growth rates in each forest type was detected, but no correlation was detected for survival rates between forest types, and support for a trade-off between growth and survival within both forest types was also identified.

Growth and mortality in old-growth and selectively logged forests

Our results suggest that most of our enrichment planted species were similar in their growth or survival over time, irrespective of forest type. This is despite the differences in both the biotic and abiotic conditions of the Danum Valley Conservation Area and the Malua Forest Reserve and was also irrespective of the differences in experimental design, particularly regarding planting density.

No clear difference in growth and survival rates between forest types for most of our 15 studied species may reflect the current capacity of this forest to recover tree biomass and recruit trees from seedling populations at a level similar to primary forests. A meta-analysis by Banin et al. (2023) synthesised evidence of growth and mortality of 176 sites across tropical and sub-tropical Asia. Within those studies, community-level analyses indicated that active restoration through tree planting can increase the speed at which tree basal area

regenerates within disturbed forests. Similarly, Philipson et al. (2020) found that actively restored forests in the Ulu Segama Forest Reserve (a secondary logged forest adjacent to the Malua Forest Reserve) had aboveground carbon recovery rates over 50% greater than naturally regenerating forest fragments. Our results could suggest that a single round of logging, as was experienced by the Malua Forest Reserve when the Sabah Biodiversity Experiment was established, does not drastically alter the forest conditions to such a degree that seedling survival and growth rates are strongly affected. Baseline data for seedling growth rates within unlogged forests are sparse, however Manokaran & Kochummen (1987) estimated that growth rates for six dipterocarp species (including *S. macroptera*, *S. parvifolia*, and *S. leprosula*) between 10-19 cm DBH ranged from 1.0 to 3.5 mm $year^{-1}$. Whilst most of our seedlings are well below this size, this growth rate is not outside the predictions for some of our larger enrichment planted seedlings.

However, it is surprising that growth and survival do not generally differ more. Studies show that tropical forest stands have slower recoveries after anthropogenic impacts than natural disturbances, including tree harvesting (Cole et al., 2014; Qie et al., 2019). Crouzeilles et al. (2016) found that forest restoration was more successful if prior disturbance was less intensive, which may be driven by a reduced availability of propagules in anthropogenically-disturbed forests (Banin et al., 2023), driven by recruitment failures and reduced canopy cover (Qie et al., 2019) resulting in disturbance-induced microclimatic condition shifts, including reduced humidity, increased radiation exposure and more extreme temperature ranges (Blonder et al., 2018; Hardwick et al., 2015; Jucker et al., 2018). We would therefore expect differences in growth and survival rates across forest types.

Although no differences in growth rates were identified for most species, slight changes to our modelling approach may yield differing results. Our model predictions suggest that, at the high end of the shared range of values, 14 of our 15 species of enrichment planted seedlings are estimated to grow larger in secondary forest plots than in primary forest plots (Fig. 5.2). Under the assumption that this is random, this gives a cumulative probability [$P(X \geq 14)$] of 0.00049 and suggests that, despite the lack of clear effects with our primary modelling approach, enrichment planted seedlings in secondary forests are growing slightly faster than their primary forest counterparts. Further, in terms of testing, although we used the Bayesian information criterion to assess the improvement of increasing model complexity, post-hoc comparison revealed that alternate model selection methods could reveal different results. For example, if the Akaike information criterion is used instead, separate smoothers are preferred for forest type for all species (Fig. D3) and then results suggests that 14 of our 15 species of enrichment planted seedlings grow faster in secondary forest plots. This highlights the wider issue of reproducibility in ecology, illustrated by a recent reproducibility study showing that 246 biologists obtained different results from the same data set depending on modelling choices such as the information criterion used (Gould et al., 2023).

If we consider our results in light of these additional analyses, an increase in growth rates for nearly all species, which includes both more light-demanding and shade-tolerant species (Saner et al., 2016), is understandable if the secondary forest is mechanistically undergoing a relatively early stage of ecological succession. Few studies have directly assessed and compared changes in tree demographic rates across levels of forest disturbance (Rozendaal & Chazdon, 2015), but we would expect growth rates to be greater early in succession for both pioneer and shade-tolerant species (Van Breugel et al., 2006).

In the context of logging, mature tree abundances are reduced and competition with established, more competitive individuals is reduced (Potvin & Dutilleul, 2009; Velázquez & Wiegand, 2020), whereas limiting resources, including light, are more readily available. Later in succession, we expect growth rates for those same species to reduce as a result of canopy closure increasing competition for resources including light (Uriarte et al., 2004). This suggests that the disturbance experienced after a single round of logging at the Sabah has not resulted in a collapse in growth and recruitment of seedlings within the first 16 years following active restoration. In line with typical observations in ecological succession, we would therefore predict a subsequent reduction in secondary forest seedling growth rates to rates similar to those observed in primary forest.

Species-specific responses to habitat degradation

Some of our studied species did show clear differences in growth and survival between forest types. There is a growing evidence base for species-specific responses to heterogeneous environmental conditions (Harrison & LaForgia, 2019; Qie et al., 2019). In an Indonesian study, Kardiman et al. (2019) showed that 38 lowland tropical tree species showed different survival rates in response to forest type, light availability, and shrub and bamboo presence within Sumatra. In the Danum Gaps-Understory experiment, O'Brien et al. (2023) showed that twelve species had a significant negative response to excess rainfall, two showed a positive response, and eleven were neutral. From this, they argue that tolerance to saturated soils due to excessive rainfall is limited to only some species due to prolonged high rainfall. Qie et al. (2019) found that naturally regenerating seedlings show species-specific responses to varying forest degradation levels in Borneo, and Clearwater et al. (1999) found that *S. johorensis* seedlings were able to acclimatise to a new post-

logging environment after three months. It may not be unreasonable, then, for certain species to be better adapted to disturbance generally.

One additional consideration relates to the tree stock used in planting. Ang et al. (2016) investigated the genetic diversity of the enrichment planted stock of *S. leprosula* and *P. malaanonan,* which were used in replanting projects including the Sabah Biodiversity Experiment and Danum Gaps-Understory Experiment. They found species-level variation in seedling stock genetic diversity due to varying numbers of parent trees for each tree species during mast fruiting events. Some species could show extreme responses as a result of limited local genetic variation and poor genetic stock. Further, the second cohort planted at the Sabah Biodiversity Experiment was planted with seedlings from a more diverse stock of parent trees, and so further work investigating the genetic diversity of all 15 studied species across both cohorts would help address this consideration.

Growth-mortality trade-off

Overall, our estimate of relative growth rate was positively correlated with mortality. This supports the idea that species differ in their ecological niches through differential investment in functional traits, manifesting as differences in growth and mortality life history traits (Huang et al., 2018). This work follows earlier analyses that identified a trade-off between growth and survival at the Sabah Biodiversity Experiment (Philipson et al., 2014; Tuck et al., 2016), but provides an update over a longer time span and demonstrates the same general trade-off is also present in the nearby primary forest of Danum Valley.

This trade-off is likely driven by specific functional traits which are important to a species' environmental adaptation, namely light (Banin et al., 2023; Giannini et al., 2017; Laughlin,

2014). On Barro Colorado Island, Panama, Welden et al. (1991) found a strong negative relationship between median annualised percent growth in gaps and annualised percent survival in the shade. Within Danum Valley, a separate study found a similar trade-off; *Shorea johorensis* and *Hopea nervosa* grew to mean heights of 10 m and four metres, respectively, in gaps environments and had survivorship of 35% and 60%, respectively, in the shaded understory over a six and a half year period (Whitmore & Brown, 1996).

We instead identified a positive correlation between growth in each forest type and no evidence of a correlation between survival rates in each forest type, which supports an earlier result seen by Philipson et al. (2014) at the Sabah Biodiversity Experiment in that, at least for growth, species are performing as well as one another despite ecological changes. This result could be due to a range of factors, such as the type of disturbance the Malua Forest Reserve underwent, the relatively long observation period, and the fact that these seedlings are planted *in situ* rather than in a controlled setting. In addition to light, studies have also reported that available of below-ground resources alter the strength of the light-based survival-growth trade-off (Dent & Burslem, 2009). Future research would benefit from a more comprehensive assessment combining data relating to forest local abiotic conditions of interest and with a greater number of species to identify any dipterocarp-wide generalisations.

Mechanistically, leaf nitrogen, leaf phosphorus, leaf thickness, dry weight, wood density, and specific leaf area are traits most widely used to describe the functional diversity of a tree community (Cosset & Edwards, 2017; Huang et al., 2018; Poorter et al., 2019; Veryard et al., 2023a). At the Sabah Biodiversity Experiment, Philipson et al. (2014) showed that seedlings' growth and mortality rates were negatively correlated with wood density. However, no correlation was observed for specific leaf area, seed mass, or leaf C:N ratio.

A similar result was found again at the Sabah Biodiversity Experiment by Tuck et al. (2016). Interestingly, Banin et al. (2023) found that wood density was negatively associated with tree growth rates but was heavily dependent on the habitat condition, with no relationship being identified in open degraded conditions. Future work at the Sabah Biodiversity Experiment and the Danum Gaps-Understory Experiment should focus on estimating study-specific functional traits to better determine how logging impacts the role of functional traits at the growth-survival trade-off.

Within-species variation and the effect of unstudied potential variables

Within each level of species and forest type we observed a large amount of variation in survival and growth rates. This variation could be explained by additional unconsidered variables. One such covariate is light, which has long been considered important for tropical niche differentiation (Denslow, 1987), and has been shown to positively affect growth at our sites previously (O'Brien et al., 2023; Philipson et al., 2014; Veryard et al., 2023b). Another potential variable is rainfall, as O'Brien et al. (2023) showed that species were largely negatively impacted by excess rainfall at the Danum Gaps-Understory Experiment. Interestingly, a meta-analysis by Banin et al. (2023) showed that elevation and climatic terms were unimportant drivers for mortality across restoration projects in Southeast Asia. Broader work directly comparing light, rainfall, and wider climatic variables to tree growth and survival across forest types is needed to provide more certainty on the ecological impacts of logging.

An additional consideration is the effect of the surrounding tree matrix. Our planted seedlings comprise a comparatively small proportion of the surrounding total tree biomass. Therefore, the level of competition experienced at each plot for each species is likely to be

substantially more variable and dependent on the surrounding matrix. Veryard et al. (2023b) mapped the spatial location, size, and species identity of surrounding matrix trees > 10 cm DBH from two planting lines of each secondary forest plot in this study and estimated that the matrix had a density of 27.4 m^2 ha^{-1}. They also showed that increasing the total matrix basal area around an enrichment planted dipterocarp increased seedling survival but did not affect growth, which may explain some of the variability seen in our survival estimates. We do not have specific estimates of tree matrix density surrounding our seedlings in the Danum Gaps-Understory Experiment, although we would expect it to be greater than the selectively logged Sabah Biodiversity Experiment. For example, Hayward et al. (2021) showed that the mean basal area of stems > 2 cm DBH in the Danum Valley Conservation Area was more than double that of the Ulu Segama Forest Reserve (adjacent to Malua Forest Reserve). Additional data on the level of matrix-tree competition will be needed to fully understand how the competitive landscape to the growth and survival of seedlings across each experimental site.

A final variable that should be considered in future studies is how the growth and survival of enrichment planted dipterocarp seedlings is impacted by El Niño drought events. The initially planted cohort at the Sabah Biodiversity Experiment coincided with an El Niño drought and experienced a much greater proportion of mortalities in the first few years of establishment (Fig. D1). Although El Niño events can now be more readily and accurately predicted (Nobre et al., 2019), active restoration projects that coincide with these extreme periods of drought risk dramatically reducing the success of enrichment planting. Given the regularity of El Niño drought events and the potential increase in extreme El Niño drought frequency linked to climate change (Cai et al., 2014; Dai, 2013), a better understanding of how El Niño drought events impact the growth and survival of enrichment

planted seedlings will be critical in better predicting the outcome of active restoration projects. Future work at the Sabah Biodiversity Experiment comparing the growth and survival rates of the initially planted cohort with the replanted cohort, whose planting did not coincide with an El Niño drought event, will provide additional insights into the impact of extreme weather events on the success of enrichment planting.

Conclusions

Here we show that selectively logged forests may still be functionally similar to old-growth counterparts despite their structural differences. We show comparable growth and survival rates for most of our 15 investigated species but also considerable variation within species and forest types and recommend that future research focuses on developing a stronger scientific understanding of seedling growth and survival in the context of their surrounding matrix and abiotic conditions. A greater focus on seedling success in primary forests may help provide suitable benchmarking targets for active restoration projects alongside naturally regenerating comparisons.

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Chapter 6: General discussion

Summary of main findings

In this thesis, I have addressed the effectiveness of active restoration in the recovery of Southeast Asian tropical forests and methods to enhance restoration efforts. I provide an up-to-date summary of the state of forest restoration science in Sabah, Malaysian Borneo, and the context for the experiments established there.

Using a long-term, field-scale experiment, I show that satellite-derived metrics of aboveground biomass increase through active restoration relative to naturally regenerating plots. I also demonstrate the positive relationship between aboveground biomass accumulation and species richness of planted seedlings following 10 years of growth. I argue, based on transgressive overyielding of aboveground biomass estimates in species-rich plots, that these effects are driven by complementarity effects and do not find strong evidence of selection effects within the Sabah Biodiversity Experiment. I explain how the lack of effect within my four-species plots is linked to the limited amount of functional diversity between plots and suggest that longer monitoring periods will be needed to potentially identify these trends in the future. Whilst I found no change in aboveground biomass estimates between sites with and without additional liana removal, I use a simple methodology, combined with the clear negative effect of liana growth on timber yields, to show that liana removal treatments have a prolonged impact on tropical forest community structure nearly 10 years after removal treatment.

I show that enrichment planted seedling survival is positively related to the surrounding matrix basal area and is driven by increased heterofamilial densities. Although alternative

explanations based on environmental stochasticity need to be investigated further, I call for this test to be repeated in primary forest conditions and hypothesize that the result, if driven by positive heterofamilial density-dependence, will be reduced in old-growth forest conditions. I also show that increased light availability in once-logged secondary forests can increase growth and survival rates.

I recommend that old-growth forests should play a more active role in the restoration of tropical landscapes by providing benchmarking data for seedling growth and survival. I show that growth and survival rates are similar between long-term primary and secondary forest experiments. Together, I suggest that community changes in terms of adult tree recruitment are driven to a greater extent by shifts in survival rates than growth rates and call for a greater understanding of benchmark ecosystem functioning in old-growth forests.

These results have strong implications for climate change mitigation, as we show that high-biodiversity active restoration measures have a strong potential to increase carbon sequestration as well as other ecosystem functioning and stability measures of tropical forests. Finally, I address design questions of the Sabah Biodiversity Experiment to improve our overall confidence in the results this experiment generates, including demonstrating the remarkable accuracy of the planting treatment design using a multi-band global navigation satellite system (GNSS) receiver and finding no evidence of seedlings being initially planted in a non-random order based on size. The Sabah Biodiversity Experiment and other long-term active restoration experiments within Southeast Asia should be prioritised for long-term monitoring so that long-term field-scale effects can be realised, helping to advance our understanding of recovering tropical forest systems.

Active restoration as an effective means of restoring selectively logged dipterocarp forest functioning

This thesis sits within the growing debate concerning the overall effectiveness of tropical forest restoration in accelerating forest recovery relative to natural regeneration (Banin et al., 2023; Crouzeilles et al., 2017; Philipson et al., 2020). Evidence against the effectiveness of active restoration includes work by Poorter et al. (2021) which showed that naturally regenerating tropical forests in the Americas and West Africa can recover to old-growth levels in two decades if post-deforestation land use intensity is low, and a global meta-analysis by Crouzeilles et al. (2017) which suggested that biodiversity and vegetation structure recovery is higher for naturally regenerating forests than actively restored forests.

In Chapter 3, I show a clear positive relationship between satellite-derived estimates of aboveground biomass and the use of active restoration techniques. This result became apparent within five years of the experiment commencing, supporting the idea that active restoration provides tangible ecological benefits within Southeast Asia (Banin et al., 2023) and improves recovery rates relative to natural regeneration. Our results, along with other work at the Sabah Biodiversity Experiment (Philipson et al., 2020; Wu et al., 2020), strongly argue that active restoration is an effective tool for increasing aboveground biomass accumulation rates in dipterocarp-dominated forests. Our results likely differ from the conclusions of Poorter et al. (2021) and Crouzeilles et al. (2017) because the ecology of the Dipterocarpaceae makes them a unique challenge in ecological restoration. Their irregular mast fruiting, short dispersal distance, and recalcitrant seeds (Ashton et al., 1988; Umarani et al., 2015) dramatically increase the impact of selective logging on forest resilience. Forests in Sabah have also experienced particularly intense selective logging

(Reynolds et al., 2011), which is known to reduce the success of natural regeneration (Banin et al., 2023).

Keller et al. (2023b) carried out an observational study at the adjacent Ulu Segama Forest Reserve which was enrichment planted using a similar methodology to the Sabah Biodiversity Experiment. They found a positive influence of active restoration management on both tree diversity and forest structure of adult trees and seedlings relative to naturally regenerating plots. The authors also found an increase in rare tree species as a result of active restoration measures. This observational result suggests a mechanism which drives the increased productivity I identified within the enrichment planted plots at the Sabah Biodiversity Experiment. When active restoration is conducted in an ecologically considerate manner (e.g., Edwards et al. (2021) and Veldman et al. (2019)), an increase in species richness should be expected to increase functioning under biodiversity-ecosystem functioning theory (Isbell et al., 2017). In particular, rare species tend to be functionally important to their ecosystems (Lyons et al., 2005), and so promoting rare species should disproportionately increase ecosystem functioning (Mouillot et al., 2013). This logic provides an additional explanation for the negative effect of active restoration identified by Crouzeilles et al. (2017), in that their meta-analysis included cases of active restoration where non-native species were planted in monoculture, which have substantially different ecological consequences and explanations relative to the methodology used at the Sabah Biodiversity Experiment.

A remaining knowledge gap in the context of active forest restoration is how financially effective these projects are. Only a handful of projects have reported the costs and additional carbon yields from active tropical restoration projects (Holl & Zahawi, 2014; Wheeler et al., 2016), including projects at the Sabah Biodiversity Experiment (Philipson

et al., 2020). Additional financial incentives beyond carbon funds may make tropical forest restoration more viable, such as through crediting systems that reward biodiversity directly which allow restored forests to generate income through increases in both biodiversity and carbon sequestration (Tedersoo et al., 2023). One clear consensus globally is that there is high variability in the outcome of active restoration (Banin et al., 2023; Crouzeilles et al., 2016), which makes forest restoration a financially risky yet potentially rewarding strategy depending on geography and land-use history.

The effect of biodiversity on ecosystem functioning

After showing that active restoration positively affects tropical forest functioning, I also investigated the role of enrichment planted seedling biodiversity on ecosystem functioning. A decade of research has highlighted the generally positive relationship between biodiversity and ecosystem functioning (Balvanera et al., 2006; Hooper et al., 2005; Loreau et al., 2022). However, most experiments have been conducted in microcosms or northern temperate grassland ecosystems and, as a result, there is a risk of over-generalising the current consensus to tropical forests. In Chapter 3, I provide evidence from a 500-ha biodiversity experiment that the success of enrichment planting, in terms of satellite-derived aboveground biomass and canopy cover, is positively associated with the species richness planted. This field-scale result supports the range of smaller tropical and subtropical biodiversity experiments that have identified a similar trend (Barrufol et al., 2013; Huang et al., 2018; Potvin & Gotelli, 2008). The experiment taking place *in situ* and the use of two separate satellite systems to provide the same qualitative result provide further credibility to my result. In terms of practical recommendations, I show that the benefits of active restoration can be enhanced even further relative to naturally regenerating plots with a more species-rich planting mix.

Biodiversity in the tropics has been shown to support other ecosystem functions beyond aboveground biomass. For instance, the hydrological cycle depends on canopy evapotranspiration rates (Bruijnzeel, 2004). Keller et al. (2023a) showed that their models of throughfall in dipterocarp forests were improved with the inclusion of the Shannon Diversity Index in some cases but did not substantially improve overall model performance. Geißler et al. (2013) found throughfall kinetic energy in a mixed evergreen broad-leaved sub-tropical forest was related to rarefied tree species richness, and Zimmermann et al. (2013) showed that rainfall interception was increased in forests with greater variation in tree size, of which species identity could be a component (Ashton, 1982).

The effect of biodiversity on ecosystem functioning was not immediately apparent. In Chapter 3, I found that the relationship between biodiversity and satellite-derived canopy openness measures could first be detected in the 2008-2012 monitoring period, though the overall effect of active restoration was apparent in the earlier 2003-2008 monitoring period. It is unsurprising, then, that some treatments in our experimental design had no identifiable effect within 10 years of investigation. This may explain the lack of a biodiversity effect on forest recovery in a Costa-Rican experiment by Gilman et al. (2016), which compared total basal areas of plots along a range of planted species richness. Since an effect of biodiversity was identified at the Sabah Biodiversity Experiment after around 10 years, the fact that Gilman et al. (2016) did not find an effect of biodiversity after 5 years is perhaps not surprising. Of the experiments collated by Banin et al. (2023), the Sabah Biodiversity Experiment is among the longest-running at approximately 240 months. Most Southeast Asian forest active restoration studies are less than 10 years old and are unlikely to continue indefinitely. As such, it may be rare to find any effects of biodiversity on tropical tree ecosystem functioning in short-running projects. Even within the Sabah Biodiversity

Experiment, subtler treatments, such as the effect of genus diversity and canopy structural complexity within four-species plots, could take much longer to become apparent, if at all. Greater focus should be placed on maintaining existing biodiversity experiments in the long term if these effects are to be fully investigated at the field scale.

Interestingly, my results in Chapter 4 found no effect of plot type (single-species or 16-species plots) on the growth or survival rates of enrichment planted seedlings, seemingly in contrast to the result identified in Chapter 3. One explanation relates to the length of each study period. In Chapter 4 seedlings were measured twice between December 2012 and May 2015, a shorter time period than the 10-year observation period used Chapter 3. Additionally, field-based assessments by Tuck et al. (2016) of the same single-species and 16-species plots analysed in Chapter 3 found no evidence of complementary species interactions in more species-rich plots as assessed by comparisons of diameter at breast height. Our satellite imagery was taken at roughly the same time as the survey data used in Tuck et al. (2016) (August 2012 and November 2011–September 2013, respectively). Combining my Chapter 3 results with those of Chapter 4 and Tuck et al. (2016), I suggest that the effects of diversity are not realised through increased survival or diameter growth of the enrichment planted seedlings. To explain the difference between these remotely sensed and field measurements, I suggest that my satellite-detected changes in aboveground biomass are due to the development of different canopy architectures in multispecies mixtures compared to single-species plots, which generates complementarity between tree crowns in plots with more complex species mixtures in a way similar to what has previously been observed in Europe (Jucker et al., 2015). Under this hypothesis, studies only estimating forest functional changes via tree stem measurements may fail to account for the complexity associated with a forest's three-dimensional structure. This canopy

architecture-driven mechanism may provide an additional explanation for the lack of a biodiversity effect observed in Gilman et al. (2016). Changes to the canopy architecture may help explain other positive relationships between biodiversity and ecosystem functioning, such as the finding by O'Brien et al. (2017a) that seedlings planted in diverse communities can better maintain growth under drought. We would expect increased crown complementarity to result in increased tree diameters in the longer term, but we do not know how long this feedback period may take. Research on the relationship between biodiversity and canopy architecture will be needed to test this hypothesis in the future. For instance, Asner et al. (2018) used a combination of airborne LiDAR and satellite imaging to determine canopy heights across Sabah and showed that unlogged forests had generally taller top-of-canopy heights than logged forests, so potential further research could use these methodologies to monitor canopy architecture in response to species diversity in an experimental setting. Use of these technologies and methodologies at the Sabah Biodiversity Experiment will ultimately allow us to quantitatively explore canopy-specific differences between plots, and test my hypothesis that the observed biodiversity effect identified in Chapter 3 is realised through different canopy architectures.

The fact that remote sensing can provide insights into forest manipulations of seedlings is a key result, although there is a lot of uncertainty as to how well satellite imagery, which is effectively a two-dimensional snapshot, can be used to make accurate estimates of biomass in a three-dimensional forest landscape (Mitchard et al., 2014) due to their limited capacity to penetrate beneath a forest canopy. In particular, the allometric equations developed by Pfeifer et al. (2016) and used in Chapter 3 have been subject to debate regarding their ability to accurately predict aboveground biomass scores. Under or over-estimating aboveground biomass in tropical forests, and consequently carbon yields, carries risk since these values

are often directly related to carbon credits, and ensuring that financial investment and public policy are not misdirected is critical. For this reason, the purpose of Chapter 3 was primarily to identify differences between plots within our experimental design rather than to estimate absolute values, since the qualitative result identified adds strongly to the growing body of support for the relationship between biodiversity and ecosystem functioning within the tropics and has strong relevance to forest management practice even without accurate quantitative estimates. Moving forward, obtaining an accurate remotely-sensed estimate of aboveground carbon accumulation is important, and will be complementary to the work I carried out in Chapter 3 in providing a more accurate and detailed estimate of the capacity for enrichment planted biodiversity to enhance carbon sequestration, and to provide additional calibration for future optical satellite estimates of ecosystem functioning at the Sabah Biodiversity Experiment.

Whilst acknowledging the risks of using optical satellite-derived measures of aboveground biomass, the estimated values I estimated in Chapter 3 are higher than I initially anticipated. After one decade, I estimated that planted forests produced 43.3 Mg ha^{-1} more aboveground biomass than our control plots, resulting in a carbon sequestration increase of approximately 2.05 Mg C $year^{-1}$ assuming that carbon content is 47.4% of total aboveground biomass (Martin & Thomas, 2011). This is larger than the estimate derived by Philipson et al. (2020), who estimated increased carbon accumulation rates of around 1.5 Mg C ha^{-1} $year^{-1}$ at the nearby Ulu Segama Forest Reserve. However, using the same methodology, I also estimate the carbon content of our control plots at the Sabah Biodiversity Experiment to be approximately 86.6 Mg C ha^{-1}, within the estimations made by Asner et al. (2018).

Implementation of the biodiversity-ecosystem functioning relationship into policy

One immediate question raised by the now clearer relationship between biodiversity and ecosystem functioning is how these results can be integrated into tropical forest management practice. The most direct method is for ecologists to translate pure ecological results into terms relevant to policy. In Chapter 3, I estimated that 16-species plots contained approximately 48 Mg ha^{-1} more aboveground biomass than single-species plots. Although there are concerns surrounding satellite remote sensing-based biomass estimates (Mitchard et al., 2014), assuming that the majority of this biomass was in the form of tree stems and that 47.4% of wood is carbon (Martin & Thomas, 2011), this result suggests that if every plot had been planted with 16 dipterocarp species it would have yielded an additional 22.8 Mg C ha^{-1} than if the site were planted with exclusively single-species plots. More widely, Huang et al. (2018) showed that, in a Chinese subtropical forest, 16-species mixtures accumulated around 1.7 times the amount of carbon found in a typical monoculture, and a global meta-analysis comparing mixed-species to single-species stands found that mixed stands increased productivity by 24% (Zhang et al., 2012). A global meta-analysis of a network of tree experiments suggested that aboveground carbon stocks were 70% higher in mixed planted forests than single-species plantations (Warner et al., 2023). By providing these results in terms directly relevant to policy, such as potential carbon yields, information can be made more easily accessible to policymakers. More practically, forest concessions should explicitly reward diversification of seedling stock and, where necessary, proactively find solutions to potential cost barriers for high-diversity restoration, including financial support as well as management advice and best practices.

Biodiversity and ecosystem functioning mechanisms

Evidence of complementarity effects

The relationship between biodiversity and ecosystem functioning has emerged as a central issue in ecology this century (Cardinale et al., 2007). Of the two main processes thought to drive the biodiversity-ecosystem functioning relationship I identified in Chapter 3, I show clear evidence for complementarity effects. For aboveground biomass, plots planted with 16 species generally outperformed all single-species plots, demonstrating overyielding. Only a single plot planted with one species yielded a comparable aboveground biomass estimate (280.6 Mg ha^{-1}, 16-species mixture average = 261.6 Mg ha^{-1}), yet several 16-species mixtures outperformed this, showing evidence for transgressive overyielding at the Sabah Biodiversity Experiment.

Complementarity is driven by niche differentiation and facilitation effects (Loreau & Hector, 2001). We expect to see niche differentiation within the Dipterocarpaceae for both light (Philipson et al., 2014) and water availability (O'Brien et al., 2020), although experiments identifying these mechanisms are limited (Grossman et al., 2018). I suggest in Chapter 3 that increased biodiversity generates different canopy architectures resulting in spatial complementarity. Tree crown architecture is critical for optimising light capture and is closely related to tree performance (Poorter et al., 2006). Evidence of canopy niche differentiation has been observed in Canada (Williams et al., 2017), Europe (Jucker et al., 2015) and China (Niklaus et al., 2017; Xu et al., 2022), although research on canopy complementarity in dipterocarp communities is limited (Huang et al., 2018). As well as aboveground resources, differential use of belowground resources like water and nutrients may also be a driver of complementarity effects in dipterocarp forests, and it has been suggested that variation in root depths, total root biomass, and root types can underlie

specialisation (Berendse, 1981; Markesteijn & Poorter, 2009). In China, Bu et al. (2017) and Sun et al. (2017) showed evidence of overyielding in response to different root traits, including root length and diameter, so spatial complementarity may extend into the soil as well as the canopy. Experiments in multi-trophic systems have also found that finer partitioning of resources can occur in high-diversity systems (Ives et al., 2005) when there is a high proportion of specialist species (Finke & Snyder, 2008), in line with classic niche partitioning theory. As dipterocarp lowland forests are among some of the most diverse communities globally (Brown, 2014), niche partitioning is expected to make up a large part of complementarity effects in the tropics.

Facilitation may also have a role in the complementarity effects observed. In the literature, this is most commonly linked to amelioration of abiotic stressors across a diversity gradient (Grossman et al., 2018). Whilst there is evidence of facilitation in grassland communities (Adair et al., 2009), there is limited evidence of an interaction between abiotic stressors and tree diversity. Kothari et al. (2021) investigated how tree diversity can ameliorate excess light stress impacting a plant's growth. They demonstrated that one of their studied temperate species showed reduced growth rates whilst in monoculture relative to a biculture, but most other species showed dominantly competitive interspecific interactions. More widely, an experimental drought gradient in Dillen et al. (2016) and the local abiotic conditions in Kröber et al. (2015) were found to not explain the biodiversity-ecosystem functioning relationships observed. Additionally, dipterocarps form ectomycorrhizal associations (Brearley, 2012), which are known to be able to facilitate carbon transfer between plants (Francis & Read, 1984) and between species (Simard et al., 1997). However, there is currently no evidence that dipterocarps connected to a community-wide ectomycorrhizal network experience facilitated growth or survival (Brearley et al., 2016b),

in contrast to the facilitation seen in other less diverse tropical forests (McGuire, 2007; Simard et al., 2012). This difference is thought to be due to the extreme host generalism of ectomycorrhizal fungi within lowland dipterocarp forests (Brearley et al., 2016b).

Complementarity effects are driven by species presenting differing functional traits, which reflect and dictate resource utilisation. In Chapter 3, I showed that species-rich mixtures also have greater values of functional diversity, aligning with the finding by Williams et al. (2017) that spatial complementarity of tree crowns was positively related to functional diversity. As we see growing arguments for community ecology to be considered from a functional perspective (McGill et al., 2006; Violle et al., 2012), in Chapter 3 I investigated the effect of altering functional diversity whilst holding species richness constant. I found no effect of functional diversity on plot-level aboveground biomass but noted that the range of functional diversity within four-species plots is relatively small. I believe that this narrow range in functional diversities is in part because species were chosen for each plot to achieve predetermined levels of genus diversity. Since nine of our 16 species belonged to the genus *Shorea*, this meant that many species (especially *D. conformis* and *D. lanceolata*) were used across many four-species plots, reducing the functional diversity gradient achieved across these plots. As it took up to 10 years for biodiversity effects to become apparent, the much narrower range of functional diversities may suggest that a significantly longer period of time is needed to show differences between four-species plots, if any are present.

Evidence of selection effects

The observed overyielding suggests complementarity effects are taking place but does not necessarily exclude selection effects. In our species-rich mixtures, a selection effect could

be realised by high-yielding species becoming dominant within a mixture, through either higher growth rates or lower mortality rates (Loreau et al., 2022). My satellite remote sensing data in Chapter 3 is unable to partition aboveground biomass to individual enrichment planted species. However, in Chapters 4 and 5, I used individual enrichment planted seedling growth and survival data for the six intensively surveyed 16-species mixtures. If selection effects are present, we would expect to see a positive relationship between the aboveground biomass estimate of species in their single-species mixtures and the growth or survival rate of those species in the sixteen-species plots (as a measure of dominance). To test this, I compared each species' remote sensed aboveground biomass estimate when in single-species mixtures to their growth and survival rates when in 16-species mixtures. I found no correlation between aboveground biomass in monocultures and relative growth rate (defined as the difference in log-transformed basal diameter (mm) over time (years) between the first and last measurement of the basal diameter of each enrichment planted seedling; $r_{(14)}$ = -0.037, 95% CI = -0.52 to 0.47) or survival ($r_{(14)}$ = -0.21, 95% CI = -0.64 to 0.31) within 16-species mixtures (Fig. 6.1). This result, combined with the identified transgressive overyielding, suggests that selection effects, if present, are less important than complementarity effects in the biodiversity-ecosystem functioning relationship in lowland dipterocarp forests.

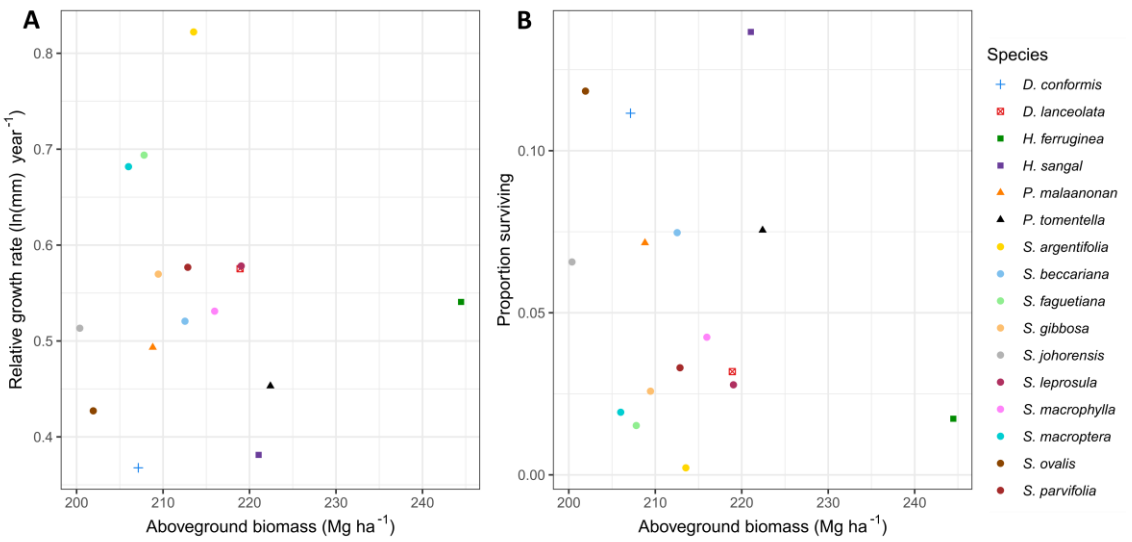

Figure 6.1 Correlations between individual species success in single-species plots and 16-species mixtures. (**A**) Correlation between satellite-based estimates of aboveground biomass in single-species plots and relative growth rate in 16-species mixtures, $r_{(14)}$ = -0.037, 95% CI = -0.52 to 0.47 (**B**) Correlation between satellite-based estimates of aboveground biomass in single-species plots and survival in 16-species mixture, $r_{(14)}$ = -0.21, 95% CI = -0.64 to 0.31.

Because tropical systems are generally species-rich (Brown, 2014), some argue that slight changes to biodiversity will have a relatively small impact on overall functioning (Clarke et al., 2017). However, in Chapter 3, we show clear benefits of increases in enrichment planted species richness. I hypothesize that this reflects the disturbed state of the secondary forest canopy, and that at relatively low biodiversity levels, increases in species richness have a stronger impact, supported by the loglinear relationship we identified between biodiversity and ecosystem functioning in Chapter 3. This relationship predicts marginal benefits from continued increases in species richness. One alternative consideration is that the Sabah Biodiversity Experiment used a range of species that covered a diverse range of physiological and functional traits (Tuck et al., 2016), and that the increases in ecosystem

functioning seen in Chapter 3 may not be as clear if we were to choose a random selection of 16 dipterocarp species found within the Malua Forest Reserve. Whilst this explanation does not dispute the qualitative result found, it would imply that the effect size may be smaller with the random inclusion of additional species.

Long-term biodiversity experiments should also consider the temporal effect on the balance between complementarity and selection effects. Theory suggests that complementarity effects will increase over time whilst selection effects remain transient (Loreau et al., 2022), initially being strong as the most competitive species rapidly establish, but falling away as the community tends towards a stable state. Fargione et al. (2007) showed in a 10-year biodiversity experiment that the mechanism driving the positive relationship between biodiversity and plant biomass production was dominated by selection effects within the first two years, and complementarity between species became dominant in the following eight years. Our strong findings of complementarity effects align with the arguments of Fargione et al. (2007) given the timespan of our experiments. It is worth acknowledging that complementarity effects and selection effects cannot be applied to the Sabah Biodiversity Experiment in the same way as weeded grassland experiments or forest plantations, since the naturally occurring trees surrounding enrichment planted seedlings have not been experimentally controlled and do not have null expectations for growth in species-rich plots. However, on the timescales relevant to forestry, we should perhaps expect complementarity effects to be dominant, and further work should focus on complementarity effects as an important mechanism to better understand tropical forest recovery rates.

Effect of liana removal

In Chapter 3 I showed that, at the time of satellite image collection in August 2012, no differences could be detected between 16-species enrichment planted plots with and without additional liana removal treatment. This is contrary to previous work that demonstrated a positive effect of liana removal on the growth and survival of dipterocarps (O'Brien et al., 2019). I suggest two explanations for this result. First, the time between the liana removal treatment (July 2011) and the image capture date (August 2012) may have been insufficiently long. Since biodiversity effects only became apparent around 10 years after planting, more time may be needed before this additional treatment yields clear results. Second, the spatial resolution for our satellite imagery ranges from five metres to 30 m, which is likely insufficient to identify differences in the aboveground biomass of trees and lianas from the canopy. A methodology that can distinguish the aboveground biomass attributed to lianas and canopy trees would help address this concern, such as technologies that can directly scan the canopy and attribute biomass to either liana or non-liana sources. For instance, terrestrial laser scanning combined with machine learning algorithms has been shown to detect 70% of liana stems in Panamanian forest plots (Moorthy et al., 2019).

Aiming to identify an effect of liana removal, I travelled to the Sabah Biodiversity Experiment in May 2023 with the original aim of conducting a drone-based mapping project to quantify the difference in aboveground biomass between the 16-species enrichment planted plots which did and did not have additional liana removal treatments applied. Unfortunately, due to a lack of response to my drone permit application, I was unable to carry out this project's primary scope. Instead, I carried out a ground-based assessment of canopy liana and non-liana vegetation cover using a canopy scope with

methods outlined in Hale & Brown (2005) and Brown et al. (2009). Eight 16-species plots with additional liana removal treatments were selected, as well as eight adjacent 16-species plots which did not undergo additional liana removal. Within the plot's central 100 x 100 m survey area, 16 regularly distributed points were identified for sampling (Fig. 6.2). At each point, a canopy scope was used to estimate the percentage of canopy scope points overlapping with open sky, lianas, or non-liana vegetation canopy. This was repeated for each cardinal direction, and the arithmetic mean was calculated.

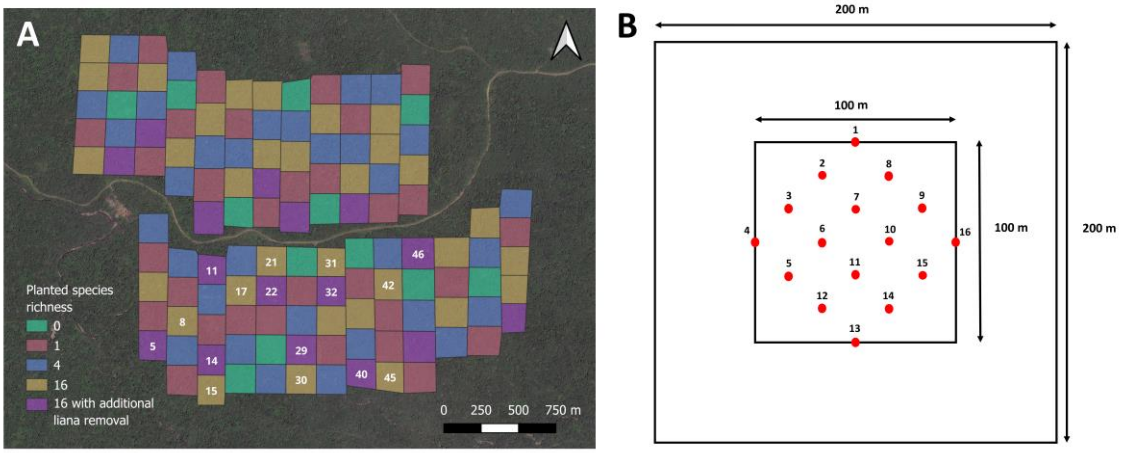

Figure 6.2 Canopy scope data collection methodology. **(A)** Data was collected from 16 plots, consisting of eight 16-species plots with the additional liana removal treatment and eight adjacent 16-species plots without additional liana removal. Numbered plots represent plots surveyed. **(B)** Within each plot, a 50 m buffer was used to create an internal 100 x 100 m subplot, and points were pre-determined using a diamond pattern as outlined in Hale & Brown (2005).

Data was analysed with a beta regression in R (version 4.3.1; R Core Team (2023)) with the 'glmmTMB' package (version 1.1.7; Brooks et al. (2017)) to identify changes in the proportion of the canopy scope recording liana, non-climber vegetation, and canopy gaps

between plots which did and did not have additional liana removal treatment. This revealed two key results. Firstly, the occurrence of lianas was reduced in the liana-removed plots (estimated proportion = 0.059, 95% CI = 0.049-0.070) compared to control plots (0.199, 95% CI = 0.176-0.223). The proportion of non-liana vegetation covering the canopy scope was also greater in liana-removed plots (0.871, 95% CI = 0.852-0.888) compared to control plots (0.697, 95% CI = 0.668-0.725). Secondly, the proportion of canopy gaps across both forest types was similar (climber-cut and control proportions = 0.086 and 0.094, 95% CI = 0.073-0.101 and 0.082-0.110, respectively; Fig. 6.3).

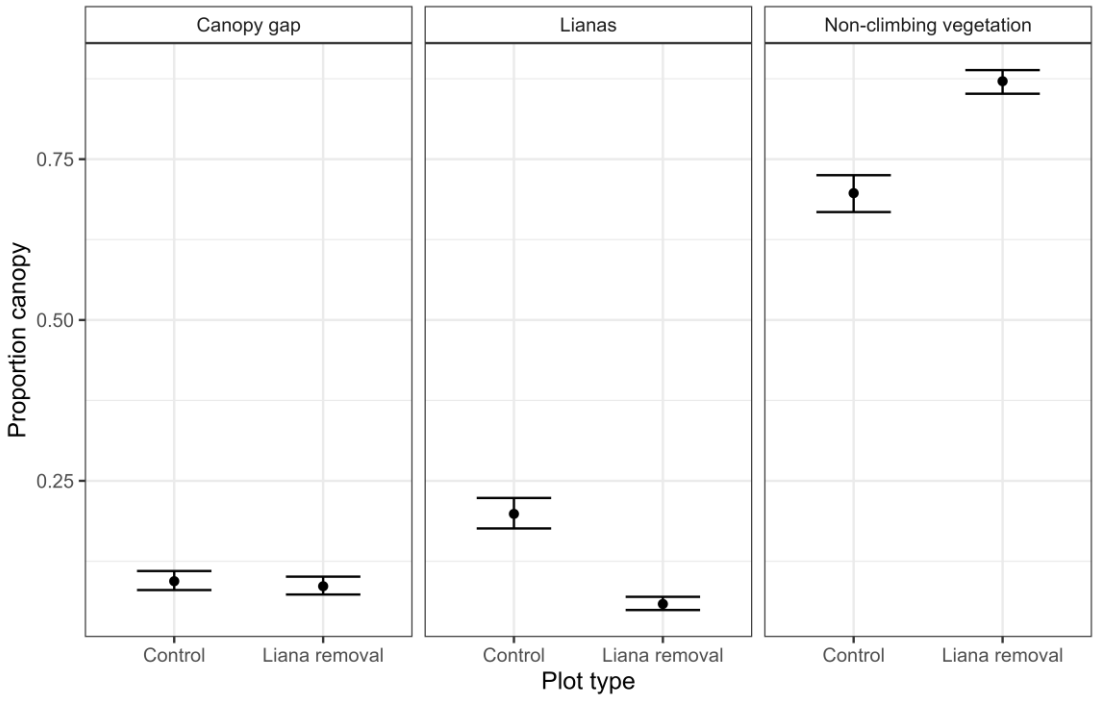

Figure 6.3 Proportion canopy occurrence across 16-species enrichment planted plots at the Sabah Biodiversity Experiment. Mean and 95% confidence intervals are provided for each assessed component of the canopy across 16-species plots with additional liana removal treatment (*Liana removal*) and those without the additional treatment (*Control*).

These results suggest that the liana removal treatment has had a continued effect on forest structure almost a decade after the most recent cutting at the Sabah Biodiversity Experiment. This is supported by a study by O'Brien et al. (2019) study at the Sabah Biodiversity Experiment, which found that liana removal reduced liana density three years after lianas were removed from plots relative to controls. The similarity in canopy gap occurrence between plot types suggests that canopy trees have successfully filled in the gaps created by liana removal and supports the idea that liana removal does have an ecological benefit to the growth of dipterocarp trees. One limitation of the Sabah Biodiversity Experiment's design is that all plots with enhanced liana removal also underwent enrichment planting. Future studies would benefit from isolating the effects of liana removal from enrichment planting within selectively logged dipterocarp forests. For instance, Finlayson et al. (2024) established five 800 x 800 m liana removal sites nearby within the Malua Forest Reserve, and used Sentinel-2 satellite imagery to suggest that canopy disturbance and fragmentation from liana removal was largely indistinguishable from control plots within one year. Still, my work in this thesis provides evidence that the cause of the lack of difference between 16-species plots with or without additional liana removal seen in Chapter 3 is due to lianas occupying parts of the canopy in control plots and suggests that their biomass is being counted towards satellite-derived estimates of aboveground biomass.

Effect of the surrounding forest matrix

In Chapter 4, I analysed the relationship between the survival of enrichment planted seedlings and the surrounding matrix basal area within 10 m of each seedling. This work addressed some of the variability associated with active restoration success at the local level, identified within Chapter 3 and more generally within active forest restoration

literature (Banin et al., 2023). I showed that increasing total surrounding matrix basal area corresponded to increases in planted seedling survival rates. Generally, the relationship between seedling survival and total matrix basal area is negative (Peters, 2003), but positive relationships have been identified when only heterospecific basal area is considered. I suggest my result is linked to the species herd protection hypothesis, where increasing the density of heterofamilial (i.e., non-dipterocarp) trees reduces the risk of family-specific pests and pathogens increasing seedling mortality (Wills & Green, 1995). Because logging in Sabah has heavily focused on extracting dipterocarp trees (Reynolds et al., 2011), increases in matrix basal area in this study were primarily driven by increases in non-dipterocarp trees. However, this theoretical mechanism has potentially simpler alternative explanations; a correlation between surrounding basal area and survival could reflect generally better growing conditions and soils that can support greater densities of trees, either as a result of soil type and topography (Gourlet-Fleury et al., 2011) or limited logging-induced disturbance (Hattori et al., 2013). Testing this alternative explanation is necessary to distinguish between a true effect of positive density-dependence and effects of heterogenous environment quality.

Indirect benefits currently seem to outweigh any direct negative impacts of competition at the Sabah Biodiversity Experiment. At the time of surveying in May 2015, the enrichment planted seedlings studied in Chapter 4 were still relatively small (median basal diameter = 0.9 cm). Because of their size, I suggest that the seedlings were not yet large enough to competitively interact with neighbouring seedlings or the surrounding matrix. For example, although most seedlings are presumably still under the canopy, a negligible amount of shading between seedlings is occurring relative to the larger biotic and abiotic pressures impacting seedling growth and survival. The apparent lack of competition could also be a

result of low mature tree densities in this once-logged forest, reducing the strength of inter- and intra-specific competition between seedlings at an early stage of development. In Chapter 4, I identified a strong positive relationship between canopy openness and the growth and survival of enrichment planted seedlings. This is an unsurprising result, given the strong evidence base for light as a limiting factor for growth within the tropics (Grubb, 1998; Philipson et al., 2012, 2014), but is certainly more complicated than the relationship we identified. For example, O'Brien et al. (2019) argued that, after liana cutting at the Sabah Biodiversity Experiment in 2014, the increased mortality relative to the 2012 cutting period was due to an interaction between increased understory light availability and drought stress. Together, my research provides further evidence that, along with water availability (O'Brien et al., 2014; O'Brien et al., 2017b), light availability is one of the strongest drivers of growth and survival within the Sabah Biodiversity Experiment.

There are some methodological considerations concerning how we collected data on local competition in Chapter 4. We assumed that competition happens within a maximum of 10 m from our seedlings, however very large trees (which were spared from logging) could be further away than this and still cast shade if their canopy is overhead (Naito et al., 2008). Although a 10 m radius was chosen as similar works suggest this distance is sufficient to capture the majority of neighbourhood effects (Fortunel et al., 2016; Lasky et al., 2014), testing this methodology further in the future, including within a primary dipterocarp forest, will help improve the confidence of the conclusions made in Chapter 4.

In Chapter 5, I found that the growth and survival of enrichment planted dipterocarp seedlings appeared unaffected by planting density. This result is interesting, as dipterocarp seedlings can grow much larger than the 0.75 x 0.75 m planting density at the Danum Gaps-Understory Experiment (Yamakura et al., 1986). The apparent lack of competition between

seedlings aligns with my hypothesis that seedlings, at their current size, are not interacting with their surrounding matrix of trees to a strong extent. However, one key unknown variable within the Danum Gaps-Understory Experiment is the degree of competition between the planted seedlings and the surrounding matrix. The surrounding matrix will almost certainly account for most local biomass and likely has a stronger influence on survival than competition exclusively between planted seedlings. However, we currently lack spatial information for the Danum Gaps-Understory Experiment, such as mapping of the pre-existing tree matrix within and around each plot. There is an opportunity to compare the strength of competition with the surrounding matrix between both experimental sites if the same FieldMap system and methodology used in Chapter 4 were to be employed at the Danum Gaps-Understory Experiment, as it would provide a standardised method to compare results with greater confidence.

I hypothesise that competition at the Danum Gaps-Understory Experiment will be stronger than in the Sabah Biodiversity Experiment. I suggest that the lack of a relationship between seedling relative growth rate and surrounding matrix basal area at the Sabah Biodiversity Experiment seen in Chapter 4 is due to the reduced number of mature trees within the forest, reducing the extent of competition between seedlings and the surrounding matrix. I also predict that the relationship between seedling survival and matrix basal area will be negative in the primary forest, as the indirect benefits hypothesised to exist at the Sabah Biodiversity Experiment, including a more hospitable and less variable microclimate, would not be relevant within the undisturbed Danum Gaps-Understory Experiment.

Primary forests as targets for restoration success

In Chapter 5, I show that species-specific survival and growth rates were similar between experiments in old-growth and selectively logged forests, despite differences in both forest reserves' abiotic and biotic conditions. Tropical forests typically recover more slowly following anthropogenic degradation than natural disturbances like treefall-induced canopy gap formation (Paquette et al., 2006). The fact that both forests are growing similarly could indicate that the forest is functioning similarly to its old-growth counterpart. Bischoff et al. (2005) observed that, for dipterocarps, mortality was not different between old-growth and selectively logged forests in Sabah, and Howlett & Davidson (2001) found that herbivory did not produce differences in dipterocarp growth or mortality across forest conditions.

As long as the forest has not converted into an alternative stable state (Beisner et al., 2003), we might expect selectively logged forests to have higher growth rates than old-growth forests (Poorter et al., 2016). In Chapter 5, I showed that 14 of our 15 studied species were predicted to grow more (if not statistically significantly so) at the Sabah Biodiversity Experiment than at the Danum Gaps-Understory Experiment, providing some support that secondary forest plots are growing faster. More widely, there is evidence that the seedling density of selectively logged forests is higher than that of unlogged forests (Kuusipalo et al., 1996), but direct experimental comparisons of seedling growth rates across forest types are limited. In Chapter 4, I identified a positive relationship between canopy openness and enrichment planted seedling growth and survival rates. With fewer mature dipterocarp trees within the Sabah Biodiversity Experiment, we may expect a greater level of canopy openness and, as a result, higher relative growth rates in our selectively logged forest (Bebber et al., 2002). An improved understanding of the light environment at the Sabah

Biodiversity Experiment and the Danum Gaps-Understory Experiment in relation to seedling growth rates will be valuable in addressing these mechanistic questions.

Interestingly, some species did show changes in growth or survival across forest types. Species-specific responses to environmental change have been investigated in Sabah previously. For instance, O'Brien et al. (2023) showed that tolerance to saturated soils from excessive rainfall was limited to only some dipterocarp species and not others, and Qie et al. (2019) found evidence for species-specific responses to forest disturbance in Borneo. Identifying which species retain their primary forest growth and survival rates in anthropogenically disturbed forests, and the mechanisms that drive these changes, will be key to optimising active restoration through species selection.

In Chapter 5, I identified a growth-survival trade-off at the old-growth Danum Gaps-Understory Experiment and the selectively logged Sabah Biodiversity Experiment. This supports previous studies both at the Sabah Biodiversity Experiment (Philipson et al., 2014; Tuck et al., 2016) and beyond (Grubb, 1977; Wright et al., 2010) which show that the growth-survival trade-off is a major element of life-history variation and allows dipterocarp species to demonstrate differential tolerances to variables including light (Philipson et al., 2012), flooding (Born et al., 2014), and drought (O'Brien & Escudero, 2022). I identified no negative correlations in survival or growth in each forest type and instead found a positive correlation between relative growth rates across forest types. Supporting this result, Philipson et al. (2012) showed that some species respond more strongly to variations in light than others but identified no rank reversal in species survival responses. I suggest that any community changes in terms of adult tree recruitment from seedlings will be driven by shifts in survival rates, rather than growth rates. In Chapter 5, my methodology for assessing survival between forest types required the removal of all trees which died before

their first census, which accounted for approximately 75% of seedlings 18 months after planting at the Sabah Biodiversity Experiment. This rate is approximately triple the mean two-year mortality rate identified in Banin et al. (2023) and is likely due to an El Niño drought event that occurred shortly after planting (Tuck et al., 2016). This argument is supported by the fact that the replanted cohort, which experienced no similar subsequent drought, experienced a considerably lower mortality rate (Fig. D1). Similarly, O'Brien et al. (2019) showed that mortality rates for seedlings in plots undergoing their first round of liana removal in 2011 exhibited lower subsequent mortality rates than the plots which underwent their first round of cutting in 2014 at the Sabah Biodiversity Experiment. They suggest that the difference in mortality was due to two subsequent El Niño droughts that occurred in quick succession after 2014. This further supports my hypothesis that community-level changes between forest types are driven by changes in survival rather than growth and that a primary mechanism for these survival-related mortality differences is drought.

Given that growth-survival trade-offs do represent important life-history parameters for dipterocarp species (Tuck et al., 2016; Wright et al., 2010), this positive correlation between growth rates across forest types provides additional evidence that selectively logged dipterocarp forests are not overly hostile, or else we might expect a more extreme change in species performance or even a collapse in the identified growth-survival relationship. This result also provides support for the role of active restoration in dipterocarp forest management, and although there are alternative considerations and explanations to the results produced in Chapter 5 (see Future work) I call for an increase in research on dipterocarp growth and survival rates within old-growth forests to create realistic and data-driven target goals for tropical forest restoration.

Active restoration as a means of climate change mitigation and adaptation

There is considerable momentum for nature-based solutions to have an active role in climate change mitigation (Seddon et al., 2021), of which forest restoration is considered a primary lever to increase ecosystem functioning and stability globally (Warner et al., 2023). These goals are highly applicable to the tropics. For example, Hutchison et al. (2018) showed that mixed stands show more stable growth and reduced mortality in response to climatic extremes relative to single-species stands. One mechanism for this climatic stability is community-level drought tolerance, where monoculture plantations have lower and less stable carbon capture rates due to reduced drought recovery times (Osuri et al., 2020; Pardos et al., 2021). In Chapter 4, I suggest one explanation for the positive relationship between enrichment planted seedling survival and the surrounding matrix basal area: the matrix basal area creates a more stable habitat, mitigating potential extremes in temperature and humidity. This benefit can be extended longitudinally – as the climate shifts and becomes more variable, greater interspecific diversity in a regenerating tropical forest could help mitigate against reductions in ecosystem service provisioning (Hisano et al., 2018).

Despite the advantages of species-rich restoration projects, climate-focused replanting efforts still typically focus on single-species restoration projects globally. Within the tropics, 45% of forest restoration commitments focus on establishing single-species stands despite stand diversification becoming a greater focus in policy (Lewis et al., 2019; Pörtner et al., 2021). Tropical forest restoration measures should more actively consider the potential climate future of the tropics when designed. My earlier hypothesis that community-level changes between forest types are driven by changes in survival, rather than growth, and that this is most apparent during periods of drought, suggests that the

extent and rate of community composition changes within secondary forests will increase as the severity and variability of extreme weather events increases (Tang, 2019). As such, we should consider how restoration management and research plans integrate with a more variable climate and how climatic uncertainty will compound the variability associated with forest restoration if it is not adequately quantified (Banin et al., 2023).

Experimental considerations

As outlined in Chapter 2, the Sabah Biodiversity Experiment was designed as a field-scale biodiversity project that could provide recommendations and insights on a scale relevant to forest management practice. Due to its size, location, and the environmental conditions surrounding this experiment, some elements of experimental design were not as practical or safe to carry out as they would have been on a smaller scale. Here, I review the impacts, if any, of some of the most important experimental considerations.

Dimensions of the Sabah Biodiversity Experiment

The Sabah Biodiversity Experiment was designed as 124 four-ha plots. These plots were measured in the field using compass bearings and tape measures. Whilst this is a practical and reliable method of measuring distance, locally, the site has an undulating terrain. If the slope was not accounted for in measuring distance, then the true overground distance of the plots could be shorter than planned.

As part of my field research at the Sabah Biodiversity Experiment, I assessed the average plot size within the southern block. Using two Emlid Reach RS2 GNSS receiver units, I obtained accurate relative positioning estimates of each plot's corner to calculate the true size of each plot. For the southern block, I navigated to each plot corner. I took a positioning

measurement with one unit and used the second to generate correction data to improve the accuracy of my estimates in post-processing (Dabove & Di Pietra, 2023). Plot corners were identified with multiple indicators. Some corners had red-painted belian wood posts, but these posts had often rotted away over the past 20 years. In other cases, corners were identified using a combination of blue and yellow border markings and the location of seedling planting lines (Fig. E1 in Appendix E). In some cases, plot corners could not be accurately identified and were decided based on the experience and personal knowledge of the research assistants who have worked at the Sabah Biodiversity Experiment for over a decade. Of the plot positions we could confidently identify, I calculated the length of each vertical and horizontal plot border using QGIS (version 3.32.3-Lima) (QGIS Development Team, 2023).

Of the plots measured, vertical borders had a mean length of 195.5 m (95% CI = 193.3-197.6 m). This is expected, as the terrain is rarely level for extended periods. Per plot, this suggests a total elevation change of 42.2 m (95% CI = 30.9-51.3 m), including ascents and descents. Despite the terrain difficulties, tape measurements and compass bearings are still remarkably accurate.

Importantly, I have shown that estimated plot positions based on an earlier perimeter mapping of the Sabah Biodiversity experiment are accurate overall, particularly within the central and western portions of the southern block (Fig. 6.4). There are greater discrepancies to the east of the southern block, which may be due to the particularly challenging terrain. For instance, I could not collect any reliable GPS coordinates in the southeast boundary of the experiment due to the presence of a large boulder (approximately 50 x 50 x 30 m).

Interestingly, vertical borders were not significantly different from the planned 200 m (198.8 m, 95% CI = 196.3-201.3 m). The presence of the clear (and often straight) logging road may have facilitated more accurate initial starting points for planting lines created using compass bearings. Overall, this data supports using my estimated plot boundaries in Chapter 3, as they largely overlap with actual plot locations.

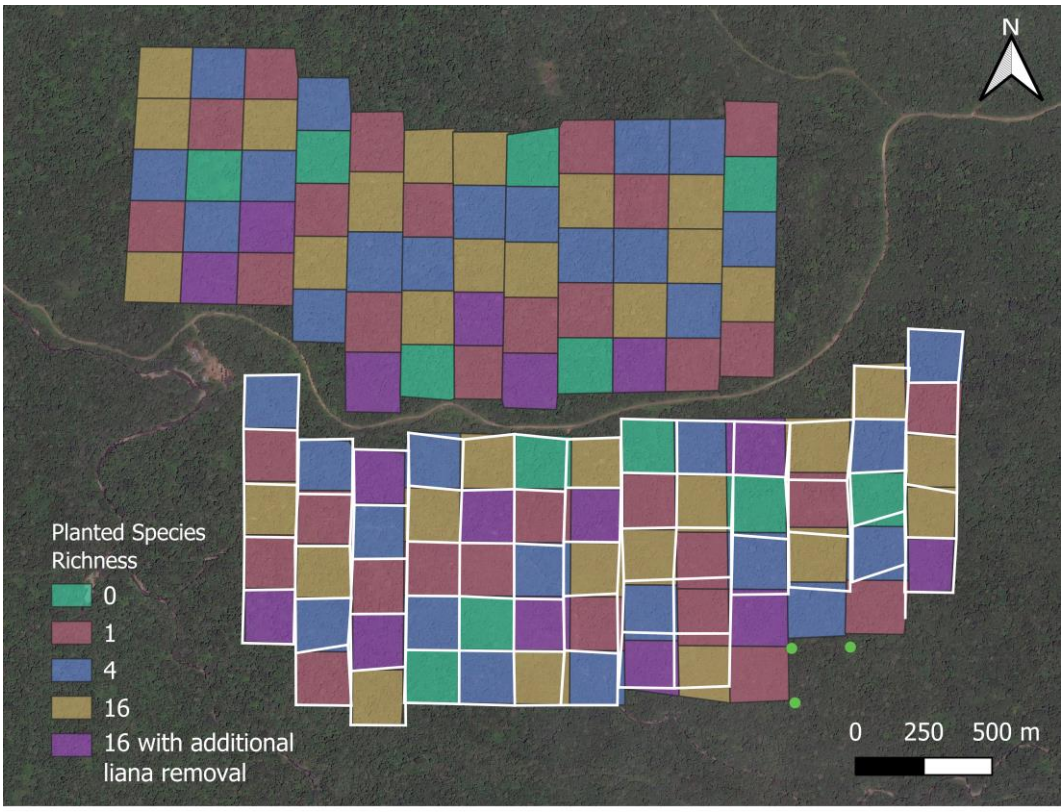

Figure 6.4 Sabah Biodiversity Experiment southern block predicted plots with actual plot locations. Coloured plots indicate the estimated plot sizes and locations based on earlier GNSS data collected at the experiment perimeter. White lines indicate the actual plot location. Plot colour indicates the treatment applied, as outlined in the legend. Note that three plot locations (green points in the southeast corner of the southern block) were carried out with low confidence and have been excluded from creating actual plot boundaries.

Non-random seedling planting order at the Sabah Biodiversity Experiment

Although the plot assignment for species richness at the Sabah Biodiversity Experiment was done randomly, the species identity for each specific position along each planting line was not done fully randomly. Planting specific species in a pre-determined order at nearly 100,000 planting locations would not have been practical, and instead, planting was done semi-randomly with researchers planting one seedling at a time from their carried load. Although species numbers for each plot were controlled to ensure evenness, there is potential for larger seedlings to be planted earlier due to the chosen methodology, as they would theoretically be more likely to be first chosen from a carried load.

To test for a non-random planting order of seedlings, I took the first surveyed size for all seedlings within the intensively surveyed plots at the Sabah Biodiversity Experiment and mapped it to their spatial location. We do not have information on the exact order in which seedlings were planted, so for this exploratory analysis I assumed that lines were planted sequentially and in alternating directions to maximise planting speed (i.e., from west to east). The following linear mixed model (*Model 6.1*) was then fitted:

Model 6.1 – Initial model of (log) mean diameter with Gaussian variance function

$$line\_number + (1|plot)$$

Where *line_number* is a covariate representing the line position within a plot, and (1|*plot*) indicates a random intercept for each plot of the intensively surveyed subsection of the Sabah Biodiversity Experiment.

Overall, I identified a weak relationship between starting size and line position, with larger seedlings planted in the western portion of each plot (i.e., closer to Malua Field Camp; Fig. 6.5). This model explains little of the total variation (adjusted R squared = 0.0337), so if there is a true effect of initial planting order it likely has a negligible impact on any data collected at the Sabah Biodiversity Experiment. Since the first survey of enrichment planted seedlings occurred around 18 months after planting, it is also difficult to say if these effects are simply a consequence of time since planting. It will be hard to draw further inferences since we lack the initial sizes from when seedlings were planted. However, this initial result suggests that a non-random planting density likely has not impacted the experimental design to any large extent.

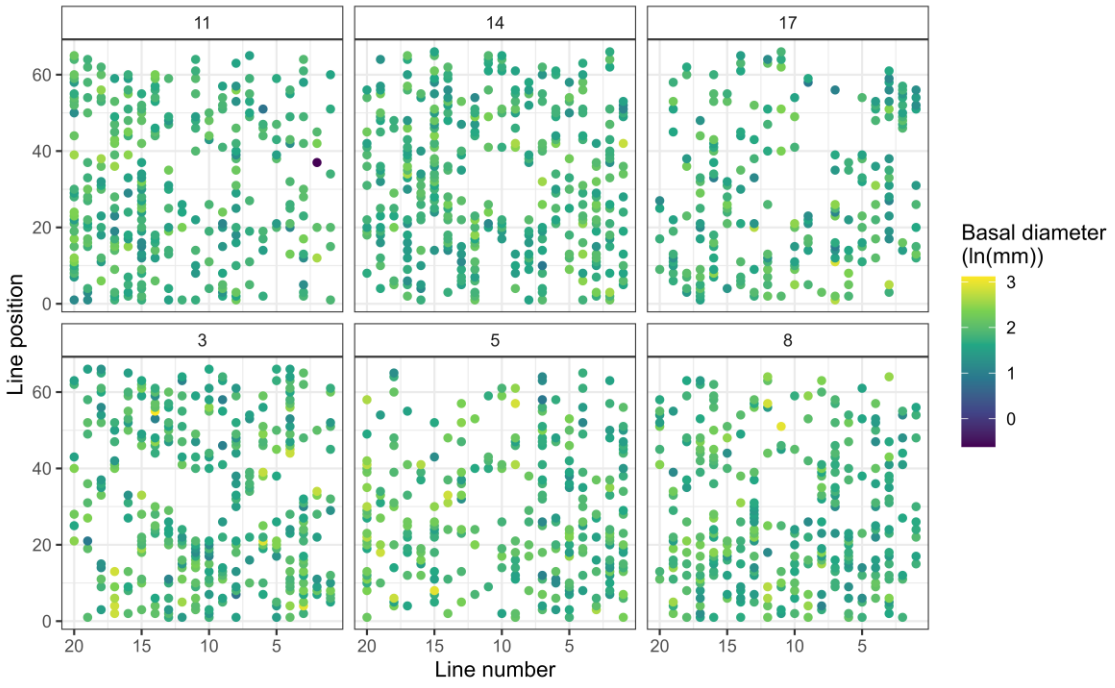

Figure 6.5 Initial sizes of planted dipterocarps within the intensively surveyed plots at the Sabah Biodiversity Experiment. Line number and position along each line have been presented to give a bird's-eye view of each plot's planting treatment within each plot's facet. Tree mean basal diameter indicated in the legend by colour. Note that for plot three, the "^" shape in the middle of the forest shows how the Malua River interrupted planting within that plot.

Seedling replacement

When replanting occurred at the Sabah Biodiversity Experiment, it was believed to have been done randomly. To confirm this, I assessed the proportion of second cohort seedlings within the intensive plot dataset and how many matched the species identity of the dead first cohort seedlings in the same planting location. Given that 16 species were planted, we would expect a 0.0625 probability of randomly replacing a dead seedling with the same species. Of the 2,985 second cohort seedlings, 196 were of the same species as the first

cohort. This produced a one-tailed probability of 0.214, and so this result provides no evidence that replacement planting was carried out non-randomly.

Future work

In Chapter 3, I found no relationship between aboveground biomass and either genus diversity or planned canopy structural complexity within the four-species plots. We might expect any effects of genus diversity to occur later than effects generated by species diversity, so additional data collection should be carried out within the Sabah Biodiversity Experiment at these four-species plots to identify any future effects. A third complete census of the Sabah Biodiversity Experiment began in late 2023, but I discuss in Chapter 3 that biodiversity effects are potentially generated via canopy architecture differences, which are not captured in standard measures of tree diameter and, to a lesser extent, from optical satellites providing effectively a two-dimensional slice of a three-dimensional landscape. Effects of genus diversity and canopy structural complexity may require additional measurements directly assessing the canopy. For instance, high-resolution ground-based LiDAR estimates have been used in the US to successfully collect structural complexity data (Atkins et al., 2018) and are becoming more common in the tropics for forestry purposes (Asner et al., 2012, 2018; Zolkos et al., 2013). Similarly, obtaining more data on the effectiveness of liana removal techniques in actively restored forests would address the remaining research questions from Chapter 3 and earlier in this general discussion. Canopy differences may not be immediately apparent from diameter measurements and would benefit from direct canopy monitoring. The Sabah Biodiversity Experiment also offers a strong opportunity for calibration of direct canopy monitoring techniques following a detailed field-based assessment of liana cover by O'Brien et al. (2019).

In Chapter 4, I identified a positive relationship between enrichment planted seedling survival and the surrounding matrix basal area. Among other explanations, this positive relationship could arise from complementarity effects enhancing overall performance by reducing extreme variations in local climate conditions (Adams et al., 2017). Forest restoration research would benefit from more research investigating these local differences spatially and temporally. We would expect local variation to occur as a result of restrictions in logging conditions, such as terrain, slope, tree diameters, and the frequency of non-timber species (e.g., *Koompassia excelsa* is spared for its role as a cultural keystone species (Axelsson et al., 2021)) to introduce heterogeneity into these landscapes (Reynolds et al., 2011). Understanding how much variation there is within typical landscapes will be important in quantifying the degree of degradation-induced heterogeneity, particularly for once, twice, and more than twice-logged forest systems. Research is also needed on the effects of heterogeneity as a result of logging on local climate patterns. Detailed longitudinal studies quantifying how microclimates vary after selective logging will provide more information concerning the causes of mortality within selectively logged forests. For instance, Blonder et al. (2018) showed that thermal ranges and spatiotemporal heterogeneity in heavily logged forests are twice that of old-growth forests and predict that the increased thermal range reduces logged forest resilience to global changes in climate patterns. More research exists on how forest-climate interactions change in response to habitat fragmentation (Laurance, 2004), but the effects of degradation are less well understood. Improving the evidence base will help inform how global climatic shifts may translate into local microclimate changes within logged forests.

In Chapter 5, I identified a knowledge gap for old-growth forest seedling growth rates to act as points of comparison for both naturally regenerating and actively restored seedlings.

Additional research to find species-specific estimations of dipterocarp growth rates in old-growth communities, particularly under varying environmental conditions, should provide comparative baselines to judge the restoration success of secondary forests against. Similarly, in Chapter 5, I cannot conclude that dipterocarps are growing equally well across our experiments in old-growth and selectively logged forests because we lack information on the structure of the surrounding matrix in the old-growth forest. The Danum Gaps-Understory Experiment will soon reach 20 years since its establishment, so understanding the context in which these seedlings have been growing will increase the applicability of the data collected beyond the experiment.

More widely, there is a need for more long-term restoration experiments globally. Most studies investigating active forest recovery are less than five years old, and few are older than 10 years (Banin et al., 2023). I have shown that around 10 years is potentially the minimum amount of time for the effects of species richness to become apparent in biodiversity experiments. Funding for restoration experiments is generally time-limited, and long-term experiments studying tree growth are relatively slow to produce results. In line with the growing demand for tree planting as a mitigation step for climate change (UNFCCC, 2015), more research on the local factors that influence the effectiveness of restoration will prove to be both ecologically rewarding and cost-effective in the long term.

Conclusions

In this thesis, I have used various methodological and analytical techniques to assess the success of active restoration in a Southeast Asian tropical forest system. I have shown that the restoration of once-logged lowland dipterocarp forests can be enhanced by active restoration methods already employed in Sabah and that these differences can become

apparent in as little as five years. I have also argued (based on transgressive overyielding and effects of functional and phylogenetic diversity) that complementarity effects drive the positive relationship between biodiversity in active restoration efforts and aboveground biomass yields. I argue that these effects arise through changes in canopy architecture and propose that future assessments of tropical forest biodiversity incorporate methodologies capable of providing enhanced, three-dimensional canopy evaluation. Although I did not find an effect of more subtle treatment effects, such as genus diversity or canopy structural complexity within four-species plots, I attribute this to the restricted functional diversity between those plot subsets, and I call for the continued monitoring of long-term experiments to allow these effects to be identified if they exist.

I demonstrate that, on the local scale, variation in the survival of enrichment planted seedlings was positively associated with the basal area of its surrounding tree matrix and may be driven by increased heterofamilial tree abundances, though wider environmental stochasticity alternatively explains this trend. I also show that both growth and survival rates of seedlings are positively related to local light levels (up to 40%). I use a nearby experiment in an old-growth forest to show that growth and survival rates are similar for most species, and I suggest that additional growth benchmarking data should be pursued in Sabah to further the understanding of what target growth rates should be. Although sustainable forest management is receiving increasing international attention, continued protection of these landscapes still needs researchers, policymakers, and the public to invest in understanding how these ecosystems function. To maximise the benefits to local communities, biodiversity, and climate change mitigation, future active restoration projects must be informed by the continued advances being made in tropical ecology.

Appendix A: Supplementary information for Chapter 2

Key towns and cities within Sabah to tropical forest research

When carrying out research at the Sabah Biodiversity Experiment, multiple immigration and research permits and passes are required. This appendix is designed to provide context and an overview of the main authorities within each town or city.

Kota Kinabalu

Kota Kinabalu is the state capital of Sabah, lying on the west coast of Sabah. It is the largest city within Sabah and the seat of governance within the state. As such, most major government buildings are present within this city, most notably Sabah's immigration Department, Income Tax Department, and main court complex. There are also many forestry and biodiversity-specific organisations based within Kota Kinabalu, notably Sabah Biodiversity Centre and Yayasan Sabah. The South East Rainforest Research Partnership (SEARRP) has an office within the city, and University Malaysia Sabah's main campus site is at the northern end of the city.

Depending on the type and location of research planned, the local collaborator, and the identity of the foreign researcher(s), several different buildings will need to be visited (see Fig. A1). In the case of foreign researchers hoping to conduct tropical forest research within Sabah, SEARRP provides detailed step-by-step instructions for navigating the application process (https://www.searrp.org/scientists/application-process), but as of 2023, Kota Kinabalu Immigration Office encourages all Professional Visitor Passes to be applied for and accepted before foreign researchers arrive in Sabah. This requires local collaborators to collate all required forms and submit them to the Kota Kinabalu Immigration Office at

least two weeks in advance of the researcher's arrival in Sabah. This is intended to avoid researchers conducting research with only a receipt of an application for two weeks before receiving a Professional Visitor Pass (as has been standard practice to date).

Lahad Datu

Lahad Datu is one of the easiest ways to access the eastern portion of the YSF Management Area, specifically the Malua and Ulu-Segama forest reserves and the Danum Valley Conservation Area. Lahad Datu airport is accessible via Kota Kinabalu and Sandakan and connects to the main logging roads that give access to the YSF Management Area. This town used to host the primary timber mill until it was closed in 2001 after the exhaustion of high timber supply volumes from Sabah's main forest reserves.

Sandakan and Sepilok

Sandakan is a city on the Sabah's northern coast and is the location of the Sabah Forestry Department headquarters. This city can be accessed via Lahad Datu and Kota Kinabalu airports. Approximately one hour west of Sandakan is the town of Sepilok, which is primarily a tourist town due to the presence of the Rainforest Discovery Centre, Bornean Sun Bear Conservation Centre, and Sepilok Orangutan Rehabilitation Centre. All three centres carry out additional conservation research and/or research support.

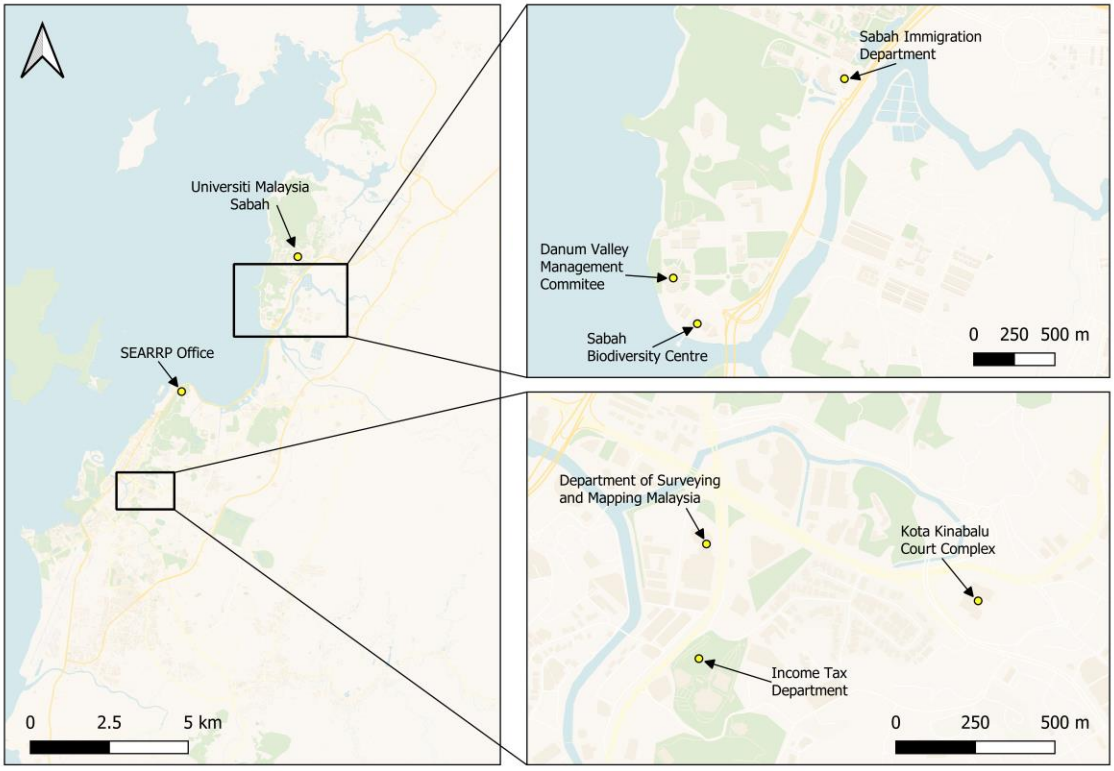

Figure A1 Map of key locations around Kota Kinabalu. To apply for a Professional Visitor Pass in Kota Kinabalu, various forms are required to be submitted to Sabah Immigration Department. Forms require payment and/or signatures from specific departments or organisations, which are indicated by arrows and yellow circles on the above map.

Table A1 Plot-level composition of the Sabah Biodiversity Experiment. Species composition values beginning with '4' refer to species compositions outlined in Table B6 in Appendix B.

Plot	Block	Species richness	Species composition
1	South	4	4.13
2	South	1	*Shorea beccariana*
3	South	16	16
4	South	1	*Hopea sangal*
5	South	16	16 with climber cutting
6	South	4	4.6
7	South	1	*Shorea leprosula*
8	South	16	16
9	South	4	4.3
10	South	1	*Dryobalanops lanceolata*
11	South	16	16 with climber cutting
12	South	4	4.10
13	South	1	*Shorea gibbosa*
14	South	16	16 with climber cutting
15	South	16	16
16	South	4	4.11
17	South	16	16
18	South	1	*Parashorea tomentalla*
19	South	4	4.5
20	South	0	Unplanted
21	South	16	16
22	South	16	16 with climber cutting
23	South	1	*Shorea parvifolia*
24	South	0	Unplanted
25	South	4	4.2
26	South	0	Unplanted
27	South	1	*Shorea macrophylla*
28	South	4	4.7
29	South	16	16 with climber cutting
30	South	16	16
31	South	16	16
32	South	16	16 with climber cutting
33	South	16	16
34	South	1	*Shorea argentifolia*
35	South	4	4.12
36	South	0	Unplanted
37	South	1	*Shorea ovalis*
38	South	16	16

39	South	4	4.9
40	South	16	16 with climber cutting
41	South	4	4.14
42	South	16	16
43	South	1	*Shorea faguetiana*
44	South	1	*Parashorea malaanonan*
45	South	16	16
46	South	16	16 with climber cutting
47	South	0	Unplanted
48	South	4	4.16
49	South	16	16 with climber cutting
50	South	1	*Shorea macroptera*
51	South	16	16
52	South	1	*Dipterocarpus conformis*
53	South	16	16
54	South	4	4.8
55	South	16	16
56	South	4	4.4
57	South	0	Unplanted
58	South	4	4.1
59	South	1	*Shorea johorensis*
60	South	4	4.15
61	South	1	*Hopea ferruginea*
62	South	16	16
63	South	16	16
64	South	16	16 with climber cutting
65	North	1	*Shorea parvifolia*
66	North	16	16
67	North	4	4.2
68	North	0	Unplanted
69	North	1	*Hopea ferruginea*
70	North	1	*Parashorea malaanonan*
71	North	4	4.8
72	North	16	16
73	North	16	16
74	North	4	4.9
75	North	16	16 with climber cutting
76	North	16	16
77	North	4	4.5
78	North	1	*Shorea faguetiana*
79	North	4	4.7
80	North	0	Unplanted
81	North	1	*Shorea macrophylla*
82	North	4	4.4
83	North	16	16
84	North	1	*Shorea beccariana*

85	North	16	16 with climber cutting
86	North	1	*Dipterocarpus conformis*
87	North	16	16
88	North	4	4.6
89	North	0	Unplanted
90	North	1	*Shorea argentifolia*
91	North	16	16 with climber cutting
92	North	16	16
93	North	4	4.10
94	North	16	16
95	North	0	Unplanted
96	North	16	16
97	North	4	4.14
98	North	1	*Parashorea tomentalla*
99	North	16	16
100	North	16	16 with climber cutting
101	North	1	*Shorea ovalis*
102	North	4	4.11
103	North	16	16
104	North	1	*Dryobalanops lanceolata*
105	North	4	4.13
106	North	16	16
107	North	1	*Shorea gibbosa*
108	North	0	Unplanted
109	North	4	4.1
110	North	1	*Shorea macroptera*
111	North	16	16 with climber cutting
112	North	4	4.16
113	North	16	16
114	North	1	*Shorea leprosula*
115	North	16	16 with climber cutting
116	North	4	4.12
117	North	0	Unplanted
118	North	1	*Hopea sangal*
119	North	4	4.3
120	North	16	16
121	North	1	*Shorea johorensis*
122	North	4	4.15
123	North	16	16
124	North	16	16

Table A2 Publications produced at the Sabah Biodiversity Experiment. Each publication produced at the Sabah Biodiversity Experiment and its corresponding publication index number.

Publication index number	Citation
1	P. Saner et a., Reduced soil respiration in gaps in logged lowland dipterocarp forests. *For. Ecol. Manage.* **258**, 2007–2012 (2009).
2	Y. Hautier et al., Effects of seed predators of different body size on seed mortality in bornean logged forest. PLoS One. **5**, e11651 (2010).
3	P. Saner et al., Positive effects of ectomycorrhizal colonization on growth of seedlings of a tropical tree across a range of forest floor light conditions. Plant Soil. **338**, 411–421 (2011).
4	A. Hector et al., The Sabah Biodiversity Experiment: a long-term test of the role of tree diversity in restoring tropical forest structure and functioning. Philos. Trans. R. Soc. B Biol. Sci. **366**, 3303–3315 (2011).
5	C. D. Philipson et al., Light-based Regeneration Niches: Evidence from 21 Dipterocarp Species using Size-specific RGRs. Biotropica. **44**, 627–636 (2012).
6	L. A. Turnbull et al., Plant growth rates and seed size: A re-evaluation. Ecology. **93**, 1283–1289 (2012).
7	P. Saner et al., Carbon stocks and fluxes in tropical lowland dipterocarp rainforests in Sabah, Malaysian Borneo. PLoS One. **7**, e29642 (2012).
8	C. E. T. Paine et al., How to fit nonlinear plant growth models and calculate growth rates: An update for ecologists. Methods Ecol. Evol. **3**, 245–256 (2012).
9	M. J. O'Brien et al., The Influence of Variable Rainfall Frequency on Germination and Early Growth of Shade-Tolerant Dipterocarp Seedlings in Borneo. PLoS One. **8**, 1–9 (2013).
10	M. J. O'Brien et al., Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. Nat. Clim. Chang. **4**, 710–714 (2014).
11	C. D. Philipson et al., A trait-based trade-off between growth and mortality: Evidence from 15 tropical tree species using size-specific relative growth rates. Ecol. Evol. **4**, 3675–3688 (2014).
12	M. J. O'Brien et al., Contrasting nonstructural carbohydrate dynamics of tropical tree seedlings under water deficit and variability. New Phytol. **205**, 1083–1094 (2015).
13	P. Saner et al., Growth rates and relative change in non-structural carbohydrates of dipterocarp seedlings in response to light acclimation. Plant Ecol. Divers. **9**, 491–504 (2016).
14	C. C. Ang et al., Genetic diversity of two tropical tree species of the

Dipterocarpaceae following logging and restoration in Borneo: high genetic diversity in plots with high species diversity. Plant Ecol. Divers. **9**, 459–469 (2016).

15 F. Q. Brearley et al., Testing the importance of a common ectomycorrhizal network for dipterocarp seedling growth and survival in tropical forests of Borneo. Plant Ecol. Divers. **9**, 563–576 (2016).

16 S. L. Tuck et al., The value of biodiversity for the functioning of tropical forests: Insurance effects during the first decade of the sabah biodiversity experiment. Proc. R. Soc. B Biol. Sci. **283**, 20161451 (2016).

17 M. J. O'Brien et al., Intra-annual plasticity of growth mediates drought resilience over multiple years in tropical seedling communities. Glob. Chang. Biol. **23**, 4235–4244 (2017).

18 A. Granados et al., Defaunation and habitat disturbance interact synergistically to alter seedling recruitment: Ecol. Appl. **27**, 2092–2101 (2017).

19 M. J. O'Brien et al., Resistance of tropical seedlings to drought is mediated by neighbourhood diversity. Nat. Ecol. Evol. **1**, 1643–1648 (2017).

20 M. J. O'Brien et al., Positive effects of liana cutting on seedlings are reduced during El Niño-induced drought. J. Appl. Ecol. **56**, 891–901 (2019).

21 J. Wu et al., Monitoring tropical forest degradation and restoration with satellite remote sensing: A test using Sabah Biodiversity Experiment. Adv. Ecol. Res. **62**, 117–146 (2020).

22 M. J. O'Brien et al., The role of soluble sugars during drought in tropical tree seedlings with contrasting tolerances. J. Plant Ecol. **13**, 389–397 (2020).

23 M. J. O'Brien et al., Topography in tropical forests enhances growth and survival differences within and among species via water availability and biotic interactions. Funct. Ecol. **36**, 686–698 (2022).

24 M. J. O'Brien et al., Demographic consequences of heterogeneity in conspecific density dependence among mast-fruiting tropical trees. Proc. R. Soc. B Biol. Sci. **289**: 20220739 (2022),

25 R. Veryard et al., Positive effects of tree diversity on tropical forest restoration in a field-scale experiment. Sci. Adv. **9**, eadf0938 (2023)

Table A3 Descriptions of the 26 dipterocarp species planted in the Sabah Biodiversity Experiment and Danum Gaps-Understory Experiment. Species names and authorities as of pre- and post-2022 updates, timber colour group (Ashton, 1982; Symington, 1943), ecology (Ashton, 1982), average nut length (Ashton, 1982), and IUCN status (with year of assessment in parentheses). An 'X' in the Sabah Biodiversity Experiment (SBE) or Danum Gaps-Understory Experiment (DGU) columns indicates that a species is present in said experiment. Modified from (Tuck et al., 2016).

Species	Timber group	Ecology	Nut length (mm)	IUCN Red List (year)	SBE	DGU
Dipterocarpus conformis Slooten	-	Rare, hill dipterocarp forest, clay-rich soils below 800 m.	-	Endangered (2019)	X	X
Dryobalanops beccarii Dyer	-	Locally abundant on leached sandy soils on coastal hills and inland ridges below 700 m.	14	Endangered (1998)		X
Dryobalanops lanceolata Burck	-	Widespread on fertile soils, abundant on undulatingland, to 700 m.	20	Least Concern (2019)	X	X
Durio graveolens Becc.	-	-	-	Vulnerable (2020)		X
Hopea ferruginea Parijs	-	Deep fertile soils in mixed dipterocarp forest below 750 m.	07	Critically Endangered (1998)	X	
Hopea sangal Korth	-	Often on or near river banks in low country and to 500 m.	07	Vulnerable (2017)	X	X
Parashorea Malaanonan (Blanco) Merr.	-	Local on clay-rich soil, rarely on riverbanks, on ridges in mountains to 1,300 m.	17	Least Concern (2019)	X	X
Parashorea tomentella (Symington) Meijer	-	Mixed dipterocarp forest on flat and undulating land below < 200 m.	20	Least Concern (2017)	X	X
Shorea acuminatissima Symington	Yellow Meranti	Mixed dipterocarp forest on sandy clay soils on hills below 500 m.	02	Vulnerable (2019)		X
Shorea argentifolia Symington	Red Meranti	Locally frequent on ridges, hillsides, and valleys, < 600 m.	14	Least Concern (2019)	X	X
Shorea beccariana Bruck	Red Meranti	Common, lowlands, and dry ridges to 1,350 m.	40	Least Concern (2019)	X	X

Shorea faguetiana F.Heim.	Yellow Meranti	Low hills and particularly ridge tops at 150–700 m, occasionally to 1,000 m.	15	Endangered (2017)	X	X
Shorea gibbosa Brandis	Yellow Meranti	Locally common on fertile clay-loam soils on undulating land and river banks to 650 m.	18	Critically Endangered (1998)	X	X
Shorea guiso (Blanco) Blume	Red Balau	Scattered in lowland forest on red soils, most common in slightly seasonal climates.	08	Vulnerable (2017)		X
Shorea johorensis Foxw.	Red Meranti	Very common on well-drained fertile soils < 600 m.	20	Critically Endangered (1998)	X	X
Shorea leprosula Miq.	Red Meranti	Widespread, fast-growing emergent, common < 700 m.	20	Near Threatened (2017)	X	X
Shorea macrophylla (de Vriese) P.S.Ashton	Red Meranti	Locally abundant on periodically flooded alluvium, rarer on hillsides, < 600 m.	60	Least Concern (2019)	X	X
Shorea macroptera Dyer	Red Meranti	Common, sandy clay soils on low hills to 600 m.	18	Least Concern (2017)	X	X
Shorea mecistopteryx Ridl.	Red Meranti	Undulating land and low hills on sandy clay soils in mixed dipterocarp forest below 400 m.	42	Vulnerable (2019)		X
Shorea oleosa Meijer	Red Meranti	Widespread on clay soils in mixed dipterocarp forest, undulating land and hillsides to 600 m.	27	Least Concern (2019)		X
Shorea ovalis Korth	Red Meranti	Scattered in lowland Mixed Dipterocarp forest, usually in moist places in valleys and low-lying ground, to 500 m.	22	Least Concern (2017)	X	X
Shorea parvifolia Dyer	Red Meranti	Perhaps the commonest dipterocarp, on clay soils on hills < 800 m.	140	Least Concern (2017)	X	X
Shorea parvistipulata F.Heim	Red Meranti	Clay-rich soils on alluvium and especially hillsides and low ridges to 1,300 m.	25	Least Concern (2019)		X
Shorea pinanga Scheff.	Red meranti	Clay-rich soils especially on ridges below 700 m.	23	Least Concern (2019)		X
Shorea smithiana Symington	Red meranti	Frequent on deep sandy clay soils on undulating land and to 400 m.	27	Vulnerable (2019)		X
Shorea superba Symington	Red Balau	Fertile clay soils at low altitudes in mixed dipterocarp forest up to 600 m.	12	Vulnerable (2019)		X

Table A4 Droughted plots within the Danum Gaps-Understory Experiment. A black cell filling indicates a subplot which has received droughting treatment. Subplots denoted by A/B.

	Gap		Understory	
Block	A	B	A	B
1		■		■
2		■		
3		■		■
4		■		
5		■		
6				
7		■		■
8		■		
9		■		
10		■		
11		■		
12				
13				
14				
15				
16		■		
17		■		
18		■		■
19		■		■
20		■		

Table A5 Initially used and most recent nomenclature of dipterocarp species used in the Sabah Biodiversity Experiment and the Danum Gaps-Understory Experiment. Where a species taxonomy has been updated, the year of this change is also provided.

Initially used species names in publications	Current species name	Year of publication
Dipterocarpus conformis Slooten	*Dipterocarpus conformis* Slooten	-
Dryobalanops beccarii Dyer	*Dryobalanops beccarii* Dyer	-
Dryobalanops lanceolata Burck	*Dryobalanops lanceolata* Burck	-
Durio graveolens Becc.	*Durio graveolens* Becc.	-
Hopea ferruginea Parijs	*Hopea ferruginea* Parijs	-
Hopea sangal Korth	*Hopea ferruginea* Parijs	-
Parashorea Malaanonan (Blanco) Merr.	*Parashorea Malaanonan* (Blanco) Merr.	-
Parashorea tomentella (Symington) Meijer	*Parashorea tomentella* (Symington) Meijer	-
Shorea acuminatissima Symington	*Richetia acuminatissima* (Symington) P.S.Ashton & J.Heck.	2022
Shorea argentifolia Symington	*Rubroshorea argentifolia* (Symington) P.S.Ashton & J.Heck.	2022
Shorea beccariana Bruck	*Rubroshorea beccariana* (Burck) P.S.Ashton & J.Heck.	2022
Shorea faguetiana F.Heim.	*Richetia faguetiana* (F.Heim) P.S.Ashton & J.Heck.	2022
Shorea gibbosa Brandis	*Richetia gibbosa* (Brandis) P.S.Ashton & J.Heck.	2022
Shorea guiso (Blanco) Blume	*Shorea guiso* (Blanco) Blume	-
Shorea johorensis Foxw.	*Rubroshorea johorensis* (Foxw.) P.S.Ashton & J.Heck.	2022
Shorea leprosula Miq.	*Rubroshorea leprosula* (Miq.) P.S.Ashton & J.Heck.	2022
Shorea macrophylla (de Vriese) P.S.Ashton	*Rubroshorea macrophylla* (de Vriese) P.S.Ashton & J.Heck.	2022
Shorea macroptera Dyer	*Rubroshorea macroptera* (Dyer) P.S.Ashton & J.Heck.	2022
Shorea mecistopteryx Ridl.	*Rubroshorea mecistopteryx* (Ridl.) P.S.Ashton & J.Heck.	2022
Shorea oleosa Meijer	*Rubroshorea fallax* (Meijer) P.S.Ashton & J.Heck.	2022

Shorea ovalis Korth	*Rubroshorea ovalis* (Korth.) P.S.Ashton & J.Heck.	2022
Shorea parvifolia Dyer	*Rubroshorea parvifolia* (Dyer) P.S.Ashton & J.Heck.	2022
Shorea parvistipulata F.Heim	*Rubroshorea parvistipulata* (F.Heim) P.S.Ashton & J.Heck.	2022
Shorea pinanga Scheff.	*Rubroshorea pinanga* (Scheff.) P.S.Ashton & J.Heck.	2022
Shorea smithiana Symington	*Rubroshorea smithiana* (Symington) P.S.Ashton & J.Heck.	2022
Shorea superba Symington	*Shorea superba* Symington	-

Appendix B: Supplementary information for Chapter 3

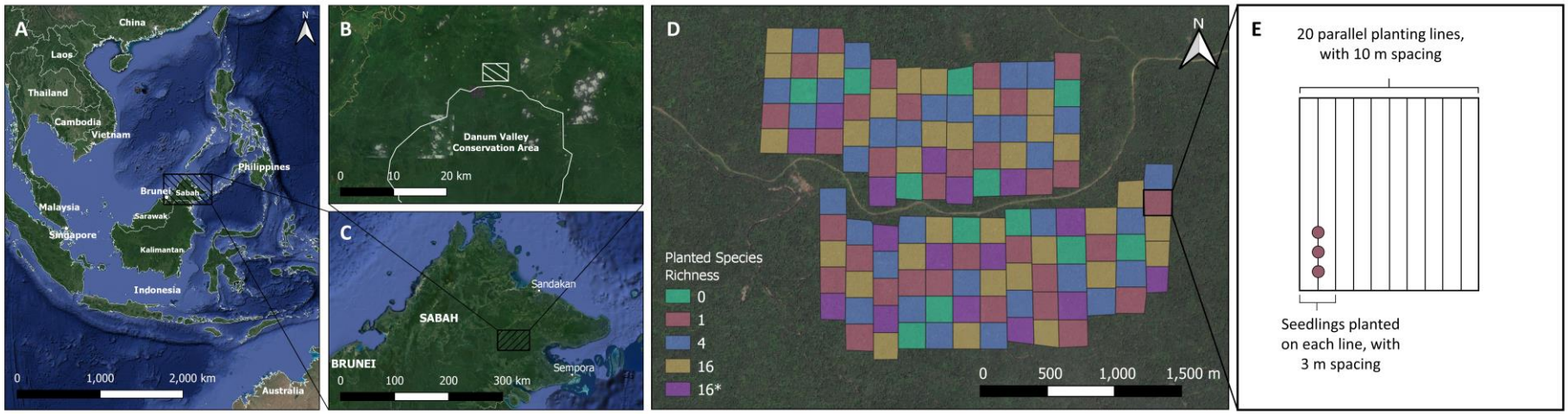

Figure B1 Location and design of the Sabah Biodiversity Experiment. (**A**) The Sabah Biodiversity Experiment is located in Sabah, Malaysian Borneo, within South East Asia. (**B**, **C**) The experimental site is located in a selectively logged area of the Malua Forest Reserve just north of the Danum Valley Conservation Area, Sabah, Malaysian Borneo. (**D**) The Sabah Biodiversity Experiment consists of 124 four-hectare plots, separated into two blocks by a logging road, with a combination of treatments that vary the species richness of enrichment planted dipterocarp seedlings (0, 1, 4, or 16 species) and restoration methodologies (liana removal (16*) or not (16)). Note that at the time of the RapidEye satellite remote sensing in 2012, only the 10 plots in the southern block had been subjected to the liana removal treatment. The six liana removal plots in the northern block are therefore treated as 16-species plots without liana removal in this analysis. (**E**) In each plot, dipterocarp seedlings were planted every 3 m along parallel lines 10 m apart.

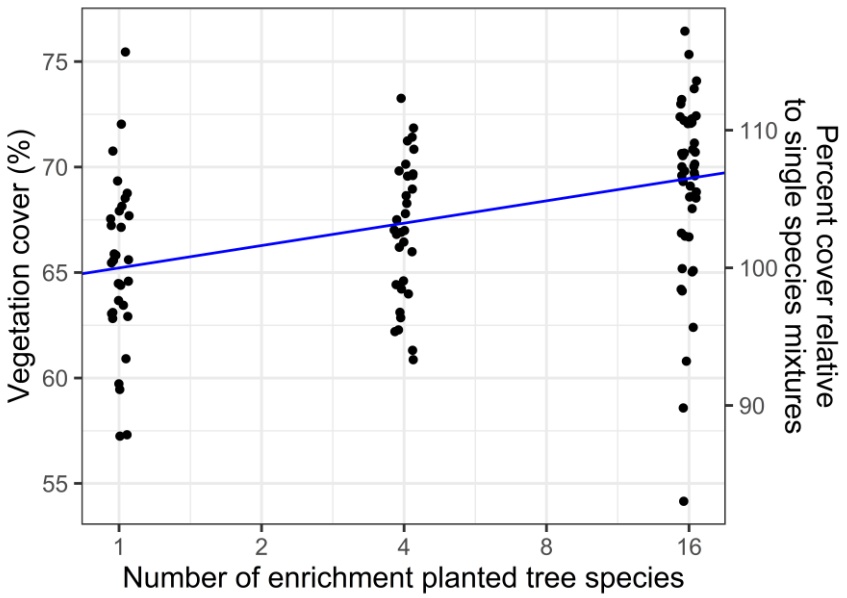

Figure B2 Effect of diversity on enrichment planted dipterocarp estimated vegetation cover. Estimated vegetation cover (RapidEye) as a function of the number of enrichment planted tree species a decade after initial planting. The line is the regression slope with the $\log_2$ number of tree species from the mixed-effects model analysis (points are jittered to avoid overlap).

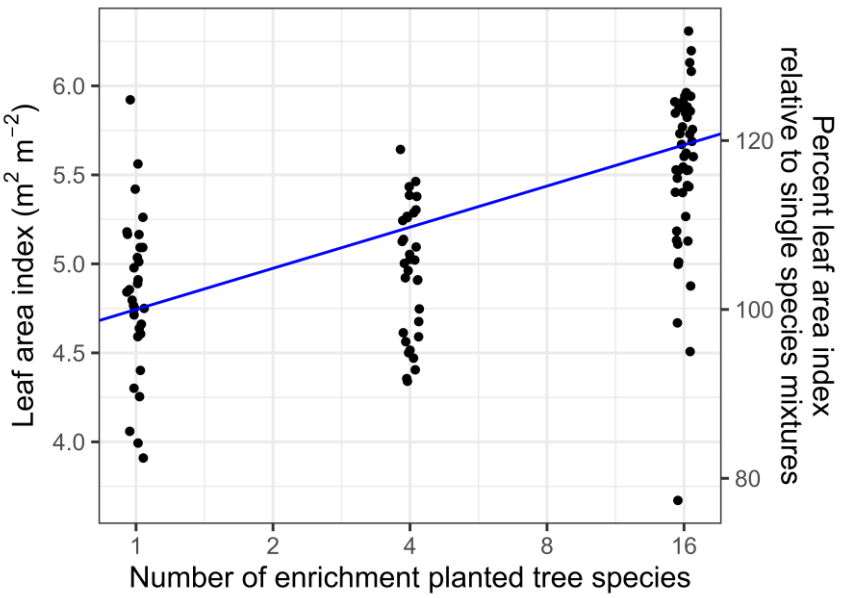

Figure B3 Effect of diversity on enrichment planted tree's estimated leaf area index. Estimated leaf area index (RapidEye) as a function of the number of enrichment planted tree species a decade after initial planting. The line is the regression slope with the $\log_2$ number of tree species from the mixed-effects model analysis (points are jittered to avoid overlap).

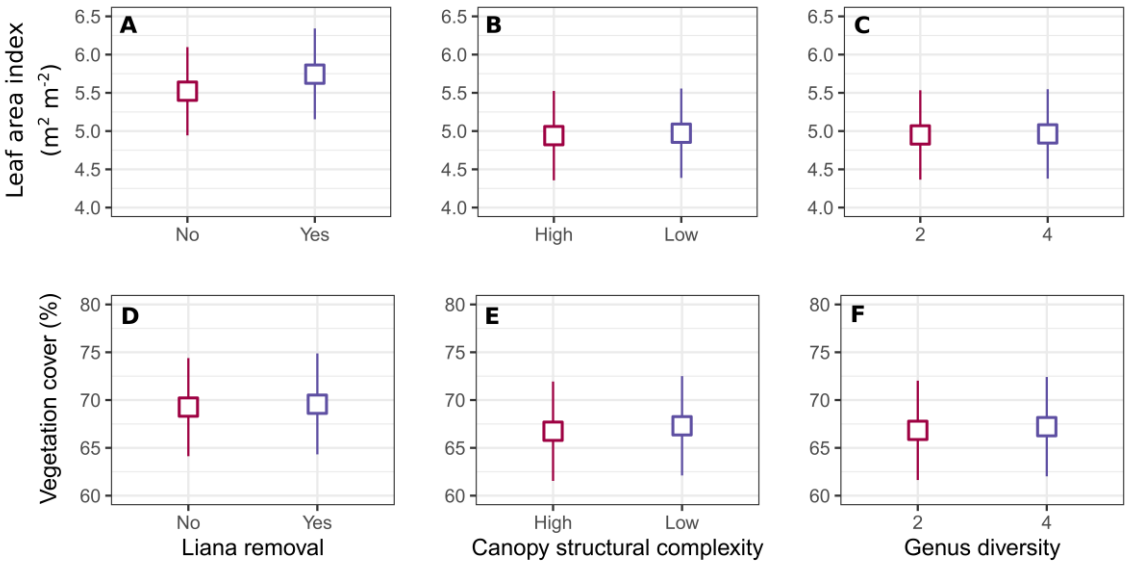

Figure B4 RapidEye satellite remote sensing estimates as a function of restoration treatment a decade after initial planting. leaf area index (**A** to **C**) and cover (**D** to **F**) as a function of (from left to right) genus diversity of plots enrichment planted with four-species (2 genera vs 4 genera); canopy complexity with four species (low vs high); and liana ('climber') cutting with 16 species.

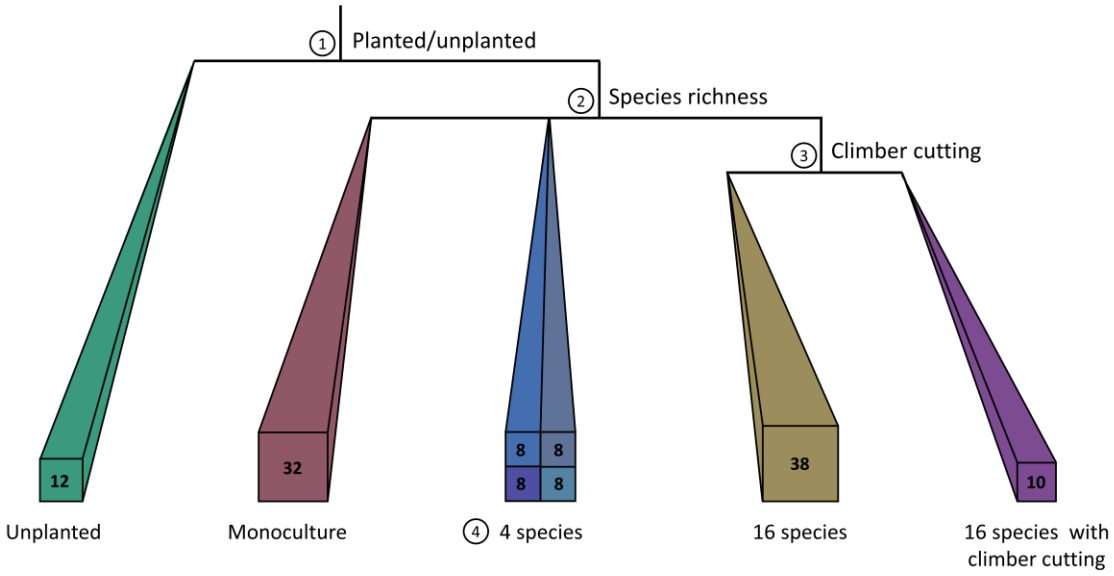

Figure B5 Summary of comparisons made by the mixed-effects model analysis. After performing an initial overall test for differences among treatment levels we performed a series of *a priori* contrasts for the comparisons of interest contained within the overall design: 1) enrichment plant vs. unplanted control plots; 2) Number (richness) of species of enrichment planted tree (both as a factor with three levels and as a regression on the $\log_2$ number of species; 3) Effects of climber cutting (16-species plots only); 4) A two-factor factorial comparison (within the 4-species plots only) of the effects of canopy structural complexity (higher and lower) and genus diversity (4 species drawn from 2 versus 4 genera).

Table B1 The 16 species of the Dipterocarpaceae family studied by the Sabah Biodiversity Experiment with relevant traits. From (Tuck et al., 2016).

Species	Relative canopy height	Ecology	Timber group	IUCN status
Dipterocarpus conformis Slooten	Tall	Rare, Hill dipterocarp forest, clay rich soils, below 800 m	-	Endangered
Dryobalanops lanceolata Burck	Tall	Widespread on fertile soils, abundant on undulating land on volcanic/calcareous soils, up to 700 m	-	Least Concern
Hopea ferruginea Parijs	Short	Deep fertile soils in mixed dipterocarp forest, below 750 m	-	Critically endangered
Hopea sangal Korth.	Short	Often on or near riverbanks in low country and up to 500 m	-	Vulnerable
Parashorea Malaanonan (Blanco) Merr.	Tall	Abundant in lowlands, typically E. Sabah, recorded up to 1300 m	-	Least concern
Parashorea tomentella (Symington) Meijer	Tall	Common on flat and undulating land, up to 200 m	-	Least concern
Shorea argentifolia Symington	Medium	Locally frequent in forests, especially clay soils on undulating land and in valleys, below 600 m	Red Meranti	Least concern
Shorea beccariana Bruck	Medium	Common on leached lowland soils and dry ridges up to 1350 m	Red Meranti	Least Concern
Shorea faguetiana Heim.	Tall	Well-drained clay soils on low hills, and particularly ridge tops at 150-100 m (typically 700 m)	Yellow Meranti	Endangered
Shorea gibbosa Brandis	Tall	Common on deep fertile soils, below 600 m	Yellow Meranti	Critically endangered
Shorea johorensis Foxw.	Tall	E. Borneo on well-drained fertile soils, below 600 m	Red Meranti	Critically endangered

Shorea leprosula Miq.	Medium	Deep clay soils in mixed dipterocarp forest below 700 m	Red Meranti	Near-threatened
Shorea macrophylla Ashton	Medium	Locally abundant on periodically flooded alluvium and riverbanks but rarer on hillsides, below 600 m	Red Meranti	Least Concern
Shorea macroptera King	Medium	Clay soils on low hills up to 600 m	Red Meranti	Least Concern
Shorea ovalis Korth.	Medium	Scattered in mixed dipterocarp forests, usually in moist or low-lying ground, up to 500 m	Red Meranti	Least Concern
Shorea parvifolia Dyer	Medium	Perhaps the commonest dipterocarp, on clay soils on hills below 800 m	Red Meranti	Least Concern

Table B2 Mixed-effects model fixed effects estimates of aboveground biomass (AGB), leaf area index (LAI), and % vegetation cover. Columns list treatment level, sample size and estimated means for each level of the primary treatment with upper and lower bounds of likelihood profile 95% confidence intervals. Mixed-effects models ANOVA *F*-tests of the treatment factor (5 levels; Satterthwaite degrees of freedom) are: AGB: $F_{4,118.5} = 132.39$, $P = < 2.2e\text{-}16$; LAI: $F_{4,118.1} = 31.84$, $P = < 2.2e\text{-}16$; Cover: $F_{4,118.11} = 14.772$, $P = 8.17e\text{-}10$. R-squared values (*R2m* and *R2c*) are for the model with all treatments included.

Index	Treatment	Number of plots	Estimate	CI 2.5% limit	CI 97.5% limit	*R2m*	*R2c*
AGB (Mg ha^{-1})	Unplanted	12	182.67	174.39	190.94	0.780	0.815
	Monoculture	32	213.89	206.99	220.79	-	-
	4 species	32	231.90	225.01	238.80	-	-
	16 species	38	261.55	254.51	268.49	-	-
	16 species with liana removal	10	265.73	256.70	274.68	-	-
LAI	Unplanted	12	4.57	3.99	5.16	0.364	0.641
	Monoculture	32	4.82	4.24	5.40	-	-
	4 species	32	4.96	4.44	5.47	-	-
	16 species	38	5.52	5.01	6.03	-	-
	16 species with liana removal	10	5.74	5.21	6.29	-	-
Cover (%)	Unplanted	12	62.05	56.81	67.28	0.210	0.563
	Monoculture	32	65.33	60.19	70.47	-	-
	4 species	32	67.03	61.89	72.17	-	-
	16 species	38	69.27	64.13	74.39	-	-
	16 species with liana removal	10	69.57	64.32	74.88	-	-

Table B3 Estimates of AGB, LAI and % vegetation cover for unplanted vs planted plots with the mean differences and 95% CI limits. R-squared values (*R2m* and *R2c*) are for the model with all treatments included.

Index	Treatment	Number of plots	Estimate	CI 2.5% limit	CI 97.5% limit	*R2m*	*R2c*
AGB (Mg ha^{-1})	Unplanted	12	182.67	153.06	212.27	0.303	0.705
	Planted	110	225.99	217.50	234.55	-	-
	Difference	-	43.33	13.33	73.20	-	-
LAI	Unplanted	12	4.57	3.89	5.26	0.042	0.572
	Planted	110	4.96	4.40	5.53	-	-
	Difference	-	0.39	-0.18	0.95	-	-
Cover (%)	Unplanted	12	62.05	56.63	67.47	0.082	0.519
	Planted	110	66.67	61.71	71.68	-	-
	Difference	-	4.63	1.08	8.07	-	-

Table B4 AGB, LAI, and % vegetation cover changes per doubling in species richness (i.e. slope of the mixed-effects regression slopes versus species richness) (log-2 transformed).

Dataset	Change per doubling in species richness	CI 2.5% limit	CI 97.5% limit	*R2m*	*R2c*
AGB (Mg ha^{-1})	12.89	10.33	15.09	0.715	0.732
LAI	0.23	0.16	0.30	0.322	0.628
Cover	1.06	0.44	1.66	0.126	0.513

Table B5 Percent vegetation cover estimates per time period and species richness group with 95% CI limits. Mixed-effects model *R2m* = 0.734, *R2c* = 0.920.

Time period	Species richness	Cover estimate (%)	CI 2.5% limit	CI 97.5% limit
1999-2002	0	71.95	71.21	72.70
1999-2002	1	72.51	72.05	72.97
1999-2002	4	72.47	72.01	72.92
1999-2002	16	72.46	72.01	72.76
2003-2008	0	72.46	71.71	73.20
2003-2008	1	75.44	74.98	75.89
2003-2008	4	75.39	74.93	75.85
2003-2008	16	76.42	75.97	76.71
2008-2012	0	72.51	71.77	73.25
2008-2012	1	75.20	74.74	75.66
2008-2012	4	77.03	76.57	77.49
2008-2012	16	78.59	78.13	79.07

Table B6 4-species mixture compositions.

A) 2-genera diversity plots

	Low structural complexity		High structural complexity
4.1	*Parashorea malaanonan* *Parashorea tomentella* *Shorea beccariana* *Shorea leprosula*	**4.5**	*Hopea sangal* *Hopea ferruginea* *Shorea beccariana* *Shorea johorensis*
4.2	*Parashorea malaanonan* *Parashorea tomentella* *Shorea macroptera* *Shorea ovalis*	**4.6**	*Hopea sangal* *Hopea ferruginea* *Shorea macroptera* *Shorea gibbosa*
4.3	*Hopea sangal* *Hopea ferruginea* *Shorea macrophylla* *Shorea parvifolia*	**4.7**	*Hopea sangal* *Hopea ferruginea* *Shorea macrophylla* *Shorea faguetiana*
4.4	*Hopea sangal* *Hopea ferruginea* *Shorea argentifolia* *Shorea parvifolia*	**4.8**	*Hopea sangal* *Hopea ferruginea* *Shorea argentifolia* *Shorea johorensis*

B) 4-genera diversity plots

	High structural complexity		High structural complexity
4.9	*Dipterocarpus conformis* *Dryobalanops lanceolata* *Parashorea malaanonan* *Shorea faguetiana*	**4.13**	*Dipterocarpus conformis* *Dryobalanops lanceolata* *Shorea macrophylla* *Hopea sangal*
4.10	*Dipterocarpus conformis* *Dryobalanops lanceolata* *Parashorea tomentella* *Shorea johorensis*	**4.14**	*Dipterocarpus conformis* *Dryobalanops lanceolata* *Shorea ovalis* *Hopea ferruginea*
4.11	*Dipterocarpus conformis* *Dryobalanops lanceolata* *Parashorea tomentella* *Shorea gibbosa*	**4.15**	*Dipterocarpus conformis* *Dryobalanops lanceolata* *Shorea ovalis* *Hopea sangal*
4.12	*Dipterocarpus conformis* *Dryobalanops lanceolata* *Parashorea malaanonan* *Shorea johorensis*	**4.16**	*Dipterocarpus conformis* *Dryobalanops lanceolata* *Shorea macrophylla* *Hopea ferruginea*

Table B7 AGB, LAI, and % vegetation cover estimates (with 95% CI limits) by genus diversity and canopy structural complexity combinations, within 4-species plot combinations. R-squared values (*R2m* and *R2c*) are for the model with all treatments included.

Index	Genera	Canopy structural complexity	Number of plots	Estimate	CI 2.5% limit	CI 97.5% limit	*R2m*	*R2c*
AGB (Mg ha^{-1})	2 genera	Low	8	231.53	222.99	240.07	0.798	0.813
		High	8	228.93	220.43	237.44	-	-
	4 genera	Low	8	234.86	226.32	243.40	-	-
		High	8	232.26	223.72	240.80	-	-
LAI	2 genera	Low	8	4.97	4.37	5.56	0.362	0.647
		High	8	4.93	4.34	5.52	-	-
	4 genera	Low	8	4.98	4.39	5.57	-	-
		High	8	4.95	4.36	5.54	-	-
Cover (%)	2 genera	Low	8	67.12	61.87	72.37	0.210	0.560
		High	8	66.55	61.29	71.80	-	-
	4 genera	Low	8	67.50	62.25	72.76	-	-
		High	8	66.93	61.68	72.19	-	-

Table B8 AGB, LAI, and % vegetation cover estimates (with 95% CI limits) for untreated and liana-removed 16-species plots. R-squared values (*R2m* and *R2c*) are for the model with all treatments included.

Index	Liana removal	Number of plots	Estimate	CI 2.5% limit	CI 97.5% limit	*R2m*	*R2c*
AGB (Mg ha^{-1})	No	38	261.55	254.51	268.49	0.798	0.813
	Yes	10	265.73	256.71	274.81	-	-
	Difference	-	4.18	-5.62	12.73	-	-
LAI	No	38	5.52	4.94	6.10	0.362	0.647
	Yes	10	5.74	5.15	6.34	-	-
	Difference	-	0.22	-0.05	0.48	-	-
Cover (%)	No	38	69.27	64.13	74.39	0.210	0.560
	Yes	10	69.57	64.32	74.88	-	-
	Difference	-	0.30	-2.13	2.63	-	-

Table B9 Aboveground biomass change per unit increase in Functional Diversity (FD) and Phylogenetic Diversity (PD) with 95% CI limits.

Index	Species richness range	Change per unit Index increase (Mg ha^{-1})	CI 2.5% limit	CI 97.5% limit	*R2m*	*R2c*
FD	1, 4, 16	12.44	9.15	15.57	0.609	0.745
FD	4 only	4.22	-44.35	52.78	0.001	0.118
PD	1, 4, 16	605.10	517.53	676.92	0.700	0.712
PD	4 only	116.97	-99.43	333.37	0.032	0.151

Table B10 Remote sensing datasets used in this study.

Data	Spatial Resolution	Temporal Resolution	Time Cover
Landsat VCF vegetation cover	30 m	5-year	2000, 2005, 2010*
RapidEye-based vegetation cover	5 m	-	Aug. 2012
RapidEye-based leaf area index	5 m	-	Aug. 2012
RapidEye-based aboveground biomass	5 m	-	Aug. 2012
MODIS MCD15A3H LAI	500 m	4-day	2001-2017

***Mid-points of the monitoring time periods ('epochs') – see main text for details.**

Appendix C: Supplementary information for Chapter 4

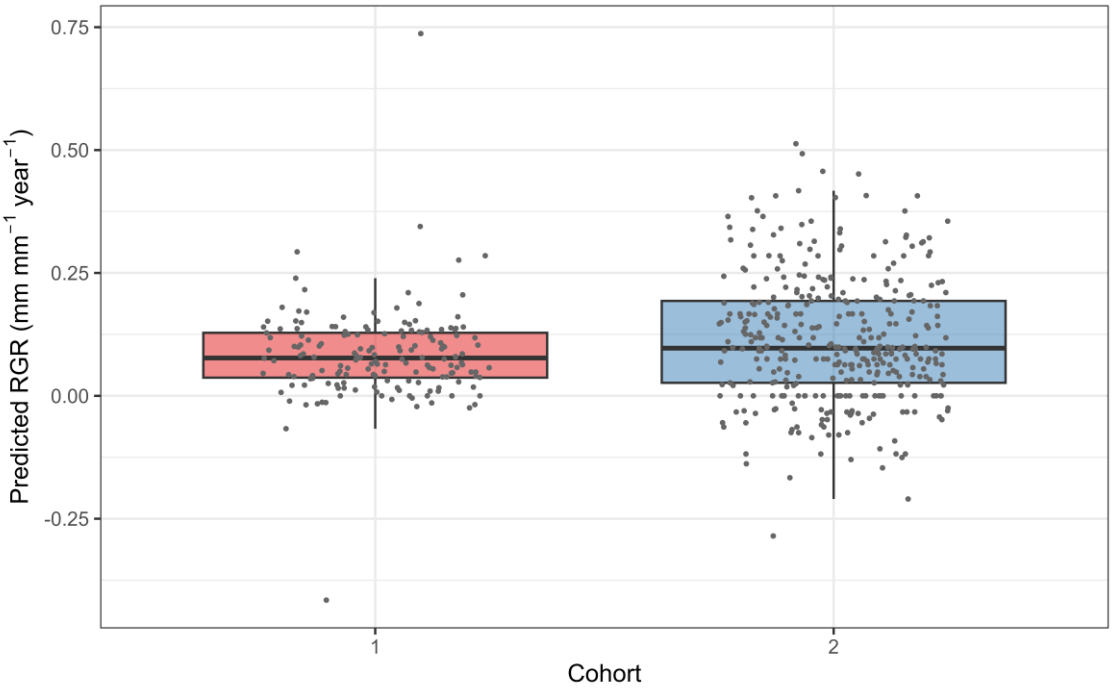

Figure C1 RGR in 2012 for cohorts 1 and 2. Points represent individual seedling values; whiskers extend 1.5 times the interquartile range (boxes). Thick lines are median values.

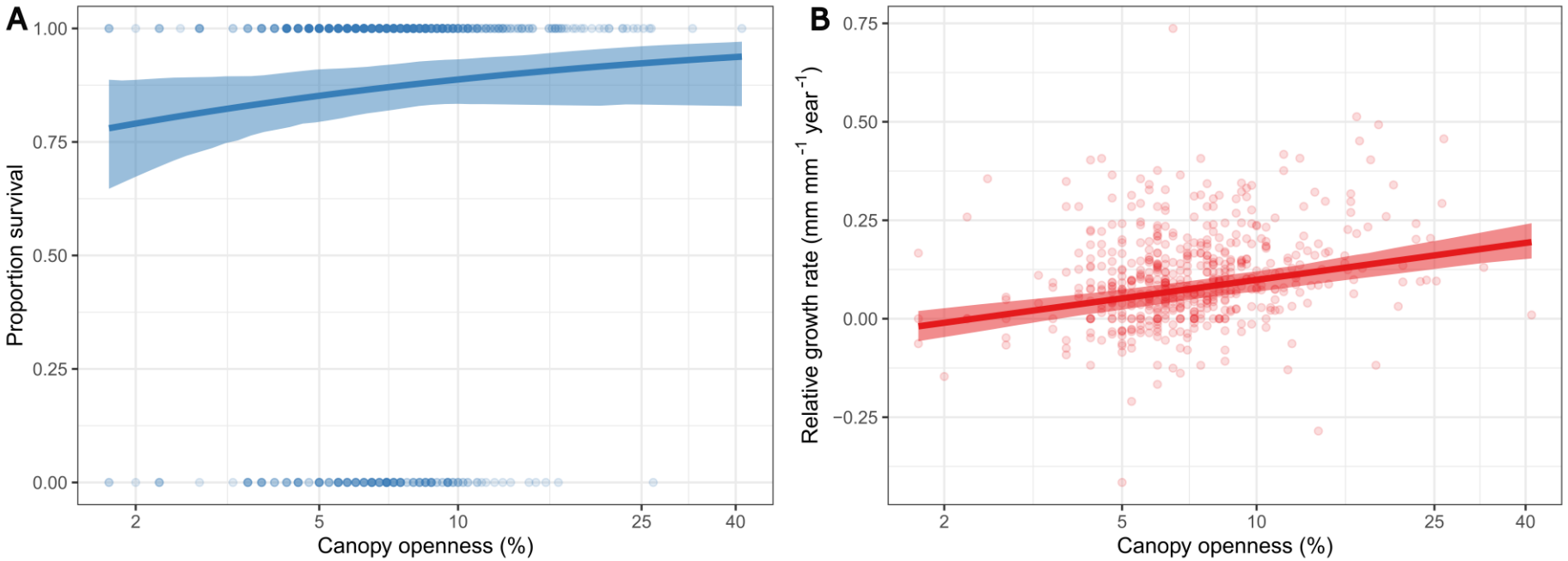

Figure C2 Estimated (**A**) survival and (**B**) RGR of dipterocarp seedlings in relation to canopy openness for cohort 1. All other covariates are held at their mean values. Coloured polygons represent the 95% confidence interval obtained through bootstrapping, and points depict the observed survival and RGR for individual enrichment planted seedlings. For both plots, $n = 194$.

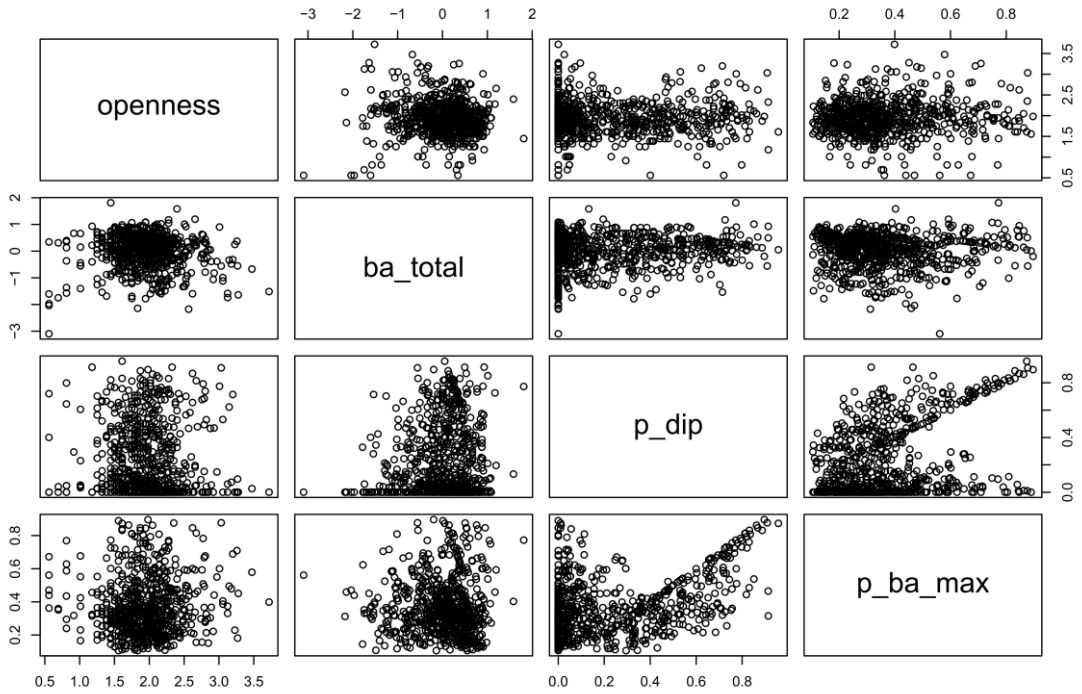

Figure C3 Correlation between combinations of canopy openness (*openness)*, total surrounding matrix area (*ba_total*), proportion largest surrounding tree (*p_ba_max*), and proportion dipterocarps (*p_dip*). Statistically significant positive Pearson product-moment correlation coefficients were identified between the proportion largest surrounding tree and proportion dipterocarps ($r_{(719)}$ = 0.390, 95% CI = 0.327 to 0.451) as well as between the proportion of trees belonging to dipterocarps and the surrounding total basal area ($r_{(719)}$ = 0.110, 95% CI = 0.037 to 0.181).

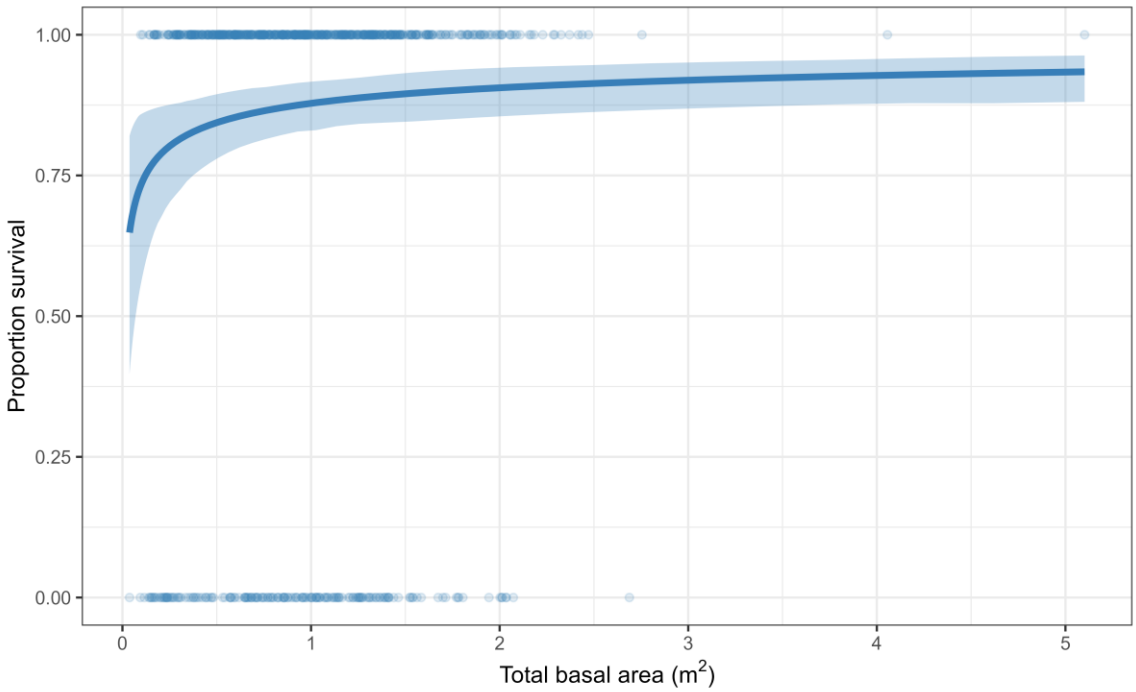

Figure C4 Estimated survival of dipterocarp seedlings in relation to the total basal area of matrix trees within a 10 m radius. Predictions are for cohort 1 seedlings, and canopy openness is held at its mean value. The blue polygon represents the 95% CI obtained through bootstrapping, and individual points depict the observed survival of planted seedlings. n = 194.

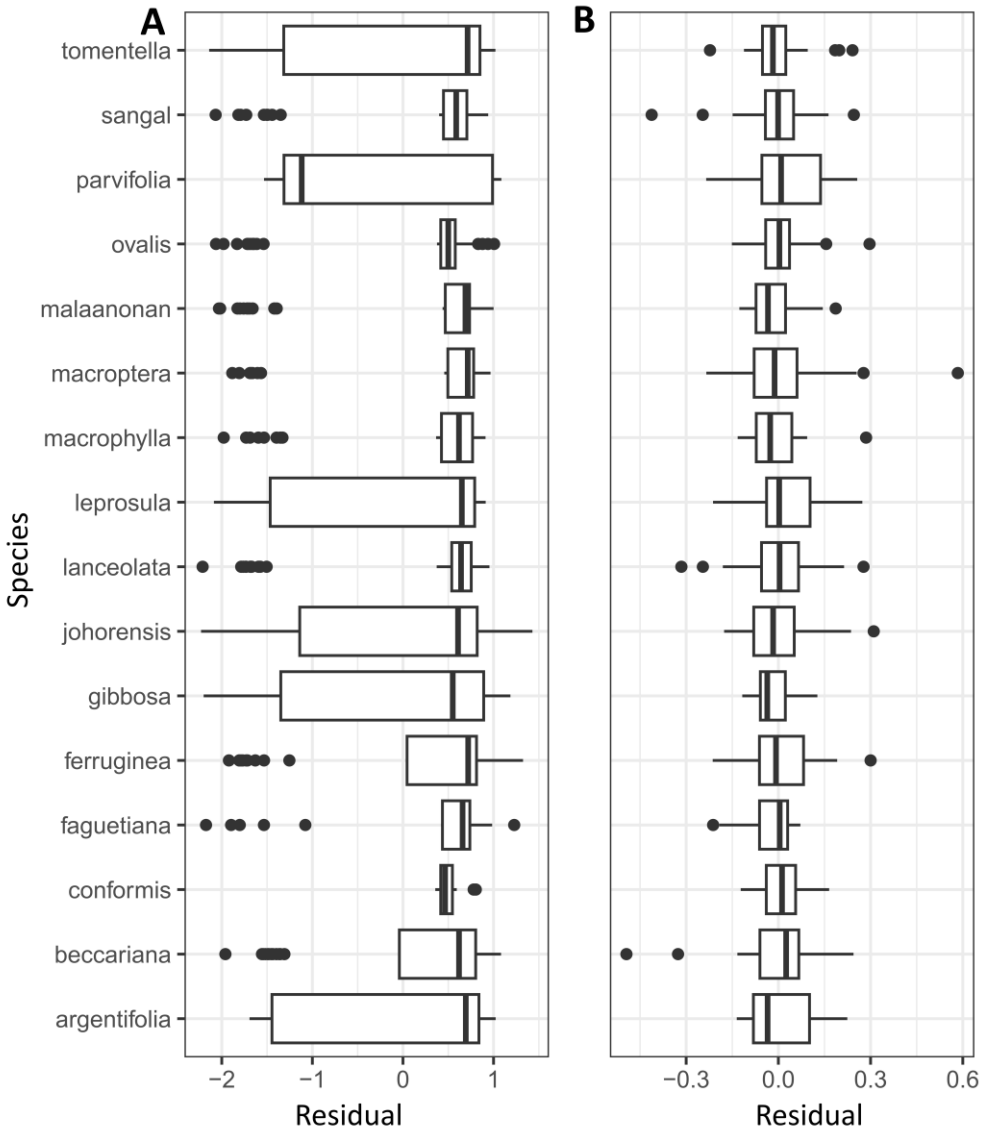

Figure C5 Residual plots for species identity in final survival (**A**) and growth (**B**) models. Boxplots contain median, 1st quartile, and 3rd quartiles. Whiskers extend from each quartile to the furthest value no greater than 1.5 times the interquartile range. Data beyond the end of whiskers are plotted as points.

Table C1 The sixteen dipterocarp species investigated at the Sabah Biodiversity Experiment.

Species	IUCN status	Date of census (year and status from prior assessment if available)
Shorea johorensis Foxw.	Critically Endangered	1998
Shorea gibbosa Brandis.	Critically Endangered	1998
Shorea faguetiana F.Heim.	Endangered	2017 (1998 EN)
Shorea leprosula Miq.	Near Threatened	2017 (1998 EN)
Shorea macrophylla Ashton	Least Concern	2019 (1998 VU)
Shorea macroptera King	Least Concern	2017
Shorea ovalis Korth.	Least Concern	2017
Shorea parvifolia Dyer.	Least Concern	2017
Shorea beccariana Bruck	Least Concern	2019
Shorea argentifolia Sym.	Least Concern	2019 (1998 EN)
Parashorea malaanonan (Blanco) Merr.	Least Concern	2019 (1998 CR)
Parashorea tomentella Meijer	Least Concern	2017
Hopea sangal Korth.	Vulnerable	2017 (1998 CR)
Hopea ferruginea Parijs	Critically Endangered	1998
Dryobalanops lanceolata Burck	Least Concern	2019 (1998 EN)
Dipterocarpus conformis Slooten	Endangered	2019

Table C2 Distribution of values for investigated covariates. For each studied covariate, the minimum and maximum observed values are provided, as well as the 1st and 3rd quartiles and median values.

Covariate	Minimum	1st quartile	Median	3rd quartile	Maximum
Canopy openness	1.75	5.50	6.75	8.75	41.25
Total basal area	0.04	0.60	0.94	1.31	5.10
Proportion dipterocarp	0.00	0.007	0.11	0.42	0.96
Proportion largest tree	0.11	0.24	0.33	0.45	0.90

Table C3 Correlation estimates (*r*) and 95% confidence intervals (CI) between the covariates included in this study. *df* = 719.

		r	2.5% CI	97.5% CI
Proportion dipterocarp	Proportion largest tree	0.390	0.327	0.451
	Basal area (logged and centred)	0.110	0.037	0.181
	Canopy openness (log scale)	0.011	-0.062	0.084
Proportion largest tree	Basal area (logged and centred)	0.003	-0.070	0.076
	Canopy openness (log scale)	0.051	-0.022	0.124
Basal area (logged and centred)	Canopy openness (log scale)	-0.047	-0.119	0.026

Appendix D: Supplementary information for Chapter 5

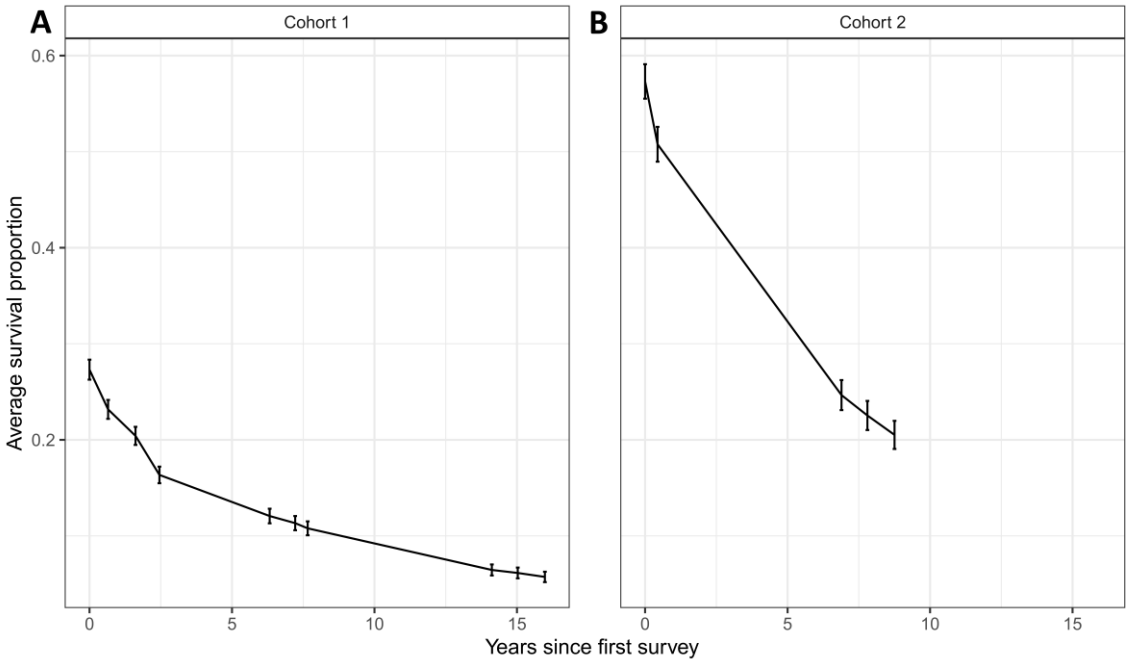

Figure D1 Survival curves for cohorts 1 (**A**) and 2 (**B**) at the Sabah Biodiversity Experiment. Vertical bars represent a 95% confidence interval for mean cohort survival at each time point, calculated from summary statistics of raw data.

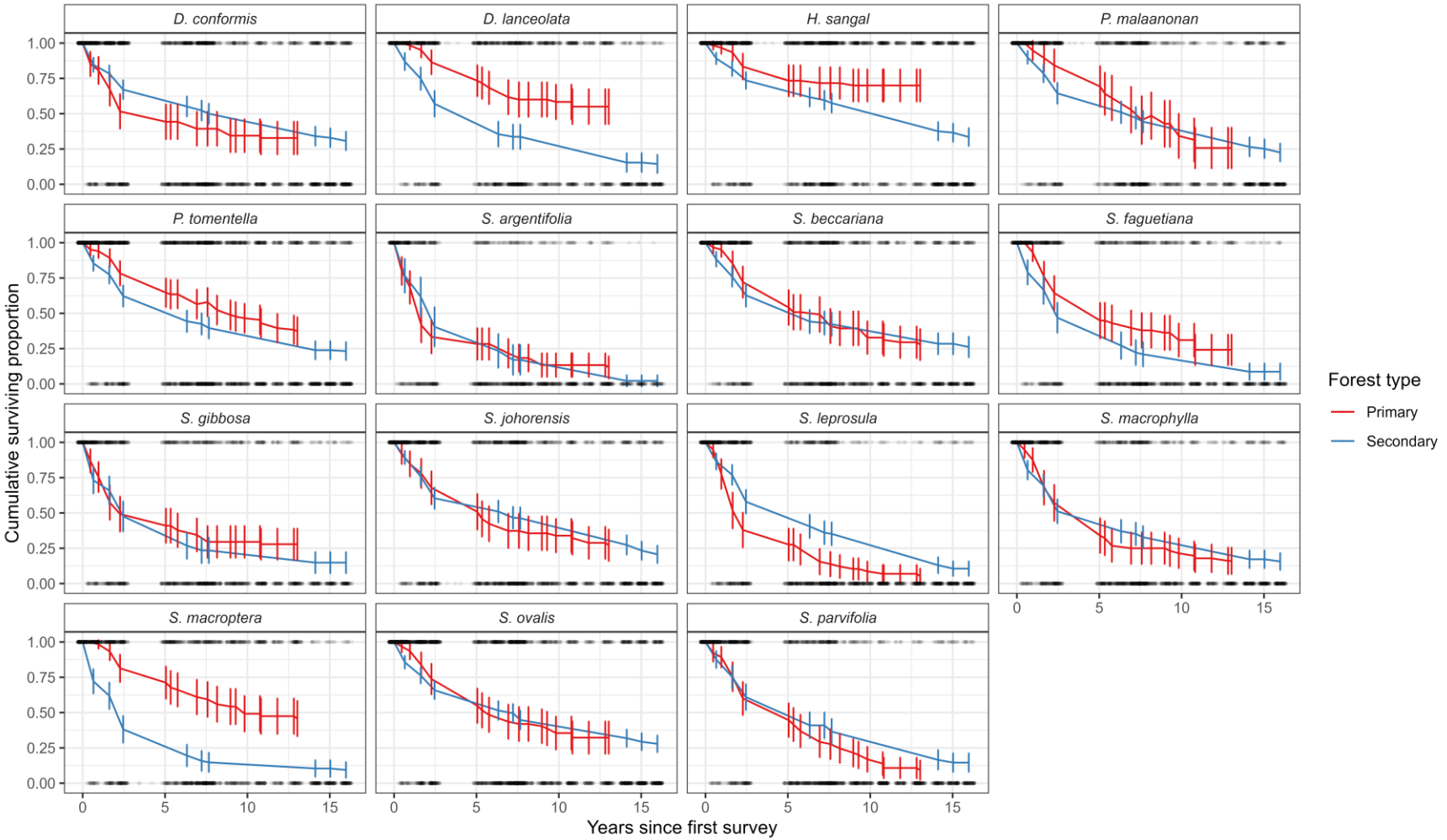

Figure D2 Survival of each tree species in each forest type since the first survey. Vertical bars represent 95% confidence interval for mean population survival at each census, calculated from summary statistics of raw data. Forest type indicated by colour in legend.

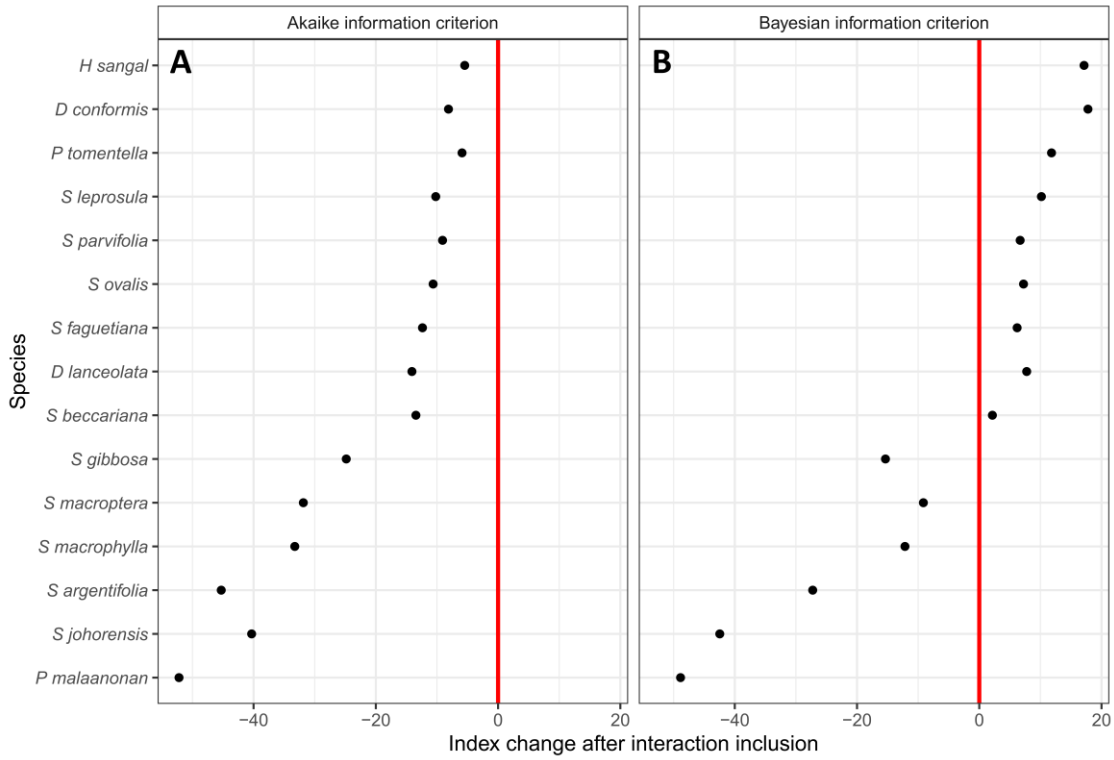

Figure D3 Growth model comparison for each species using Akaike (**A**) and Bayesian (**B**) information criteria. Negative values (left of the red vertical line) indicate species which produce a lower score when individual smoothers are fitted for each forest type across time. Positive values indicate species which show no clear difference in growth rates between forest types.

Table D1 Descriptions of the 26 dipterocarp species planted in the Sabah Biodiversity Experiment and Danum Gaps-Understory Experiment. Species names and authorities as of pre- and post-2022 updates, timber colour group (Ashton, 1982; Symington, 1943), ecology (Ashton, 1982), average nut length (Ashton, 1982), and IUCN status (with year of assessment in parentheses). An 'X' in the Sabah Biodiversity Experiment (SBE) or Danum Gaps-Understory Experiment (DGU) columns indicates that a species is present in either experiment.

Species	Timber group	Ecology	Nut length (mm)	IUCN Red List (year)	SBE	DGU
Dipterocarpus conformis Slooten	-	Rare, hill dipterocarp forest, clay-rich soils below 800 m.	-	Endangered (2019)	X	X
Dryobalanops beccarii Dyer	-	Locally abundant on leached sandy soils on coastal hills and inland ridges below 700 m.	14	Endangered (1998)		X
Dryobalanops lanceolata Burck	-	Widespread on fertile soils, abundant on undulating land, to 700 m.	20	Least Concern (2019)	X	X
Durio graveolens Becc.	-	-	-	Vulnerable (2020)		X
Hopea ferruginea Parijs	-	Deep fertile soils in mixed dipterocarp forest below 750 m.	07	Critically Endangered (1998)	X	
Hopea sangal Korth	-	Often on or near river banks in low country and to 500 m.	07	Vulnerable (2017)	X	X
Parashorea Malaanonan (Blanco) Merr.	-	Local on clay-rich soil, rarely on riverbanks, on ridges in mountains to 1,300 m.	17	Least Concern (2019)	X	X

Parashorea tomentella (Symington) Meijer	-	Mixed dipterocarp forest on flat and undulating land below < 200 m.	20	Least Concern (2017)	X	X
Shorea acuminatissima Symington	Yellow Meranti	Mixed dipterocarp forest on sandy clay soils on hills below 500 m.	02	Vulnerable (2019)		X
Shorea argentifolia Symington	Red Meranti	Locally frequent on ridges, hillsides, and valleys, < 600 m.	14	Least Concern (2019)	X	X
Shorea beccariana Bruck	Red Meranti	Common, lowlands, and dry ridges to 1,350 m.	40	Least Concern (2019)	X	X
Shorea faguetiana F.Heim.	Yellow Meranti	Low hills and particularly ridge tops at 150–700 m, occasionally to 1,000 m.	15	Endangered (2017)	X	X
Shorea gibbosa Brandis	Yellow Meranti	Locally common on fertile clay-loam soils on undulating land and river banks to 650 m.	18	Critically Endangered (1998)	X	X
Shorea guiso (Blanco) Blume	Red Balau	Scattered in lowland forest on red soils, most common in slightly seasonal climates.	08	Vulnerable (2017)		X
Shorea johorensis Foxw.	Red Meranti	Very common on well-drained fertile soils < 600 m.	20	Critically Endangered (1998)	X	X
Shorea leprosula Miq.	Red Meranti	Widespread, fast-growing emergent, common < 700 m.	20	Near Threatened (2017)	X	X
Shorea macrophylla (de Vriese) P.S.Ashton	Red Meranti	Locally abundant on periodically flooded alluvium, rarer on hillsides, < 600 m.	60	Least Concern (2019)	X	X
Shorea macroptera Dyer	Red Meranti	Common, sandy clay soils on low hills to 600 m.	18	Least Concern (2017)	X	X

Shorea mecistopteryx Ridl.	Red Meranti	Undulating land and low hills on sandy clay soils in mixed dipterocarp forest below 400 m.	42	Vulnerable (2019)		X
Shorea oleosa Meijer	Red Meranti	Widespread on clay soils in mixed dipterocarp forest, undulating land and hillsides to 600 m.	27	Least Concern (2019)		X
Shorea ovalis Korth	Red Meranti	Scattered in lowland Mixed Dipterocarp forest, usually in moist places in valleys and low-lying ground, to 500 m.	22	Least Concern (2017)	X	X
Shorea parvifolia Dyer	Red Meranti	Perhaps the commonest dipterocarp, on clay soils on hills < 800 m.	140	Least Concern (2017)	X	X
Shorea parvistipulata F.Heim	Red Meranti	Clay-rich soils on alluvium and especially hillsides and low ridges to 1,300 m.	25	Least Concern (2019)		X
Shorea pinanga Scheff.	Red meranti	Clay-rich soils especially on ridges below 700 m.	23	Least Concern (2019)		X
Shorea smithiana Symington	Red meranti	Frequent on deep sandy clay soils on undulating land and to 400 m.	27	Vulnerable (2019)		X
Shorea superba Symington	Red Balau	Fertile clay soils at low altitudes in mixed dipterocarp forest up to 600 m.	12	Vulnerable (2019)		X

Table D2 Site characteristics of Danum Valley Conservation Area and Malua Forest Reserve. Site characteristics carried out in 1983. From Saner et al. (2012).

Site characteristic	Danum Valley Conservation Area	Malua Forest Reserve
Elevation	<250 m	<250 m
Topography	Slopes 15-25°	Slopes 0-20°
Parent material	Mudstone	Mudstone
Soil type	Orthic acriosol	Orthic acriosol
Soil family	Tanjong Lipat	Tanjong Lipat
Soil association	Bang	Kretam and Mentapok
Est. pre-logging volume	178-230 m^3 ha^{-1}	193-221 m^3 ha^{-1}
Est. dipterocarp volume	149-225 m^3 ha^{-1}	180-216 m^3 ha^{-1}

Table D3 Initial and final seedling numbers across forest type for each species.

Species	Primary forest		Secondary forest	
	Initial surviving (Nov 2004)	Final surviving (Nov 2017)	Initial surviving (Apr 2004)	Final surviving (Mar 2020)
D. conformis	62	20	176	54
D. lanceolata	61	33	107	15
H. sangal	61	43	193	66
P. malaanonan	39	9	149	34
P. tomentella	83	32	151	36
S. argentifolia	60	8	47	1
S. beccariana	61	17	129	34
S. faguetiana	58	14	81	7
S. gibbosa	61	17	82	12
S. johorensis	60	16	149	31
S. leprosula	58	4	126	13
S. macrophylla	56	10	128	20
S. macroptera	61	29	97	9
S. ovalis	62	21	202	56
S. parvifolia	65	6	105	15

Table D4 BIC values for generalised additive models with and without separate smoothing terms for forest type, as well as the difference. Values are given for each species-specific pair of models. Species which show an improved model with separate smoothers are shown in bold text.

Species	Single smoother	Separate smoothers	BIC difference
D. conformis	1517.4	1535.1	17.8
D. lanceolata	1573.3	1581.0	7.8
H. sangal	2517.6	2534.8	17.1
P. malaanonan	1365.6	1316.8	-48.9
P. tomentella	1922.5	1934.3	11.8
S. argentifolia	937.8	910.5	-27.2
S. beccariana	1777.4	1779.5	2.1
S. faguetiana	896.9	903.1	6.2
S. gibbosa	678.7	663.4	-15.3
S. johorensis	2091.2	2048.8	-42.5
S. leprosula	1491.6	1501.8	10.2
S. macrophylla	1671.6	1659.5	-12.2
S. macroptera	1194.6	1185.4	-9.1
S. ovalis	1936.7	1943.9	7.2
S. parvifolia	1542.9	1549.6	6.7

Table D5 Survival proportions for individual species across each forest type and estimated difference between forest types (with 95% CI limits). Mixed-effects model *R2m* = 0.152, *R2c* = 0.188. Species which show a statistically significant difference in survival proportions are shown in bold text.

	Primary forest			Secondary forest		
Species	Estimate	2.5% CI	97.5% CI	Estimate	2.5% CI	97.5% CI
D. conformis	0.325	0.215	0.460	0.333	0.244	0.436
D. lanceolata	0.556	0.420	0.684	0.151	0.088	0.248
H. sangal	0.710	0.576	0.815	0.374	0.282	0.477
P. malaanonan	0.255	0.135	0.429	0.257	0.177	0.358
P. tomentella	0.368	0.265	0.484	0.229	0.155	0.324
S. argentifolia	0.111	0.053	0.219	0.022	0.003	0.137
S. beccariana	0.273	0.172	0.404	0.280	0.192	0.388
S. faguetiana	0.232	0.138	0.362	0.083	0.038	0.172
S. gibbosa	0.273	0.172	0.405	0.139	0.075	0.243
S. johorensis	0.267	0.165	0.400	0.265	0.183	0.367
S. leprosula	0.050	0.016	0.144	0.121	0.070	0.202
S. macrophylla	0.153	0.079	0.274	0.165	0.102	0.256
S. macroptera	0.462	0.331	0.598	0.099	0.051	0.185
S. ovalis	0.317	0.209	0.450	0.318	0.233	0.416
S. parvifolia	0.087	0.039	0.182	0.164	0.097	0.264

Appendix E: Supplementary information for Chapter 6

Figure E1 Plot boundary markers within the Sabah Biodiversity Experiment. **(A)** A red-painted belian marker indicates a plot corner. **(B)** A tree with blue paint markings indicates part of a plot's vertical boundary. **(C)** A tree with yellow paint indicates a part of a plot's horizontal boundary. **(D)** A planted seedling with a tree identification tag indicating it is part of planted line 20 (bottom tag).

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