Restoring Dipterocarp Rainforest Diversity

Tree Regeneration, Life-history traits and the Light Factor

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Cover: Fisheye photo of a seed tree in the Sow-a-Seed project, Sabah, Borneo (photo: A. Lojingi and M. Gustafsson)

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Restoring Dipterocarp Rainforest Diversity. Tree Regeneration, Life-history traits and the Light Factor

Abstract

Rainforest restoration is an important application in today's multipurpose management of secondary forests. In the Malaysian state Sabah (Borneo) most forests have been selectively logged, but many still hold potential for high biodiversity and carbon sequestration, as well as future timber production. Restoration for biodiversity is increasing, but knowledge concerning tree species growth and adaptations are insufficient for foresters to make good decisions for sustainable management. The PhD research was mainly conducted in the Sow-a-Seed project (Sabah) that started in 1998 to restore rainforest biodiversity degraded from logging and wildfire. Within the project area a common garden experiment was established in 2008, involving 34 tree taxa. There, tree species responses to increased light were predicted with the help of species traits, and related to a pioneer-climax continuum of life history characteristics. Some of these traits, e.g. wood density, specific leaf area and foliar nutrient concentration were major factors in predicting the trees growth responses. Also in the common garden, young trees growth under different levels of canopy cover were studied to examine the potential increase in growth under higher levels of light, and the occurrence of species specific light optima for growth. The tree species showed varied growth performances under different levels of light, e.g. that species with climax properties had optima at lower light levels than species with pioneer properties; and life-history traits were used to model these variations among species. Further, diversity patterns among naturally regenerated trees (≥10 cm diameter at breast height) were studied over 10 years after selective timber harvesting, using a gradient of harvest intensities (0–16 trees cut ha^{-1}). Results showed that for optimum biodiversity harvest intensities should not exceed 8 trees ha^{-1}; since species richness was highest at an intermediate level of extraction, after which it started to decline. Also the broadest range of traits was achieved at intermediate levels of disturbance. Tree species richness influence on the diversity of foliar lichens and canopy arthropods was also studied. Results indicated that a foundation species approach could be useful for selecting trees that promote high biodiversity. The work in this thesis highlights that the biodiversity of regenerating forests can potentially be enhanced with suitable post-disturbance management.

Keywords: canopy cover treatment, *Dipterocarpaceae*, late successional species, resource investment strategies, tree seedling, tropical forest, visible sky.

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Dedication

To my parents (all four of you) for believing in me.

Trees are sanctuaries. Whoever knows how to speak to them, whoever knows how to listen to them, can learn the truth

Hermann Hesse

Contents

List of Publications

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

I Gustafsson, M., Gustafsson, L., Alloysius, D., Falck, J., Yap, S., Karlsson, A. & Ilstedt, U. (2016). Life-history traits predict the response to increased light among 33 tropical rainforest tree species. *Forest Ecology and Management* 362, 20–28.

II Gustafsson, M., Gustafsson, L., Alloysius, D., Falck, J., Yap, S., Karlsson, A. & Ilstedt, U. A life-history traits model explains differences in light growth responses among young tropical rain forest trees. *Manuscript*.

III Axelsson, E.P., Gustafsson, M., Lussetti, D., Karlsson, A. & Ilstedt, U. The intermediate disturbance hypothesis applies to the in-growth of understorey trees in selectively logged tropical forests. *Submitted manuscript*.

IV Grady, K.; Gustafsson, M.; Garnas, J.; Frisch, A.; Axelsson, P.; Ilstedt, U.; Vairappan, C. S.; Gustafsson L. A foundation tree species approach for restoring degraded tropical forests: lichens and invertebrates as bio-indicators of foundation status. *Manuscript*.

Papers I is reproduced with the permission of the publisher, Journal of Forest Ecology and Management. Paper III is submitted to Journal of Functional Ecology.

Preface

2 April 2014

I’m back in Camp Marimba, about 2 hour’s bumpy car ride from my base in Luasong village, southeast Sabah, Borneo. Gibbon monkeys are singing the morning to life, and a monitor lizard hunts for fish in the jungle river below the camp. The forest is contradictory with its intense peacefulness and beauty.

Marimba is home away from home for many of the project staff who carefully manages this great rainforest infrastructure. It is remote… no cell phone signals reach here. It is wild… I even saw a clouded leopard cross the bush road one early morning not far from the camp. I feel such bliss to – for a short moment – be part of this amazing wilderness. I am forever grateful.

1 Introduction

1.1 Secondary rainforest

Disturbance and forest loss are part of the natural successional dynamics in tropical rainforests, through processes such as natural fires, droughts, landslides, diseases and extreme weather. However, anthropogenic activities have shown accelerating effects on the natural forest succession (Brancalion *et al.*, 2013). Secondary forests have been defined in many ways (Box 1), and in this thesis I use a definition from Brown & Lugo (1990) "forests formed as a consequence of human impact on forest lands", excluding both plantation forests and secondary forests resulting from natural disturbances.

Box 1. Definitions of secondary forest and old-growth forest

Secondary forest
Forest with simple structure and low biodiversity that is dominated by tree species with pioneer characteristics; the term generally refers to any forest subjected to logging. Brown & Lugo (1990) use the term to describe human induced forest degradation, while Ghazoul & Sheil (2010) also include natural disturbance in the term. Secondary forest, also called second-growth or regrowth forests, can refer to forests that are re-established on previously forested land after complete or almost complete natural or human induced clearing, (Chazdon, 2014; Kammesheidt, 2002)

Old-growth forest
Late successional forest with high biodiversity and dense canopy cover that have reached a stabile stage in structure and species composition, and where the tree species composition is dominated by tree species with climax properties; also called mature, pristine or virgin forest (e.g. Chazdon, 2014; Ghazoul & Sheil, 2010).

Secondary rainforests may have been exposed to various degrees of degradation; for instance anything from a single selective logging operation to repeated wood harvesting over an extended time period (Kammesheidt, 2002; Brown & Lugo, 1990). The disturbance intensity affects the forest structure and species composition (Mouillot *et al.*, 2013), and a majority of these disturbed forests have undergone changes in vegetation structure and soil properties that may influence productivity and processes related to ecosystem services (Chazdon, 2008). Also, degraded biodiversity is common in secondary forests and researchers have expressed their concerns regarding the conditions of the expanding areas of degraded forests (Barlow *et al.*, 2016; Keenan *et al.*, 2015). Nevertheless, many of today's secondary forests hold high species richness and potential to recover from previous disturbances (Gibson *et al.*, 2011).

Human-modified landscapes are expanding in the tropics mainly due to conversion of natural ecosystems into production focused land-uses (Gibson et al., 2011). Todays' tropical rainforest degradations are mainly due to selective logging and large scale conversions into industrial agriculture or timber plantations, but also shifting cultivation (Fao, 2015); the lack of adequate forest management constitute an additional influential factor in many countries (Kobayashi, 2004). Even though there are indications that the net rate loss of tropical forests has slowed down over the last 25 years, there has still been a decline in forest cover by 10 percent between 1990 and 2015 (Keenan *et al.*, 2015). A study from the University of Maryland using satellite data show a yearly trend in tropical deforestation by 2101 km^2 between the years 2000 and 2012, despite that the satellite data also indicate high levels of reforestation (Hansen *et al.*, 2013). It is reported that the trends of tropical deforestation are actually declining in some areas, very likely a consequence of deforestation having had a high priority on international policy agendas over the last decades (Barlow *et al.*, 2016; Fao, 2015). The tree cover has even been expanding in some tropical regions due to reforestation and tree plantations (Fao, 2015). All in all, todays' about 1770 M ha tropical forests are facing challenges such as large-scale degradation and fragmentation, diminishing biodiversity and reduced genetic diversity in expanding monoculture plantations (Keenan *et al.*, 2015).

In the repeatedly selectively logged forests of Southeast Asia deforestation rates are declining at a slower pace compared to many other forested regions, while secondary forest areas are increasing rapidly (Keenan *et al.*, 2015). For example, on the Island of Borneo almost 50 percent (~26.3 M ha) of the original forest had been lost and another 25 percent (~13.6 M ha) had been selectively logged in 2010 (Figure 1), while an additional 42 percent (6.6 M ha) of the remaining Bornean primary forests are expected to be logged since they are designated within the ‘production forest’ land-use class (Gaveau *et al.*, 2014).

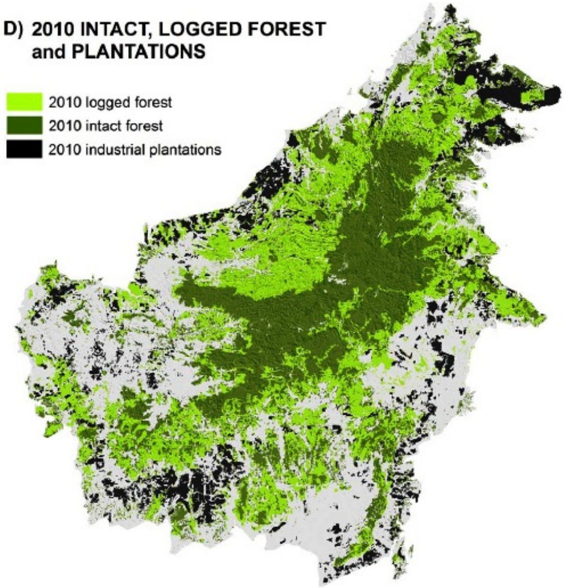

Figure 1. Map of Borneo illustrating the forests cover in year 2010; intact forest (dark green), logged forest (light green), and industrial timber and oil palm plantations (black). Map and caption courtesy of Gaveau *et al.*(2014).

1.2 In the light of species coexistence

Primary tropical forests are known to sustain a seemingly incomprehensible diversity of trees. A recent pantropical study estimate that the number of tropical tree species might exceed 50 000, which is an enormous contrast to the about 130 tree species native to temperate Europe (Slik *et al.*, 2015). On the island of Borneo around 3000 native tree species have been identified (MacKinnon *et al.*, 1996), and 200-300 different tree species can be found in just one hectare (Richards, 1952). Tropical rainforest biodiversity is supported by a large variation in habitats that the tree diversity offers (Baltzer & Thomas, 2010). High species richness causes competition for resources, and many theories aim to explain the co-existence of life forms. One commonly suggested mechanism is niche differentiation (Poorter & Bongers, 2006; Wright, 2002), i.e. that the rainforest heterogeneity reduces interspecific competition and provides for coexistence of many species with different resource requirements and competitive abilities in various temporal and spatial scales.

The available light is generally the most limiting resource for growth among seedlings and young trees in evergreen tropical rainforest (Rozendaal *et al.*, 2006; Poorter, 1999); where the multi-layered canopy and gaps create a diverse and dynamic forest light environment. It might be surprising that these equatorial forest trees suffer from limited light, but imagine a closed canopy as a roof where very little light is let through to the forest floor and where stochastic events cause gaps that, for a short while, increase light and boost plant growth. Under an intact canopy, only about 1-2 percent of the photosynthetically active radiation will reach the understory plants and seedlings (Romell *et al.*, 2009; Chazdon & Fetcher, 1984). A vertical light resource gradient ranges from the dark forest floor where tree seedlings usually have to compete with dense understory vegetation, to the emergent tree crowns in bright sun light. A disturbance – human or natural – can cause gaps that are big enough to make a new successional regeneration cycle possible (Romell *et al.*, 2009; Brown & Whitmore, 1992). Secondary forests are found in different stages of succession depending on the intensity of and time since the last disturbance, and successional processes that lead to variabilities in the forest light environment constitute key drivers for tree species composition (Walker & Wardle, 2014).

1.3 Tree resource investments explained by life-history traits

The heterogeneous rainforests support a large diversity in ecological strategies of trees relating to their life histories (Figure 2). These strategies govern different dimensions of plant function, such as regeneration adaptations, disturbance tolerance, and response capacity to light or nutrient limitations (Wright *et al.*, 2003; Westoby *et al.*, 2002). Varieties in plant function are expressed in functional traits, i.e. characteristics that have effects on individual trees physiological functions, and thus directly influence organism performance and fitness (e.g. Kunstler *et al.*, 2015; Lebrija-Trejos *et al.*, 2010; Wright *et al.*, 2010). A plants actual fitness is obtained by compromises (trade-offs) in life-history traits; i.e. those acquisitive or conservative strategies that influence the plants life history, like reproductive behaviour, growth rate, shade tolerance, and resilience (Philipson *et al.*, 2014; Wright *et al.*, 2010; Poorter & Bongers, 2006).

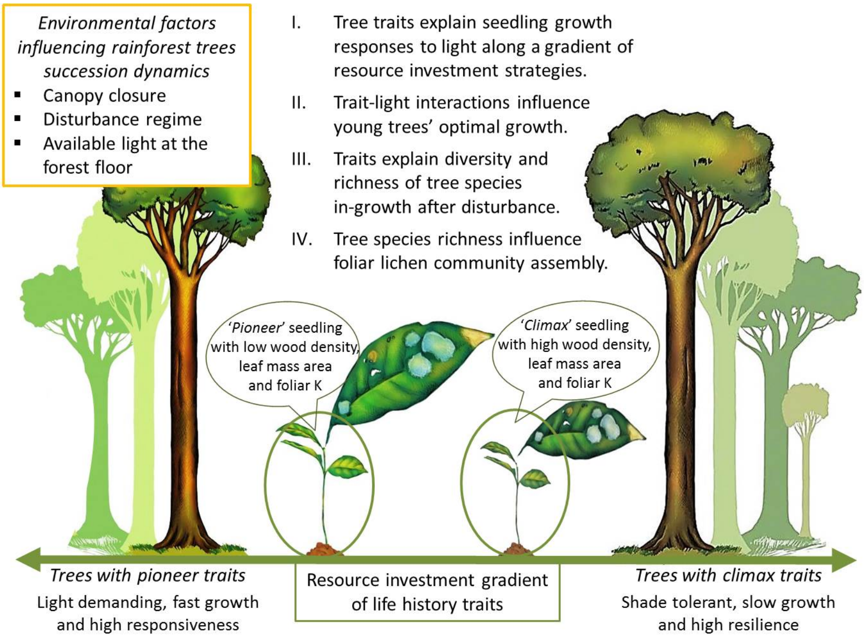

Figure 2. Successional dynamics of trees in secondary lowland dipterocarp rainforest described from a gradient of resource investment strategies based on life-history traits. The studies in the thesis are listed as I - IV. Illustration by Karina Kaliadka

Rainforest trees' different light requirements for regeneration can be illustrated with a resource investment axis; at one extreme with trees having 'climax' properties (e.g. shade tolerance, slow growth and high leaf mass per area) that limits tree growth in favour of stability and resilience, and at the opposite side of the gradient light-demanding trees displaying contrasting fast-growing 'pioneer' properties (Baltzer & Thomas, 2007; Rozendaal *et al.*, 2006). Shade tolerant trees with climax properties will invest in long leaf lifespan with thick leaves or high leaf tissue density, while trees with pioneer properties are associated with fast relative height growth and thin leaves with short leaf lifespan (Asanok *et al.*, 2013; Wright *et al.*, 2004). Although forests never actually reach that climax equilibrium stage of succession, the term is still useful in explaining basic non-pioneer tree species characteristics and adaptations. The pioneer–climax gradient shows a trade-off in life-history traits among trees; for instance a young tree that experience rapid growth in bright light will likely have a larger mortality rate in the dark understory shade compared to an individual with a slower growth rate. Thus, different adaptions of tree species to site conditions are visible in their resource investment strategies through the life-history traits (Salguero-Gómez *et al.*, 2016; Philipson *et al.*, 2014). The prevailing stage in forest succession after disturbance determines the species community composition through predictable patterns in life-history traits and vital rates (Wright *et al.*, 2010; King *et al.*, 2006; Davies & Ashton, 1999).

1.4 Dipterocarps – rainforest giants

One tree family – the *Dipterocarpaceae* – dominates the lowland rainforests of Southeast Asia; ecologically in forest biomass, but also from an economic aspect since many valuable timber species belong to this family (Ashton, 1988). The dipterocarps are long-lived tree species with strong habitat associations and are generally described as late successional with climax properties, all though it is becoming more and more recognized that there are large variations in resource requirements also within the dipterocarp family (Born *et al.*, 2015; Ashton & Kettle, 2012; Kettle *et al.*, 2012 and Paper I). Still, there are large knowledge gaps concerning dipterocarp resource investment strategies and adaptations to site conditions. Due to intensive harvest over the last decades many dipterocarp species are now listed as endangered or even critically endangered in the IUCN Red List of Threatened Species (IUCN, 2016). For instance, out of the 195 dipterocarp species native to Sabah 44 species are listed as critically endangered, 20 species as endangered and 1 species as vulnerable in the Red List (IUCN, 2016). Noteworthy is that Maycock *et al.* (2012) have questioned current conservation assessments of Sabah dipterocarps for not considering the full aspects of the species' ecology. By using ecological niche models sensitive to ecological factors their estimates indicated greater habitat loss within dipterocarp species' historic distributions in lowland rainforest than earlier reported. Still, the Maycock *et al.* study (2012) estimated a lower category of threat for most of the studied species compared to the estimates by IUCN in 2010, and they concluded that other dipterocarps likely are more threatened. Overall, the dipterocarps are among the tree species in most need of management measures like restoration for biodiversity.

1.5 Foundation tree species

Foundation species, i.e. species with disproportionately large effect on associated biodiversity of organisms, create and maintain habitats that locally support other species and structure communities; they also tend to have a stabilizing influence on ecosystem processes (Whitham *et al.*, 2006; Ellison *et al.*, 2005). Late successional tree species truly construct the characteristic rainforest architecture, and some of these tree species may well act as foundation species. Slik *et al.* (2013) recognize the importance of large old trees in a forest ecosystem, and that their (life-history) traits can influence ecosystem dynamics, e.g. in influencing hydrological processes, storing large quantities of carbon and creating niches such as nesting and sheltering sites. However, also young individuals of certain tree species may have a facilitating influence on other species groups in the local environment, and thus acquire the status of foundation species.

1.6 Management for multi-functional forests and biodiversity

Managers are facing many challenges in reversing the current trends in forest degradation. New measures of management for biodiversity are required to meet the needs of the widespread areas of secondary tropical rainforests recovering from disturbances like fragmentation and loss of biodiversity. Our levels of understanding are hampered from insufficient knowledge regarding e.g. forest recovery processes and drivers of species community assembly (Lebrija-Trejos *et al.*, 2010; Clark & Clark, 1992). It has been shown that ecosystem functioning and biodiversity are closely related during secondary succession (Bu *et al.*, 2014), and in order to enhance degraded biodiversity we need to increase our knowledge regarding such processes and drivers.

The fitness of a tree, i.e. the individuals reproductive success in a specific environment, illustrates a relationship between phenotypic variation and environmental conditions that reflect the adaptive value of the trees life-history traits (Ackerly, 2003). By studying life history strategies we can better understand forest successions and the relationships between functional traits and demographic rates among tropical rainforest trees. Many traits are difficult to measure, while others are easier to acquire and easier to use in practice. Traits usefulness mainly lies in their rapid and consistent responses - regardless of taxa - to the complex processes caused by major changes in the environment (Mouillot *et al.*, 2013). There are numerous studies on traits interspecific variations (among species), while intraspecific variations (within species) have been less researched. Tree traits have been proven useful for modelling the variation among species to better understand species interactions and responses to disturbance (e.g. Philipson *et al.*, 2014; Poorter *et al.*, 2008), and trait-based approaches have helped gaining significant understanding in how the environment affects the species community composition (e.g. Kunstler *et al.*, 2015; Asanok *et al.*, 2013). This is valuable knowledge indicating how relatively easily measured traits that can be obtained for large numbers of species can be used to predict tree resource requirements for less studied species in the highly diverse tropical forests. Predicting tree species strategies for resource use is important for management focusing on production and ecosystem services, and it also applies to biodiversity focused management (Baltzer & Thomas, 2010).

Today’s declining deforestation rates are partly due to earlier reforestation and timber plantation operations for wood production purposes (which often used only a limited number of species, usually <5), and often monocultures of highly productive exotic tree species (Lamb *et al.*, 2005). Now reforestation can have different aims, for instance to restore biodiversity and to enhance carbon sequestration (Kettle, 2010; Chazdon, 2008; Brown & Lugo, 1994). Restoration methods include support of naturally regenerated seedlings and enrichment planting of absent species (Hector *et al.*, 2011; Ådjers *et al.*, 1995); for instance focusing on foundation plant species (Ellison *et al.*, 2005). Ecological restoration for biodiversity raise the interest to involve a much more diverse tree species pool compared to traditional reforestation, but so far practical experience from enrichment plantings with more than a handful species is scarce.

My PhD research was conducted in the INIKEA Sow-a-Seed project, which started in 1998 in Sabah to restore rainforest degraded from logging and wildfire. The main aim of the Sow-a-Seed project has been to improve biodiversity by planting a multitude of native tree species; mainly Dipterocarps, but also other climax species and fruit trees. Today about 13000 ha have been treated, and almost 100 tree species have been included in the restoration efforts. Two enrichment planting methods – line planting and gap-cluster planting – has been used alongside assisting the natural regeneration by canopy reduction and removal of competing herbaceous vegetation (Alloysius *et al.*, 2010). The project now holds great knowledge from planting and managing these many species. Trees’ survival rates vary between 25-80 percent, and the largest trees after 18 years have reached almost 60 cm diameter at breast height, while many individuals are smaller (around 10 cm diameter at breast height). The main question of the project is no longer whether it is possible to plant many species; instead the focus is on fine-tuning methods to enhance tree survival and forest structure. The experiences from restoration efforts have greatly enhanced our understandings of the restoration process. At the start there was a focus on how to restore a degraded rainforest in a wide sense, whilst now the questions are much more specific, e.g. regarding the impact of certain tree planting methods and tree species interactions with site conditions. Still we only have a very limited degree of understanding the whole system. I seek with this thesis to contribute to increased knowledge regarding management of secondary rainforest.

1.7 Objectives

The overarching aim of my PhD thesis was to improve future forest restoration by enhancing the understanding of post-disturbance processes in secondary lowland dipterocarp rainforest. Based on life history theory I aimed to investigate relationships between tree traits and interactions with site factors by modelling tree species responses to limiting resources and to disturbance. I aimed to use life-history traits of a diverse selection of tree species to gain general knowledge of tree dynamics through multivariate models, and thereby also to increase the understanding of lesser known tree species. I also scaled up from the species level to the community level to gain a broader understanding of the secondary forest system. Thus, I examined tree species' responses to disturbance, as well as the community composition of trees regenerating and growing into the tree strata after disturbance (Paper III). Further I examined the influence of the tree community on the diversity of other life forms (Paper IV).

The central research questions of this thesis are:

I. Can models based on life-history traits predict tree species' responses to increased light; and do these responses relate to a possible pioneer–climax continuum of resource investment strategies?

II. Can life-history trait interactions with light predict young trees growth – irrespectively of species identity; and is it then possible to identify optimal light conditions for growth?

III. Does an intermediate level of disturbance benefit the diversity of trees growing into the strata after selective logging, and can life-history traits be used to predict species-specific patterns of post-disturbance in-growth?

IV. Does a higher number of planted tree species promote the diversity of other life forms (e.g. lichens and insects); and is it then possible to optimize tree species selection by using foundation species, or with the help of life-history traits?

2 Study system

The PhD studies were conducted in two forest reserves in southeast Sabah, a Malaysian state on the Island of Borneo, and managed by Yayasan Sabah a State Government statutory body. The area consists of undulating lowland dipterocarp rainforest (altitudes between 300 m and 600 m a.s.l.) with tropical humid equatorial climate and mean annual temperatures around 27°C. The monthly precipitation exceeds 100 mm throughout the year, with moderately more intense rainfalls between October and February (Peel 2007). Mean annual precipitation has been measured to 2517 mm in the project area (SD 760 mm) for the years 2002–2013. Today the production forests surrounding the forest reserves have been selectively logged and large parts have been converted into oil palm plantations.

2.1 Field sampling

Most of the research in this thesis (Paper I, II and IV) was conducted in the Sow-a-seed restoration project area, a 18,500 hectare experimental forest within the Sg. Tiagau Forest Reserve (approximately 4°360’N, 117°120’E). This area was logged in the 1970’s and subsequently burned in the 1982-1983 ENSO event resulting in one of the most extensive forest fires in recent times (Goldammer, 2006). The wildfire event resulted in secondary forest largely dominated by pioneer trees, primarily from the *Macaranga* genus (Figure 3b), while some areas that were subjected to a higher degree of disturbance had a large element of herbaceous vegetation mixed with the pioneer trees (Figure 3a). Still a few adult canopy trees with climax properties could be located in most parts of the project area, as well as fragments of primary forest (Figure 3c). In 1998 the project was initiated with the aim to restore the forest biodiversity by using enrichment planting methods, and to date more than 2 million native trees have been planted.

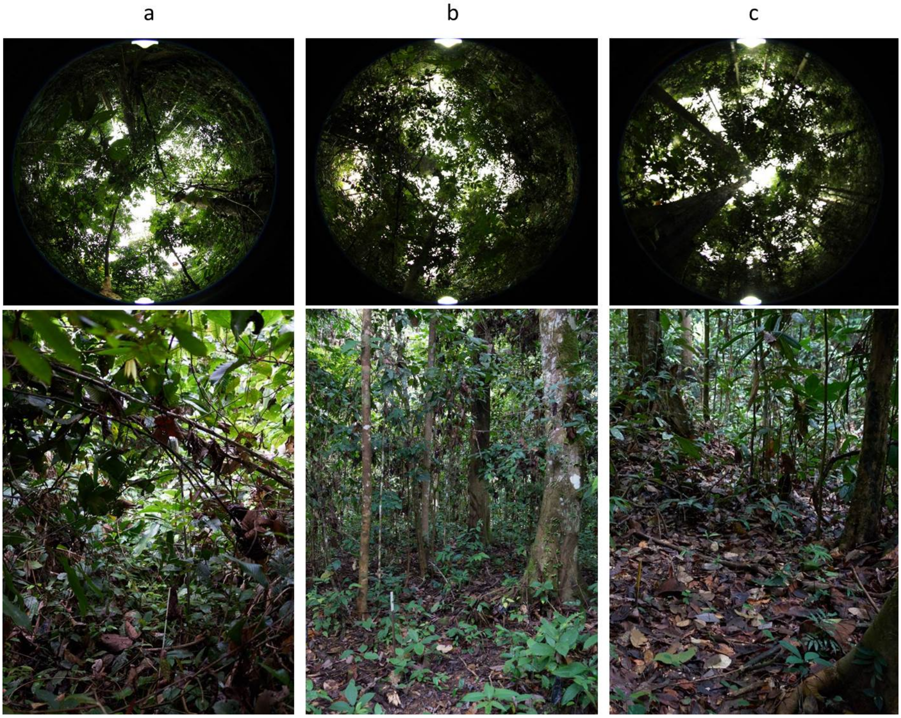

Figure 3 (a-c). Forest types based on levels of degradation in a secondary lowland dipterocarp rainforest subjected to selective logging and wildfires over 30 years ago in Sabah, Borneo. Fisheye photos illustrate the canopy cover of the forest types (top row), and photos show the vegetation at the forest floor (bottom row). A mix of herbaceous vegetation and pioneer trees create the broken canopy that dominate the areas that were subjected to the highest level of degradation (a), while the most common forest type that was subjected to an intermediate level of disturbance is dominated by pioneer tree species (b). In areas that were less degraded adult late-successional tree species mixed with pioneer tree species form a more closed canopy (c). Fisheye photos by Lukas Holmström and photos by Ulrik Ilstedt.

In 2008 a 3 ha field trial study plot was established in the interior of the project area where plants were propagated in a relatively homogenous environment. Trees from 34 species replicated 20 times were planted 3 m apart with a random distribution along lines with 10 m apart over the study area (Figure 4). This “common garden” approach allowed studies of the interspecific tree variation within a standard environment - the suitable set up for studying tree species common in forest restoration, their traits and response to light. There was also conducted a study on the relationship between the tree species richness and the diversity of other life forms, i.e. foliar lichens (Figure 5) and canopy arthropods.

The study for Paper III was conducted in the Gunung Rara Forest Reserve (approximately 4°33’N, 117°02’E) about 40 km from the Sow-a-seed project area. The experimental area comprised 20 study plots (6 ha study plots, with enumerated 100x100 m net plots) established in 1992 in primary forest, with the initial aim to evaluate the impact of different tree harvest methods, where logging was carried out in 1993. Based on this long-term selective logging experiment the study of Paper III was focused on in-growth development of trees (≥10 cm diameter at breast height) over a period of 10 years after logging, using a gradient of selective logging intensities i.e. number of harvested trees per ha. More detailed information on study sites and sampling methodology can be found in respective Paper.

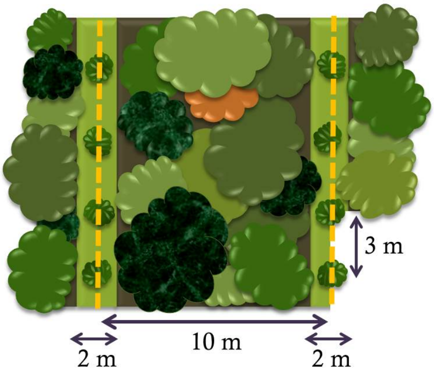

Figure 4. Schematic description of line planting as implemented in the Sow-a-seed restoration project, an 18,500 hectare experimental forest within the Sg. Tiagau Forest Reserve, Sabah Malaysia.

Figure 5. Foliar lichens on a leaf from a tree planted in the common garden experiment of the Sow-a-Seed project in Sabah, Borneo.

2.2 Life-history traits

Functional traits are known to have strong correlations to growth and response to light (Wright *et al.*, 2010; King *et al.*, 2005 and Paper I), and life-history traits have frequently been used to examine species' resource requirements (Salguero-Gómez *et al.*, 2016; Kunstler *et al.*, 2015; Born *et al.*, 2014). For instance have wood density historically been used to group tree species into different timber categories (e.g. light or heavy hardwood); while it today also is used in trait-based analyses, indicating tree species resource investment strategies (i.e. acquisitive or conservative) along a pioneer–climax continuum (Rozendaal *et al.*, 2006; Swaine & Whitmore, 1988). Trees with high wood density have more robust stems that are resistant to herbivores and pathogens, while trees with low wood density instead invest in high volume growth per synthesised carbon compound. Specific leaf area (and its inverse, leaf mass area) represents the cost of light absorption at leaf level and indicating trees leaf strategies for resource capture, where high specific leaf area indicates resources invested in pioneer properties e.g. fast growth and strong responses (Díaz *et al.*, 2015; Lambers & Poorter, 1992). Specific leaf area is a good indicator of plant functioning (e.g. photosynthetic and respiratory rates), and plays an important role in plants responses to both light and nutrient availability (Wright *et al.*, 2010). Further, I also examined leaf nutrient concentrations (i.e. nitrogen, phosphorous and potassium). Pioneer properties such as fast growth and high photosynthetic capacity can be linked to high levels of both nitrogen (an essential component of both chlorophyll and amino acids) and phosphorous (for instance necessary in the regulation of photosynthetic capacity) (Wright *et al.*, 2010; Mengel & Kirkby, 1987). Potassium leaf concentrations effects on trees growth and resource use is much less studied, but it has been linked to species investment in resilience e.g. unpalatable and disease resistant leaves (Tripler *et al.*, 2006). I have taken use of a selection of life-history traits commonly used in studies on trees growth performance to examine the variation among tree species resource investment strategies (Table 1, next spread).

2.3 Canopy cover and forest light conditions

I used two complementary methods to estimate the light environment; image-based measurements of the visible sky to reflect the proportion canopy openness, and the subjective crown illumination index, CII (Jennings *et al.*, 1999; Clark & Clark, 1992) to estimate the light that actually reaches a tree crown. A canopy reduction treatment was conducted to mimic a natural (or human induced) gap dynamic process and I took measurements before and after treatment to calculate the overall change in forest light conditions for the two canopy/light parameters. The canopy openness (percentage of visible sky) from 1.30 m above the forest floor was estimated by analyzing circular 180° hemispherical photographs (Figure 6). The light environment for an individual tree was calculated using the mean values from two photographs, taken at 1.5 m from each planting point in both directions of a planting line (in total >1500 photos*2 inventories). CII was based on a subjective scale where 1.0 indicated no direct light on the tree crown, while 5.0 indicated a fully illuminated tree crown (Jennings *et al.*, 1999; Clark & Clark, 1992). A more detailed description of the light estimates can be found in Paper I.

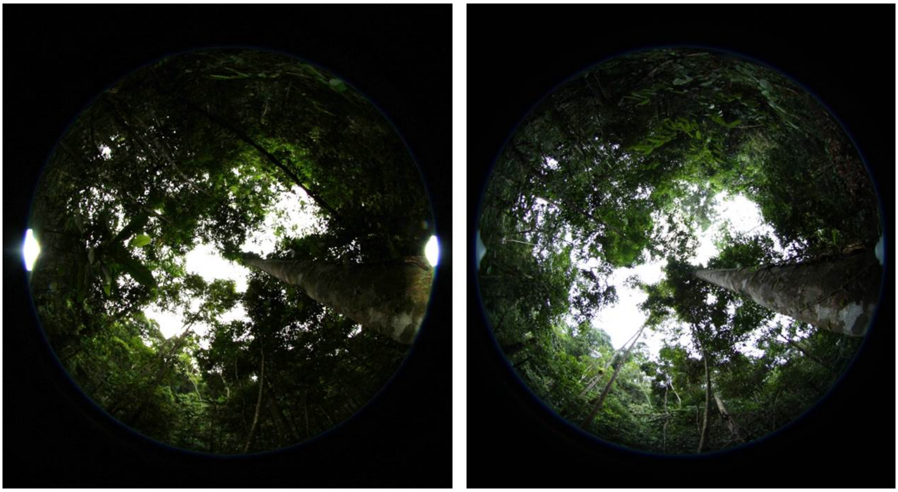

Figure 6. Canopy openness before (left) and after (right) a canopy reduction treatment in the common garden experiment of the Sow-a-Seed project in Sabah (Borneo), measured using hemispherical fisheye photos.

Table 1. *Tree species' life history traits and related resource investment strategies in the pioneer–climax continuum. Variables (Var.) are shown as predicted (P) or explanatory (e) in the trait-based models.*

Life-history traits	**Var.**	**Resource investment strategies in pioneer–climax continuum**	**Evidence for trait function**
Relative height growth rate $(\log[h^{final}] - \log[h^{initial}])/(time^{final} - time^{initial})$	P	Monthly height (h) increment from stem base to top of the crown. Species with pioneer properties grows faster compared to species with climax properties.	E.g. Paine *et al.* (2015) and Philipson *et al.* (2011).
Height growth response (cm/month)	P	Monthly response in height growth to increased light. Stronger response for species with pioneer properties compared to species with climax properties.	E.g. Paine *et al.* (2012) and Baker *et al.* (2003).
In-growth (stems/ha)	P	Trees growing into the forest after disturbance. Pioneer properties dominate early succession stages, with an increasing element of climax properties in later stages.	Molino and Sabatier (2001).
Potential response in height growth (cm/month)	P	The 75percent quantile of a species' HGR response. The growth response of individuals less limited by other factors from each species.	Wright *et al.* (2010).
Crown depth (m)	e	Vertical measurement from lowest branch to top of the crown. High values indicate a tall crown, fast growth and pioneer properties.	E.g. Kitajima *et al.* (2005) and Poorter *et al.* (2003).
Crown depth/tree height ratio (m/m)	e	Tall trees have high values, potentially indicating climax properties. Light limitation can potentially be indicated by a tall and slim individual with short crown depth.	Sterck *et al.* (2001).
Crown width (m)	e	Mean horizontal crown width, measured in two directions. Wide crowns indicate fast growth and pioneer properties.	E.g. Iida *et al.* (2014) and King *et al.* (2005).
Early height growth (m)	e	Height growth from six months after planting to 12 months after planting. Strong early height growth can potentially indicate pioneer properties.	N.a.
Foliar potassium concentration (mg/g)	e	Measured with an atomic absorption spectrometer. High values indicate conservative climax properties e.g. reduced herbivory and strong resistance to disease.	Tripler *et al.* (2006).
Leaf mass area (g/cm^2)	e	Leaf dry mass per unit area. High values indicate climax properties e.g. thick long-lived leaves.	E.g. Díaz *et al.* (2015) and Wright *et al.* (2004).
Leaved stem length (cm)	e	Total length of leaf display on a branch. Indicates recent extension growth, e.g. high values reflect high growth rates, and indicate pioneer properties.	King and Clark (2004).

Mortality rate (log[N^{initial}] - log[N^{final}])/time	e	Young tree mortality (excluding the six first months after planting). High values indicate pioneer properties e.g. investments in early growth.	E.g. Philipson *et al.* (2014) and Wright *et al.* (2010).
Maximum diameter at breast height (m)	e	Trunk diameter measured at 1.3 m above stem base. High values indicate investments in climax properties, e.g. investment in stability.	King *et al.* (2006).
Maximum height stature (m)	e	Tree height from stem base to tip of the crown. High values indicate investments in climax properties, e.g. investment in stability.	E.g. Kunstler *et al.* (2015) and Wright *et al.* (2010).
Foliar nitrogen concentration (mg/g)	e	Measured using an autoanalyzer. Essential for plant growth and photosynthesis, and high levels indicate pioneer properties.	E.g. Baltzer and Thomas (2007) and Wright *et al.* (2004)
Foliar phosphorous concentration (mg/g)	e	Determined using the molybdenum-blue method. High levels indicate pioneer properties. Low levels can result in stunted growth in young plants.	E.g. Baltzer and Thomas (2007) and Tripler *et al.* (2006).
Specific leaf area (cm^2 g^{-1})	e	The inverse of LMA. High values indicate pioneer properties e.g. thin leaves with short lifespan.	E.g. Philipson *et al.* (2014) and Poorter and Bongers (2006).
Wood density (g/cm^3)	e	Dry weight per unit volume wood. High values indicate climax properties, e.g. stability and resilience.	E.g. Kunstler *et al.* (2015) and Iida *et al.* (2014).

2.4 Trait-based multivariate analysis

I have based a large part of the statistical analyses of my PhD research on multivariate Partial Least Square Regressions (PLS) analyses (Paper I, II and III), mainly in an attempt to capture and examine as much of the variation as possible in a highly diverse lowland dipterocarp rainforest. There are still numerous unidentified species and many to us unknown basic ecosystem processes i.e. species community assembly, interspecific competition and response to disturbance, and thus relationships between species traits and site factors. Hence, PLS is an adequate analysis method to examine such a complex and unknown system since it allows the inclusion of several correlated dependent variables (Eriksson *et al.*, 2013).

PLS is a multivariate extension of a multiple linear regression (MLR) that, similarly to a Principal Component Analysis (PCA), summarizes the variation in the data by calculating linear components. New components are created as long as Q^2 (predicted variance based on cross-validation) is increasing. The PLS identifies a linear (or polynomial) relationship between two matrixes of predicted Y-variables and explanatory X-variables (i.e. traits or site factors). Thus in contrast to PCA the PLS components are optimized to predict Y-variables based on the X matrix (Eriksson *et al.*, 2013). Consequently the explanatory variables do not need to be independent as in MLR, and it is also possible to use several y-variables. In Paper II and III, squared terms of the environmental variables (i.e. light and disturbance, respectively) and their interactions with the traits, i.e. trait*trait, site*site and trait*site*site, were include to explore the presence of young trees relative height growth optima in relation to light availability (Paper II), and the disturbance intensity required for optimal tree species diversity establishment after selective logging (Paper III). More detailed descriptions of the PLS analysis method can be found in Paper I and II.

3 Results and Discussion

3.1 Life-history traits' predictive power

Modelling tree's functional traits have been proven useful for creating a better understanding of forest structure, plant life history strategies and response to a changing environment (Salguero-Gómez *et al.*, 2016; Díaz *et al.*, 2015; Poorter & Bongers, 2006). There are traits that seem to correlate positively with patterns of genetic diversity, for instance seed dispersal syndromes (e.g. gyration, wind, animal) for maternally-inherited markers (Thomas *et al.*, 2014). Building on previous knowledge, the studies of this thesis have shown that trait-based models can be used for predicting general patterns of tree species resource use strategies and thus how they responded to an altered light environment (Paper I), but also to predict relative growth for individual trees at different levels of light (Paper II) and tree species in-growth after disturbance (Paper III). The model's explained variance ranged between 20-50 percent (20 percent, 30 percent and 47 percent for Paper I, II and III respectively), quite promising results considering that they were examining a hyper diverse tropical rainforest ecosystem. In addition to the variables included in these models, there were probably numerous other factors influencing the tree growth. For instance competing vegetation, i.e. climbers, herbaceous understory vegetation and early successional trees, would likely have influenced the monitored trees, as well as available soil nutrients, erosion, compaction during logging operations, herbivory and pathogens.

With the multivariate models I aimed to identify a limited number of traits that could explain a large part of the variation influencing the studied system; more specifically I wanted to examine the extent of variation in resource investment strategies among a large group of late-successional 'climax' species, but also study the variation among a selection of taxa from different families. The trees in the common garden were germinated from seeds collected from the same area and planted under realistic conditions in this degraded forest, which is in contrast to many studies conducted in tropical rainforest that have been examining either existing natural regeneration (e.g. Holste *et al.*, 2011; Whitmore & Brown, 1996; Clark & Clark, 1992) or seedlings in "greenhouse-like" environments (e.g. Paine *et al.*, 2012; Philipson *et al.*, 2011; Wright & Westoby, 1999). In a study with similar methodology and from similar conditions as my common garden experiment Philipson *et al.* (2014) identify a trade-off in life history characteristics between trees with different ecological strategies, and they highlight wood density as an especially useful trait when examining variation among trees life history strategies. My prediction models also showed systematic patterns among trees life history strategies that could be related to a pioneer–climax continuum, i.e. that tree species exhibit a continuum of resource investment strategies related to their successional status (Paper I). Further, by including a canopy reduction treatment I could also relate the trees responses to increased light to the pioneer–climax continuum (Paper I). The light factor was later also used in analyses that showed that young trees light requirements for optimal growth varied with resource investment strategies (Paper II). Additionally, by examining tree species in-growth after disturbance I showed that mild disturbance can enhance tree species richness and thereby influence life history trait diversity (Paper III). The results are consistent with other studies that have shown how relationships between life history adaptations and vital rates (e.g. relative height growth) vary along a pioneer–climax gradient of resource investment strategies (Díaz *et al.*, 2015; Wright *et al.*, 2010).

The rich flora of lowland dipterocarp rainforest partly belongs to tree species that are still unknown or unidentified. I showed in Paper I and II that by applying traits-based models to lesser known tree species it was possible to predict e.g. growth or response patterns for species where that information were not known to us, and thus broaden the understanding of rainforest trees interspecific competition and community assembly. Based on the trait-based model (Paper I) I created a prediction plot, where some of the species in the study were used to predict the values of the remaining species in a cross-validation approach (Figure 7). The result showed a clear correlation between measured and predicted values - indicating the models strong predictive power. The species positions along the 1:1 line (blue in Figure 7) indicated a pioneer–climax continuum, where species with high response indicated pioneer properties. Both dipterocarps and non-dipterocarps were found in the full range from weak to strong response to the change in light conditions, but the majority of our dipterocarps exhibited a high response.

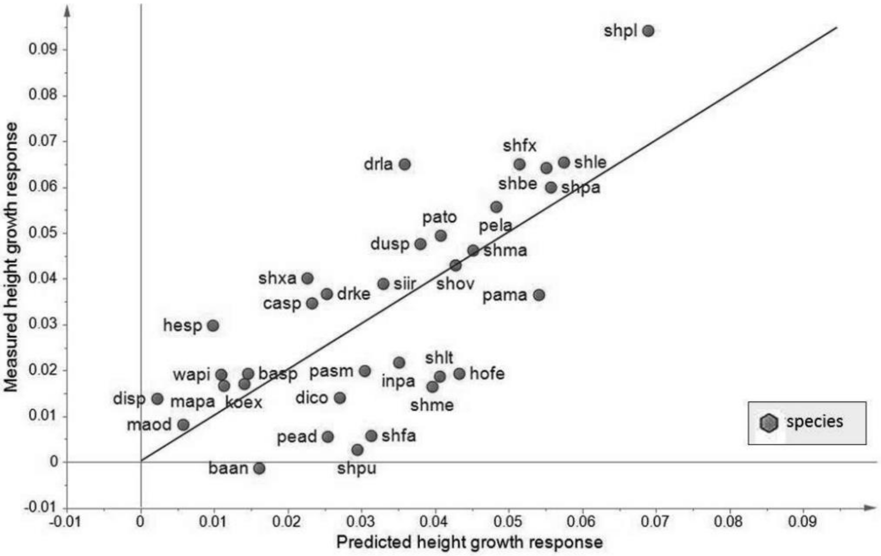

Figure 7. Response prediction plot for height growth response (m). The Y-axis represents measured values and the X-axis predicted values of the potential height growth response, where the positions along the 1:1 line (blue) indicates a pioneer–climax continuum among 33 planted native tree species in Sabah, Borneo. For full methodology and tree species' codes see Paper I.

I used a large number of life-history traits in this thesis (Table 1), all with the aim to address different aspects of tree resource investment strategies and thus to increase our understanding of secondary rainforest dynamics. The traits can show different explained variance, depending on the focus of the study as well as the species included. For instance, when examining different tree species response in height growth to an increased irradiance (Paper I) a suit of traits related to pioneer properties showed high explained variance, i.e. fast early height growth and large tree crown (i.e. long leaved stem length, large crown width and long crown depth). Trees acquisitive or conservative strategies can influence competitive dominance through resource requirements and responsive abilities (Kunstler et al., 2015; Walker & Wardle, 2014). Consequently, life-history traits affect the rainforest tree community composition. The traits interspecific variations are drivers for a growth–mortality trade-off (Philipson et al., 2014; Wright et al., 2010; Ackerly, 2003; Kitajima & Bolker, 2003), where adaptations related to fast growth (e.g. high SLA and mortality) are opposing adaptations related to stability and resilience (e.g. high wood density and foliar K concentrations) illustrated in Paper I, II and III.

In my studies a few traits stood out as especially well-suited to predict tree species' growth and responses, as well as their resource investment strategies;

foliar potassium concentration consistently showed high explained variance with high values indicating climax properties, so did also wood density and leaf mass area (or its inverse specific leaf area). Wood density is a well-known trait that has been used for decades in the timber industry to group tree species after timber density and thus approximate values can be found for most tree species (Faridah Hanum & Van Der Maesen, 1997). I used wood density values from the literature, which probably decreased the models degrees of explanation. Still wood density had a large impact in my models, for instance showing a strong negative correlation between wood density and the response to light (Paper I). Also foliar K concentration – up until now rarely used as a life history trait in trait-based modelling – was negatively correlated with both tree height growth response (Paper I) and relative height growth rate for young trees (Paper II), as well as the response to disturbance (Paper III); indicating that high values of K can be an evidence of climax properties. Also lichen community composition was correlated to foliar K concentrations (Paper IV). Based on my results I would strongly support further inclusion of foliar K concentration in life history trait studies.

3.2 The light factor

The forest light environment plays a key role in this thesis (Paper I, II, III and IV). In general it is dark at the rainforest floor, also under a broken canopy (Figure 3). The levels of transmitted radiation reaching the planted trees in our common garden study (Paper II) ranged from complete shade to just above ten percent canopy openness in the largest gaps (Figure 8). Only three percent of the seedlings were found in bright light (CII level 4 and 5). Under the closed canopy at CII level 1 a median value of 4.1 percent visible sky (1st quartile 0.035 /3rd quartile 0.048) was measured; while the least shaded points at CII 4 showed a median value of 7.5 percent visible sky (1st quartile 0.055 /3rd quartile 0.086) and at CII 5 a median value of 11.3 percent visible sky (1st quartile 0.068 /3rd quartile 0.130). An additional value of the dual light measurements is that the results indicated that crown illumination index – a simple and cheap estimation method – can estimate the forest light environment with reasonable accuracy.

I performed a canopy reduction treatment 50 months after planting to study the young trees growth responses to increased light (Paper I). The post-treatment increase in visible sky from 4.8 percent to 7.3 percent might seem small, but it is actually an increase in canopy openness of 34 percent (Figure 9). Other studies from the same region show similar levels of light after disturbance; e.g. a study examining naturally created gaps in Sabah show canopy openness of 11.2 percent in the gaps and 2.4 percent in the shaded understory (Born et al., 2015). Another study in lowland dipterocarp forest in Sabah with a slightly higher level of disturbance compared to the common garden show levels of visible sky at 8.8–10.7 percent before treatment (Romell *et al.*, 2009).

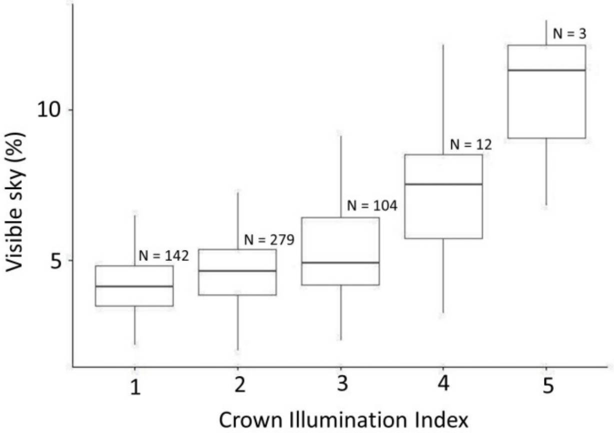

Figure 8. Box plot illustrating the relationship between the measured percentages of visible sky (or canopy openness) and the estimated values of crown illumination index (CII) for young planted trees in a common garden experiment in Sabah, Borneo. CII level 1 indicates a tree crown in complete shade, while CII level 5 indicates a fully illuminated tree crown. N is the number of individuals for each CII category. For full methodology see Paper II.

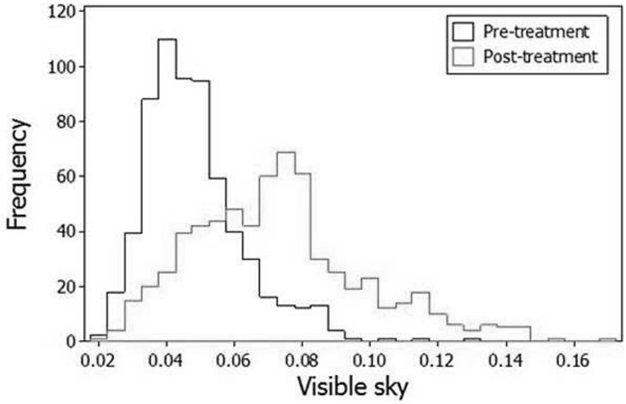

Figure 9. Frequency of visible sky (i.e. canopy openness) at individual planting points before (black) and after (grey) a canopy reduction treatment in a common garden experiment in Sabah, Borneo. For full methodology see Paper I.

3.3 Trait – light interactions influence growth

Rainforest trees have to compete for resources and their establishment at suitable sites are decisive for trees to obtain optimal fitness (Philipson *et al.*, 2014; Ackerly, 2003). Fast growth and strong responses will depend on how well a tree is adapted to its site conditions as well as the amount of available light at its growing site. Trees adaptations to site factors can be examined through trade-offs in regeneration strategies, and multivariate trait-based analyses can model relationships between species' traits and site factors (Legendre & Legendre, 2012; Dray & Legendre, 2008). In Paper I it was possible to predict tree species height growth responses to increased light succeeding a canopy reduction treatment based on traits (Paper I). Further, by combining traits and light factors as explanatory variables in multivariate models more of the variation among tree species, but also among individual trees could be explained (Paper II).

In accordance with Poorter et al. (2003) my results showed that pioneer traits related positively to species with requirements of high light levels across a large number of species and genera (dipterocarps and other genera). Additionally, by using a taxon-free approach it was possible to identify different resource investment strategies, and light levels for optimal growth among the young planted trees (Paper II), where trees with acquisitive pioneer growth patterns had optima at higher light levels than trees with conservative climax growth patterns (Figure 10). The models' best fit was achieved by including quadratic terms, indicating non-linear relationships between traits and light.

It has been debated whether species with high growth rates in comparatively open environments also exhibit better growth in light-poor environments (Bloor & Grubb, 2003; Poorter, 1999; Clark & Clark, 1992), or if species change ranks when not growing in their optimal light (Philipson *et al.*, 2014; Sack & Grubb, 2001). In Paper II the response surface with respect to the leaf mass area variable indicated a week rank reversal between young trees adapted to bright light or full shade; i.e. that trees not only experienced an optimal light for growth, but also decreased growth rates in less favourable light environments. However, the identified differences were small and it is doubtful whether they are important for population dynamics, and the differences in survival were probably larger and thus had greater impact in low light conditions

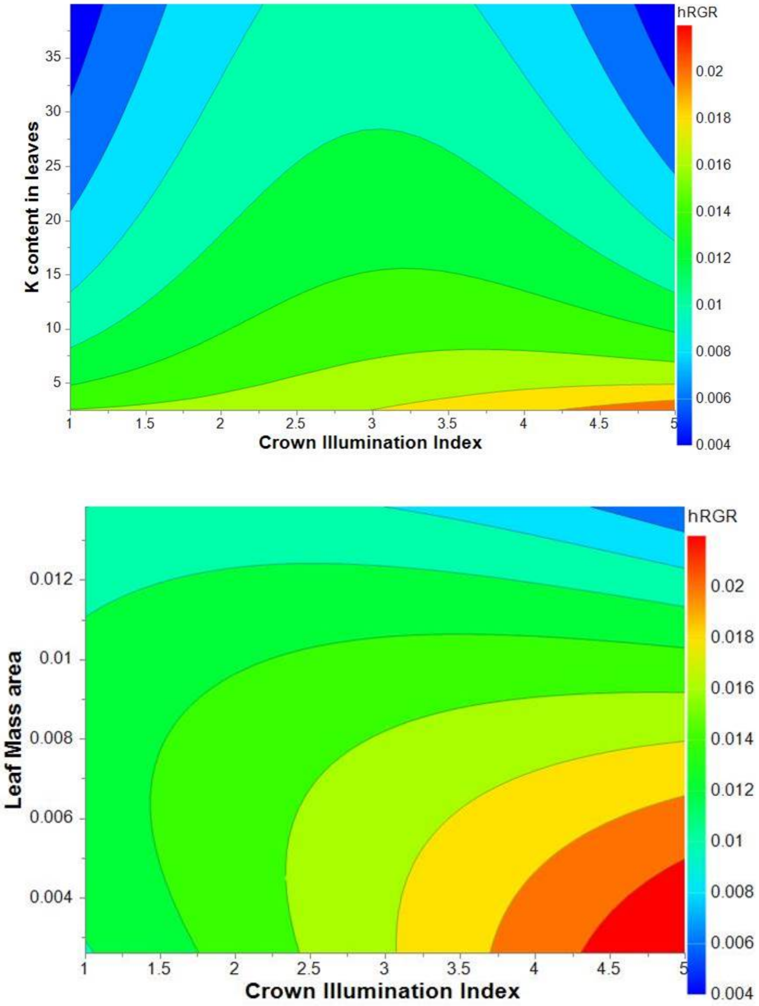

Figure 10 (a and b). Response surfaces based on a PLS regression model illustrating young trees relative height growth rate (hRGR, m/month) among 34 tree species at different levels of forest light under rainforest canopy predicted by traits in a common garden experiment in Sabah, Borneo. (a) Total foliar K concentration (K, mg/g), (b) Leaf mass area (LMA, g/m^2). The Y-axes represents a continuum of life-history traits, with pioneer properties (e.g. low K and LMA) at low levels and properties of shade tolerant species (i.e. high K and LMA) at the high levels. The forest light (X-axis) is qualitatively estimated using the crown illumination index, where level 1 indicates complete shade and level 5 indicates total canopy openness. The colour scheme indicates increasing hRGR from blue to red colour. For full methodology see Paper I.

3.4 Disturbance effects on tree species coexistence

The forest light environment is closely linked to the forest disturbance regime, may it be of natural cause or induced by human activities. Trees exhibit different adaptations to disturbance based on a natural succession dynamic that can be illustrated with the pioneer–climax gradient in species resource investment strategies (Rozendaal *et al.*, 2006; Wright *et al.*, 2003, as well as Paper I and III). Patterns of tree species in-growth after selective logging could be illustrated by relating tree wood densities to number of harvested trees (Paper III); where for instance, species with pioneer properties might have been favoured by the increased light and soil exposure after harvest (Figure 11). Disturbance is therefore an important factor for tree growth and survival, and thus a driver of tree species community composition (Kunstler *et al.*, 2015; McConkey *et al.*, 2012). Interspecific variations in demographic rates are primarily observed in tree's early life stages, and growth variations among young trees are often linked to theories on coexistence, such as gap dynamics and niche partitioning (Ghazoul & Sheil, 2010). These coexistence theories are supported by the results in Paper II, showing differences in optimal growth among young trees that can be related to the forest light conditions after disturbance. Frequent and intense disturbance events such as forest fires or overharvesting of forest resources will likely change tree species composition and generate homogeneous low-diversity forests (Lamb *et al.*, 2005; Woods, 1989). Conversely, low disturbance intensities can support spatial heterogeneity and higher life-history traits diversity, and thus a larger tree species pool (Paper III). The polynomial diversity–disturbance relationship in Paper III indicates that low harvest intensities of 2-8 trees ha^{-1} increased species richness of trees growing into the tree strata by giving disturbance favoured species a chance to establish in newly formed gaps in the forest vegetation. The study provides a mechanistic understanding of individual tree species disturbance responses under different competitive conditions. However, Paper III provides a comparatively strong evidence since it is based on a replicated, long-term and controlled experiment. In this respect, it seems like moderate selective logging does not involve substantial damage to biodiversity.

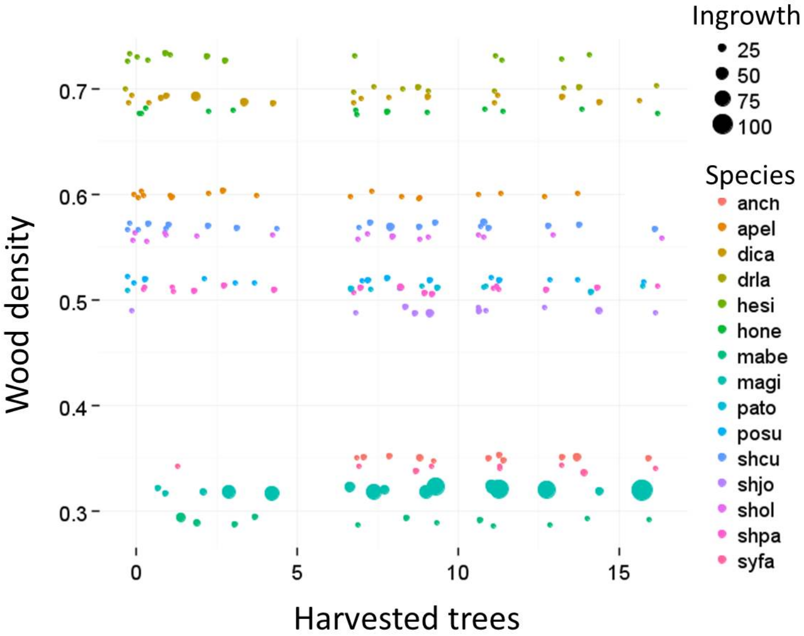

Figure 11. Patterns of in-growth for 15 tree species, in relation to wood density (g cm^{-3}) and disturbance (number of harvested trees per hectare). Tree species are marked in different colours and the in-growth over 10 years (number of stems per hectare; diameter at breast height ≥ 10 cm) is illustrated with different sized dots (a larger dot indicates greater in-growth). See Paper III for full methodology and a key to the species abbreviations.

3.5 Trait-based management applications

The diversity of trees' life-history traits influence tree species communities response to disturbances and other factors changing the environment (Thomas *et al.*, 2014), subsequently these traits facilitate rainforest resilience and evolutionary potential. Restoration for biodiversity can therefore be improved by reliable predictions of e.g. tree species life-history traits and growth response potentials (Paper I) and optimal light for growth (Paper II). By planting a mix of tree species with different life history adaptations it may be possible to regenerate a rich climax tree species community, where certain tree species are foundation species supporting the diversity of other life forms (Paper IV). With current increasing interest in management for biodiversity and other ecosystem services it will be necessary to restore a rich and diverse tree species pool. Consequently, traditional knowledge from conventional management operations using a very limited number of tree species for regeneration and timber production are no longer sufficient to accommodate this broad spectrum of life history adaptations and interactions with other species groups. Mace et al. (2012) highlight the importance of including functional trait diversity in largescale research on biodiversity and ecosystem services. Hence, to ensure positive outcomes of restoration for biodiversity we need to enhance tree diversity, but also secure high trait diversity. The generalizing predictive power of multivariate trait-based analyses can be used to enhance planted tree survival and fitness in forest restorations, as showed in Paper I and II. For instance, for tree species whose traits indicate lower than general survival rates managers can compensate by planting more individuals of that species to reach a certain target. Also, the use of native species in management operations like enrichment plantings enable a possible enhancement in e.g. genetic diversity, inter- and intraspecific interactions, as well as interactions with their environment (Thomas *et al.*, 2014).

Life-history traits were proven useful in predicting e.g. tree growth rates and responses to site conditions (Paper I and II). Hence, I showed that cost effective tools based on easily observed traits can facilitate species-site matchings and thus species selection for forest restoration. For instance, the strong relationship between initial growth rates of trees and their response to increased light and other traits in Paper I propose a possibility to make a fast screening of species with unknown characteristics, which can be of great value in practical forest management. This is of particular importance at present when knowledge is lacking on most rain forest tree species. Potentially traits or combinations of traits can be used in forest management to optimize between production focused values, e.g. timber, and ecosystem services. It was also possible to predict effects of harvest operations impacts on tree diversity and species composition (Paper III). Life-history traits provide increased insight into the understanding of forest drivers and processes, based on that we can make targeted management operations that imitate forest dynamics and give long lasting support to biodiversity.

3.6 Tree species and other life forms

In order to evaluate the success of restoration for biodiversity the entire system needs to be taken into consideration – including species variation among taxonomic groups, but also genetic variation and the diversity of natural communities and habitats; therefore I looked beyond the tree diversity by including other species groups. In an attempt to assess whether the efforts of including a large tree species pool in the restoration will enhance the diversity of other life forms I conducted an inventory of foliar lichens, where a total of 102 lichen taxa from 17 families were identified across 18 tree species in our common garden (Paper IV). I found significant differences of lichen taxa diversity and abundance among host tree species with tree species average values of 0.6–14.6 lichens per tree species, and 0 to 29 lichens were found per individual tree. About 25 percent (24 taxa) of the lichens preferred certain tree species hosts, and 11 of these taxa were host-specific to one unique tree species. Trait-based analyses indicated some evidence that life-history traits can predict lichen community structure and lichen richness, i.e. lichen community composition was correlated to foliar potassium concentration, and that lichen richness was predicted by lichen abundance. In addition to the common garden a wildland survey was conducted at a nearby site with high tree species biodiversity (within the Sow-a-seed project area), to examine the lichen community of a less degraded site with fewer pioneer trees and several adult individuals of late successional tree species. It showed that the same tree species that promoted high lichen richness in the common garden also did so in the wildland area. Three tree species (*Shorea fallax*, *Canarium* sp., and *Pentance adenophora*) with the highest number of indicator species (from 7 to 11 species) hosted 76 percent of all lichen taxa. Furthermore, I also performed a small study on the diversity of canopy arthropods, examining 5 of the tree species included in the lichen inventory. The results showed that the arthropod richness was significantly though negatively correlated to lichen taxa richness. My studies indicated that different tree species were needed to support both lichen and arthropod richness, and that a significant part of the lichen taxa were host-specific. Based on these results I concluded that in forest management for biodiversity it can be of value to include a large diversity of tree species.

Enrichment plantings can promote a relatively rapid recovery of the tree community in degraded rainforest (Yeong *et al.*, 2016), and increased tree diversity may support the recovery of other life forms. A study from Sabah on the bird community within rainforest regenerating after selective logging showed that avian species richness and diversity were significantly lower in naturally regenerating forest, compared to restored forest where values were similar to unlogged forest (Edwards *et al.*, 2009). Identifying tree species with a strong association to one or (preferably if possible) several other taxa to include in enrichment plantings could likely enhance the outcome of the restoration efforts for biodiversity. This kind of foundation species approach has not been previously tested during restoration or in tropical forests of Southeast Asia. The lichen inventory in Paper IV showed that the three tree species with the highest lichen richness supported nearly 75 percent of all identified lichen taxa; hence, I suggest that a foundation species approach may be a useful for selecting trees that promote high biodiversity.

3.7 Conclusions

The research presented in this thesis was based on the various aspects of restoration ecology in secondary forest, even though the research questions had elements of a more general ecological nature. This resulted in studies where the general ecological findings could be presented with recommendations for management.

Based on the results presented in this thesis I here address my four research questions (Objectives, section 1.7):

I In the common garden, I predicted young tree species responses to increased light with the help of species traits, and related these responses to a possible pioneer-climax continuum of life history characteristics. I found significant tree species responses in height growth to the increased light. In accordance to my hypotheses the results showed that resource investment related traits, such as wood density, specific leaf area and foliar nutrient concentration, were major factors in predicting species average growth responses. This was especially the case for the least limited trees of each species, representing the tree species potential in growth response. I found systematic patterns that earlier have been recorded for a small number of species in green house studies or among naturally regenerated seedlings also were applicable under conditions with a diverse range of predominantly late successional 'climax' species relevant for practical restoration plantings. In Paper I, II and III, I have presented indications that these differences are due to variations in tree species traits, and thus how a trait-based approach can be used to understand and predict species responses.

II Secondly, also in the common garden, I studied growth of young trees under different levels of canopy cover to explore if an increase in light under a dense canopy boost growth for all species, or if there are species specific light optima for growth. The results showed that young trees of different species have varied growth performances under different levels of light, and that life history traits can be used to model these variations among species. It was possible to identify different species light optima for growth with traits, e.g. that species with pioneer properties had optima at higher light levels than species with climax properties. With these findings we can make more successful species-site matchings in future management operations in tropical rainforests.

III Moderate selective logging does not involve substantial impact on life history trait diversity or tree species richness. Both tree in-growth and tree species richness increased after the selectively logging. Number of regenerated trees increased from about 6 trees ha^{-1} $year^{-1}$ in uncut forests to about 25 trees ha^{-1} $year^{-1}$ in forest that had been harvested (averaged across harvest intensity). The findings indicated that in order to promote high tree species richness harvest intensities should not exceed 8 trees ha^{-1}; since species richness was highest at an intermediate level of extraction, after which it started to decline. The trait-based approach also showed that the broadest range of traits was achieved at intermediate levels of disturbance and that a species in-growth could be predicted by its traits.

IV A substantial part of the lichen taxa (about 25 percent) had high affinity for specific tree hosts, which highlights a potential positive effect of including a large variety of tree species in enrichment plantings for biodiversity. Furthermore, the foundation species approach indicated that a few tree species tend to drive the diversity of other life forms. Lichen diversity varied by tree species host with an average richness of 0.6–14.6 across tree species, and 27 of 102 lichen taxa showed high affinity for specific tree hosts. Hence, the study indicated that a foundation species approach can be useful for selecting trees that promote high biodiversity. For instance, the three tree species with the highest lichen richness supported nearly 75 percent of all lichen taxa. Associated trait-based multivariate analyses indicated low explained variance, although tree species with a low compared to high number of indicator species had 20 and 23 percent more foliar N and P concentration, respectively. Also, lichen taxa richness was negatively correlated to arthropod richness, thus supporting the idea that planting more tree species promotes diversity of other life forms.

3.8 Future research recommendations

The biodiversity of regenerating forests can potentially be enhanced with suitable post-disturbance management. Restoration has in recent years gained recognition as an important management option for today's large areas of degraded secondary rainforest. Though, current knowledge of tree traits diversity and adaptations expressed in resource use strategies is limited to very few taxa, while studies often are confounded by methodological shortcomings such as insufficient replication or edge effects (Barlow *et al.*, 2007). This thesis presented trait-based methods that can be used to better match available tree species in a forest restoration operation to suitable planting sites. Systematic patterns among tree species (Paper I and II) indicated that it is possible to use a trait-based model to make predictions also for trees with unknown resource requirements – using only a small number of easily acquired traits, e.g. leaf mass area, foliar potassium content and wood density. Also the trait "early height growth" showed a strong degree of explanation in Paper I, and may be used to quickly (within a few months in the nursery or in a "common garden") obtain valuable information for species with "unknown" properties. By increasing both survival and growth for these planted or naturally regenerated young trees that need to compete for light in the forest understory it might be possible to enhance the success rate of future forest restorations. For instance, for the maintenance of species with high ecologic or economic value (such as a foundation species) but low survival rate, it may be useful to increase the number of planted individuals and thus enhance the total number of surviving individuals. In the future – to further add to this knowledgebase – it would be useful to also study interactions with more species and combinations of species, as well as the within-species variation due to traits plasticity.

Scaling out to the tree community level, and to better understand forest structure and dynamics it was important to include environmental factors in the models. Available light may often be the most limiting factor for tree growth in tropical rainforest, but there are also other environmental factors that can have large impact on the young trees. For instance, different habitat associations of trees to specific soil types can influence species coexistence mechanisms (Born *et al.*, 2014). I suggest that one succeeding step could be continued studies in the common garden experiment to examine the edaphic properties of the site and make similar experiments in other sites with contrasting conditions. Also Paper III would benefit from including soil properties in the analyses. Logging operations are known to cause soil degradation (Chazdon, 2008), thus the explained variance of the trait-based analyses in Paper III might be improved by adding interactions between disturbance and soil properties. Multivariate models can increase our understanding of lowland dipterocarp forest dynamics, and further improvements of life-history traits modelling can be accomplished with new field experiments where environmental factors are systematically controlled.

In Paper IV, the study was manly focused on different aspects of foliar lichen diversity – to my knowledge this is the first detailed diversity study on foliar lichens in Southeast Asia, but there occur some studies from Australia and Latin America (e.g. Anthony *et al.*, 2002; Lücking & Matzer, 2001). My study was conducted only six years after the inventoried trees were planted, and over 30 years after the selective logging and forest fires took place. Hence, this study was a ‘snapshot’ of the development in forest structure after enrichment planting in degraded secondary forest. It could be of great value for future forest management for biodiversity to follow up on these results with more extensive studies on the occurrence and influence of foundation species in tropical rainforest. In a recent study on rainforest restorations' influence on dung beetle species diversity along a restoration chronosequence, it is showed that both species richness and community composition are improved in the latter stages of restoration (Derhé *et al.*, 2016). I suggest that future studies in the Sow-a-Seed project will apply a similar approach, where we follow the development in species diversity and community composition (e.g. foliar lichens) over a longer time period to gain further understanding of species interactions and forest structure development after restoration. There are numerous other aspects related to the foliar lichens that would be of interest to study; for example possible impact that the lichens have on the trees e.g. facilitative properties, protection against herbivores, nitrogen fixating properties, or influence on the photosynthesis of the host tree, as well as further studies on the relationships between foliar lichens and different tree life-history traits.

Restoration is at present an accepted and common management practice in secondary rainforest, but in a long-term perspective we need to further quantify and understand the biodiversity of these amazing ecosystems in order to keep them healthy, productive and resilient. For instance, tropical deforestation is a substantial contributor to climate change, whereas rainforest restoration is recognised to be a potentially powerful management option for climate change mitigation (Imai *et al.*, 2014; Kettle, 2012). Building on that, knowledge derived from trait-based modelling and life-history traits can be useful for climate change mitigating forest management. For example in Paper I, there was a general correlation between tree traits (e.g. wood density) and the growth response, but there was also variation between species. These intraspecific variations could potentially be used to find tree species that are particularly good at binding carbon.

Late successional rainforest trees have long regeneration cycles that require a lot of time for a planted seedling to become a productive seed tree. The future of a rainforest relies on wise management and policy decisions extending over long time periods. Kettle et al. (2011) highlights the inadequacy of existing policy instruments, financial mechanisms, and forestry infrastructure to sufficiently manage future forest restorations, for example concerning the management of the large seed resources that come from synchronized – but unpredictable – mass fruiting events of forest trees in Borneo. But all is not lost; a new global study shows the positive impacts of protected areas for local biodiversity (Gray *et al.*, 2016). This is favourable for the Sow-a-Seed project area (a land area owned by the state of Sabah) that in was 2014 placed under the highest form of protection, i.e. Protection Class 1, including full protection of the trees that have been planted in the project.

All in all, areas of restored tropical rainforest will most likely increase globally over the coming decades, and thus it will require adaptive forest management to mitigate future biodiversity losses and for these dynamic systems to withstand the stresses of climate change and other anthropogenic effects. My research contributes to generalizations that can facilitate the restoration of rainforest biodiversity.

References

Ackerly, D.D. (2003). Community Assembly, Niche Conservatism, and Adaptive Evolution in Changing Environments. pp. pp. S165-S184.

Ådjers, G., Hadengganan, S., Kuusipalo, J., Nuryanto, K. & Vesa, L. (1995). Enrichment planting of dipterocarps in logged-over secondary forests: effect of width, direction and maintenance method of planting line on selected Shorea species. *Forest Ecology and Management,* 73(1-3), pp. 259-270.

Alloysius, D., Falck, J., Wai, Y. & Karlsson, A. An attempt to rehabilitate a degraded tropical rainforest in Borneo: the biological results and the social benefits of the IKEA investment, an analysis after ten years. In: *Proceedings of XXIII IUFRO World Congress*2010.

Anthony, P.A., Holtum, J.A.M. & Jackes, B.R. (2002). Shade acclimation of rainforest leaves to colonization by lichens. *Functional Ecology,* 16(6), pp. 808-816.

Asanok, L., Marod, D., Duengkae, P., Pranmongkol, U., Kurokawa, H., Aiba, M., Katabuchi, M. & Nakashizuka, T. (2013). Relationships between functional traits and the ability of forest tree species to reestablish in secondary forest and enrichment plantations in the uplands of northern Thailand. *Forest Ecology and Management,* 296, pp. 9-23.

Ashton, P. & Kettle, C.J. (2012). Dipterocarp Biology as a Window to the Understanding of Tropical Forest Structure: Where are we Looking Now? *Biotropica,* 44(5), pp. 575-576.

Ashton, P.S. (1988). Dipterocarp Biology as a Window to the Understanding of Tropical Forest Structure.

Baker, T.R., Swaine, M.D. & Burslem, D.F.R.P. (2003). Variation in tropical forest growth rates: combined effects of functional group composition and resource availability. *Perspectives in Plant Ecology, Evolution and Systematics,* 6(1-2), pp. 21-36.

Baltzer, J.L. & Thomas, S.C. (2007). Determinants of whole-plant light requirements in Bornean rain forest tree saplings. *Journal of Ecology,* 95(6), pp. 1208-1221.

Baltzer, J.L. & Thomas, S.C. (2010). A Second Dimension to the Leaf Economics Spectrum Predicts Edaphic Habitat Association in a Tropical Forest. *PLoS ONE,* 5(10), pp. e13163-e13163.

Barlow, J., Gardner, T.A., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C. & Peres, C.A. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences,* 104(47), pp. 18555-18560.

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Nally, R.M., Thomson, J.R., Ferraz, S.F.d.B., Louzada, J., Oliveira, V.H.F., Parry, L., Ribeiro de Castro Solar, R., Vieira, I.C.G., Aragão, L.E.O.C., Begotti, R.A., Braga, R.F., Cardoso, T.M., Jr, R.C.d.O., Souza Jr, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F.Z., Veiga, R.C.S., Venturieri, A. & Gardner, T.A. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature,* 535(7610), pp. 144-147.

Bloor, J.M.G. & Grubb, P.J. (2003). Growth and mortality in high and low light: trends among 15 shade-tolerant tropical rain forest tree species. *Journal of Ecology,* 91(1), pp. 77-85.

Born, J., Bagchi, R., Burslem, D., Nilus, R., Tellenbach, C., Pluess, A.R. & Ghazoul, J. (2015). Differential Responses of Dipterocarp Seedlings to Soil Moisture and Microtopography. *Biotropica,* 47(1), pp. 49-58.

Born, J., Pluess, A.R., Burslem, D.F.R.P., Nilus, R., Maycock, C.R. & Ghazoul, J. (2014). Differing Life History Characteristics Support Coexistence of Tree Soil Generalist and Specialist Species in Tropical Rain Forests. *Biotropica,* 46(1), pp. 58-68.

Brancalion, P.H.S., Melo, F.P.L., Tabarelli, M., Rodrigues, R.R. & Ricardo, R. (2013). Biodiversity persistence in highly humanmodified tropical landscapes depends on ecological restoration. *Tropical Conservation Science,* 6(6), pp. 705-710.

Brown, N.D. & Whitmore, T.C. (1992). Do Dipterocarp Seedlings Really Partition Tropical Rain Forest Gaps? *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences,* 335(1275), pp. 369-378.

Brown, S. & Lugo, A.E. (1990). Tropical Secondary Forests. *Journal of Tropical Ecology,* 6(1), pp. 1-32.

Brown, S. & Lugo, A.E. (1994). Rehabilitation of Tropical Lands: A Key to Sustaining Development. *Restoration Ecology,* 2(2), pp. 97-111.

Bu, W., Zang, R. & Ding, Y. (2014). Field observed relationships between biodiversity and ecosystem functioning during secondary succession in a tropical lowland rainforest. *Acta Oecologica,* 55, pp. 1-7.

Chazdon, R.L. (2008). Beyond Deforestation: Restoring Forests and Ecosystem Services on Degraded Lands. *Science,* 320(5882), pp. 1458-1460.

Chazdon, R.L. (2014). *Second growth: the promise of tropical forest regeneration in an age of deforestation*: University of Chicago Press.

Chazdon, R.L. & Fetcher, N. (1984). Photosynthetic Light Environments in a Lowland Tropical Rain Forest in Costa Rica. pp. 553-564.

Clark, D.A. & Clark, D.B. (1992). Life History Diversity of Canopy and Emergent Trees in a Neotropical Rain Forest. *Ecological Monographs,* 62(3), pp. 315-344.

Davies, S.J. & Ashton, P.S. (1999). Phenology and fecundity in 11 sympatric pioneer species of Macaranga (Euphorbiaceae)in Borneo. *Am. J. Botany,* 86(12), pp. 1786-1795.

Derhé, M.A., Murphy, H., Monteith, G. & Menéndez, R. (2016). Measuring the success of reforestation for restoring biodiversity and ecosystem functioning. *Journal of Applied Ecology*.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D. & Gorné, L.D. (2015). The global spectrum of plant form and function. *Nature,* 529(7585), pp. 167-171.

Dray, S. & Legendre, P. (2008). Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology,* 89(12), pp. 3400-3412.

Edwards, D.P., Ansell, F.A., Ahmad, A.H., Nilus, R. & Hamer, K.C. (2009). The Value of Rehabilitating Logged Rainforest for Birds El Valor de la Rehabilitación de un Bosque Tropical Lluvioso para Aves. *Conservation Biology,* 23(6), pp. 1628-1633.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B. & Webster, J.R. (2005). Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment,* 3(9), pp. 479-486.

Eriksson, L., Byrne, T., Johansson, E., Trygg, J. & Vikström, C. (2013). *Multi-And Megavariate Data Analysis : Basic Principles And Applications*. Third revi. ed: MKS Umetrics AB.

Fao (2015). *Global Forest Resource Assessment*. Rome.

Faridah Hanum, I. & Van Der Maesen, L. (1997). *Plant resources of South-East Asia No. 11. Auxiliary plants*: Backhuys Publishers.

Gaveau, D.L.A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N.K., Ancrenaz, M., Nasi, R., Quinones, M., Wielaard, N. & Meijaard, E. (2014). Four decades of forest persistence, clearance and logging on Borneo. *PLoS ONE,* 9(7), pp. e101654-e101654.

Ghazoul, J. & Sheil, D. (2010). *Tropical rain forest ecology, diversity, and conservation*. Oxford: Oxford University Press.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.a., Laurance, W.F., Lovejoy, T.E. & Sodhi, N.S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature,* 478(7369), pp. 378-381.

Goldammer, J.G. (2006). History of equatorial vegetation fires and fire research in Southeast Asia before the 1997–98 episode: A reconstruction of creeping environmental changes. *Mitigation and Adaptation Strategies for Global Change,* 12(1), pp. 13-32.

Gray, C.L., Hill, S.L.L., Newbold, T., Hudson, L.N., Borger, L., Contu, S., Hoskins, A.J., Ferrier, S., Purvis, A. & Scharlemann, J.P.W. (2016). Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nat Commun,* 7.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.a., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, a., Egorov, A., Chini, L., Justice, C.O. & Townshend, J.R.G. (2013). High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science,* 342(6160), pp. 850-853.

Hector, A., Philipson, C., Saner, P., Chamagne, J., Dzulkifli, D., O'Brien, M., Snaddon, J.L., Ulok, P., Weilenmann, M., Reynolds, G. & Godfray, H.C.J. (2011). The Sabah Biodiversity Experiment: a long-term test of the role of tree diversity in restoring tropical forest structure and functioning. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 366(1582), pp. 3303-3315.

Holste, E.K., Kobe, R.K. & Vriesendorp, C.F. (2011). Seedling growth responses to soil resources in the understory of a wet tropical forest. *Ecology,* 92(9), pp. 1828-1838.

Iida, Y., Poorter, L., Sterck, F., Kassim, A.R., Potts, M.D., Kubo, T. & Kohyama, T.S. (2014). Linking size-dependent growth and mortality with architectural traits across 145 co-occurring tropical tree species. *Ecology,* 95(2), pp. 353-363.

Imai, N., Tanaka, A., Samejima, H., Sugau, J.B., Pereira, J.T., Titin, J., Kurniawan, Y. & Kitayama, K. (2014). Tree community composition as an indicator in biodiversity monitoring of REDD+. *Forest Ecology and Management,* 313(0), pp. 169-179.

Jennings, S.B., Brown, N.D. & Sheil, D. (1999). Assessing forest canopies and understory illumination: canopy closure, canopy cover and other measures. *Forestry,* 72(1), pp. 59-73.

Kammesheidt, L. (2002). Perspectives on secondary forest management in tropical humid lowland America. *AMBIO: A Journal of the Human Environment,* 31(3), pp. 243-250.

Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A. & Lindquist, E. (2015). Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. *Forest Ecology and Management,* 352, pp. 9-20.

Kettle, C. (2010). Ecological considerations for using dipterocarps for restoration of lowland rainforest in Southeast Asia. *Biodiversity and Conservation,* 19(4), pp. 1137-1151.

Kettle, C.J. (2012). Seeding ecological restoration of tropical forests: Priority setting under REDD+. *Biological Conservation,* 154, pp. 34-41.

Kettle, C.J., Ghazoul, J., Ashton, P., Cannon, C.H., Chong, L., Diway, B., Faridah, E., Harrison, R., Hector, A., Hollingsworth, P., Koh, L.P., Khoo, E., Kitayama, K., Kartawinata, K., Marshall, A.J., Maycock, C., Nanami, S., Paoli, G., Potts, M.D., Samsoedin, I., Sheil, D., Tan, S., Tomoaki, I., Webb, C., Yamakura, T. & Burslem, D.F.R.P.R.P. (2011). Seeing the fruit for the trees in Borneo. *Conservation Letters,* 4(3), pp. 184-191.

Kettle, C.J., Maycock, C.R. & Burslem, D. (2012). New Directions in Dipterocarp Biology and Conservation: A Synthesis. *Biotropica,* 44(5), pp. 658-660.

King, D.a. & Clark, D.B. (2004). Inferring Growth Rates from Leaf Display in Tropical Forest Saplings. *Journal of Tropical Ecology,* 20(3), pp. 351-354.

King, D.A., Davies, S.J. & Noor, N.S.M. (2006). Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. *Forest Ecology and Management,* 223(1-3), pp. 152-158.

King, D.A., Davies, S.J., Supardi, M.N.N. & Tan, S. (2005). Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Functional Ecology,* 19(3), pp. 445-453.

Kitajima, K., Mulkey, S.S. & Wright, S.J. (2005). Variation in Crown Light Utilization Characteristics among Tropical Canopy Trees. *Annals of Botany,* 95(3), pp. 535-547.

Kobayashi, S. (2004). Landscape rehabilitation of degraded tropical forest ecosystems: Case study of the CIFOR/Japan project in Indonesia and Peru. *Forest Ecology and Management,* 201(1), pp. 13-22.

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H.C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., Onoda, Y., Peñuelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, I.F., Ståhl, G., Swenson, N.G., Thompson, J., Westerlund, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E. & Westoby, M. (2015). Plant functional traits have globally consistent effects on competition. *Nature,* 529(7585), pp. 204-207.

Lamb, D., Erskine, P.D. & Parrotta, J.A. (2005). Restoration of Degraded Tropical Forest Landscapes. *Science,* 310(5754), pp. 1628-1632.

Lambers, H. & Poorter, H. (1992). Inherent Variation in Growth Rate Between Higher Plants: A Search for Physiological Causes and Ecological Consequences. In:23), pp. 187-261. Available from: http://www.sciencedirect.com/science/article/pii/S0065250408601488.

Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bongers, F. & Poorter, L. (2010). Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology,* 91(2), pp. 386-398.

Legendre, P. & Legendre, L.F.J. (2012). *Numerical Ecology*: Elsevier. Available from: https://books.google.com/books?hl=en&lr=&id=6ZBOA-iDviQC&pgis=1.

Lücking, R. & Matzer, M. (2001). High foliicolous lichen alpha-diversity on individual leaves in Costa Rica and Amazonian Ecuador. *Biodiversity & Conservation,* 10(12), pp. 2139-2152.

Mace, G.M., Norris, K., Fitter, A.H., Mace, K., Fitter, A.H.G.M. & Norris (2012). Biodiversity and ecosystem services: a multilayered relationship. *Trends in Ecology & Evolution,* 27(1), pp. 19-26.

MacKinnon, K., Hatta, G., Halim, H. & Mangalik, A. (1996). *The ecology of Kalimantan: Vol. III*: Periplus Editions (HK) Ltd. Available from: http://library.wur.nl/WebQuery/clc/966166.

Maycock, C.R., Kettle, C.J., Khoo, E., Pereira, J.T., Sugau, J.B., Nilus, R., Ong, R.C., Amaludin, N.A., Newman, M.F. & Burslem, D.F.R.P. (2012). A Revised Conservation Assessment of Dipterocarps in Sabah. *Biotropica*, pp. n/a-n/a.

McConkey, K.R., Prasad, S., Corlett, R.T., Campos-Arceiz, A., Brodie, J.F., Rogers, H. & Santamaria, L. (2012). Seed dispersal in changing landscapes. *Biological Conservation,* 146(1), pp. 1-13.

Mengel, K. & Kirkby, E.A. (1987). *Principles of plant nutrition*: International Potash Institute.

Molino, J.F. & Sabatier, D. (2001). Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science (New York, N.Y.),* 294(5547), pp. 1702-4.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution,* 28(3), pp. 167-177.

Paine, C.E.T., Amissah, L., Auge, H., Baraloto, C., Baruffol, M., Bourland, N., Bruelheide, H., Daïnou, K., de Gouvenain, R.C., Doucet, J.-L., Doust, S., Fine, P.V.A., Fortunel, C., Haase, J., Holl, K.D., Jactel, H., Li, X., Kitajima, K., Koricheva, J., Martínez-Garza, C., Messier, C., Paquette, A., Philipson, C., Piotto, D., Poorter, L., Posada, J.M., Potvin, C., Rainio, K., Russo, S.E., Ruiz-Jaen, M., Scherer-Lorenzen, M., Webb, C.O., Wright, S.J., Zahawi, R.A. & Hector, A. (2015). Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. *Journal of Ecology,* 103(4), pp. 978-989.

Paine, C.E.T., Stenflo, M., Philipson, C.D., Saner, P., Bagchi, R., Ong, R.C. & Hector, A. (2012). Differential growth responses in seedlings of ten species of Dipterocarpaceae to experimental shading and defoliation. *Journal of Tropical Ecology,* 28(04), pp. 377-384.

Philipson, C.D., Dent, D.H., O'Brien, M.J., Chamagne, J., Dzulkifli, D., Nilus, R., Philips, S., Reynolds, G., Saner, P. & Hector, A. (2014). A trait-based trade-off between growth and mortality: evidence from 15 tropical tree species using size-specific relative growth rates. *Ecology and Evolution,* 4(18), pp. 3675-88.

Philipson, C.D., Saner, P., Marthews, T.R., Nilus, R., Reynolds, G., Turnbull, L.A., Hector, A. & Rgrs, S.-s. (2011). Light-based Regeneration Niches: Evidence from 21 Dipterocarp Species using Size-specific RGRs. *Biotropica,* 0(0), pp. n/a-n/a.

Poorter, L. (1999). Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology,* 13(3), pp. 396-410.

Poorter, L. & Bongers, F. (2006). Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology,* 87(7), pp. 1733-1743.

Poorter, L., Bongers, F., Sterck, F.J. & Wöll, H. (2003). Architecture of 53 rain forest tree species differing in adult stature and shade tolerance. *Ecology,* 84(3), pp. 602-608.

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G., Harms, K.E., Licona, J.C., Martínez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Peña-Claros, M., Webb, C.O., Wright, I.J. & Peña-Claros, M. (2008). Are functional traits good predictors of demographic rates? Evidense from five neotropical forests. *Ecology,* 89(7), pp. 1908-1920.

Richards, P.W. (1952). The tropical rain forest: an ecological study. *The tropical rain forest: an ecological study.*

Romell, E., Hallsby, G. & Karlsson, A. (2009). Forest floor light conditions in a secondary tropical rain forest after artificial gap creation in northern Borneo. *Agricultural and Forest Meteorology,* 149(6-7), pp. 929-937.

Rozendaal, D.M.A., Hurtado, V.H. & Poorter, L. (2006). Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology,* 20(2), pp. 207-216.

Sack, L. & Grubb, P.J. (2001). Why do species of woody seedlings change rank in relative growth rate between low and high irradiance? *Functional Ecology,* 15(2), pp. 145-154.

Salguero-Gómez, R., Jones, O.R., Jongejans, E., Blomberg, S.P., Hodgson, D.J., Mbeau-Ache, C., Zuidema, P.A., de Kroon, H. & Buckley, Y.M. (2016). Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences of the United States of America,* 113(1), pp. 230-5.

Slik, J.W.F., Arroyo-Rodríguez, V., Aiba, S.-I., Alvarez-Loayza, P., Alves, L.F., Ashton, P., Balvanera, P., Bastian, M.L., Bellingham, P.J., van den Berg, E., Bernacci, L., da Conceição Bispo, P., Blanc, L., Böhning-Gaese, K., Boeckx, P., Bongers, F., Boyle, B., Bradford, M., Brearley, F.Q., Breuer-Ndoundou Hockemba, M., Bunyavejchewin, S., Calderado Leal Matos, D., Castillo-Santiago, M., Catharino, E.L.M., Chai, S.-L., Chen, Y., Colwell, R.K., Robin, C.L., Clark, C., Clark, D.B., Clark, D.A., Culmsee, H., Damas, K., Dattaraja, H.S., Dauby, G., Davidar, P., DeWalt, S.J., Doucet, J.-L., Duque, A., Durigan, G., Eichhorn, K.A.O., Eisenlohr, P.V., Eler, E., Ewango, C., Farwig, N., Feeley, K.J., Ferreira, L., Field, R., de Oliveira Filho, A.T., Fletcher, C., Forshed, O., Franco, G., Fredriksson, G., Gillespie, T., Gillet, J.-F., Amarnath, G., Griffith, D.M., Grogan, J., Gunatilleke, N., Harris, D., Harrison, R., Hector, A., Homeier, J., Imai, N., Itoh, A., Jansen, P.A., Joly, C.A., de Jong, B.H.J., Kartawinata, K., Kearsley, E., Kelly, D.L., Kenfack, D., Kessler, M., Kitayama, K., Kooyman, R., Larney, E., Laumonier, Y., Laurance, S., Laurance, W.F., Lawes, M.J., Amaral, I.L.d., Letcher, S.G., Lindsell, J., Lu, X., Mansor, A., Marjokorpi, A., Martin, E.H., Meilby, H., Melo, F.P.L., Metcalfe, D.J., Medjibe, V.P., Metzger, J.P., Millet, J., Mohandass, D., Montero, J.C., de Morisson Valeriano, M., Mugerwa, B., Nagamasu, H., Nilus, R., Ochoa-Gaona, S., Page, N., Parolin, P., Parren, M., Parthasarathy, N., Paudel, E., Permana, A., Piedade, M.T.F., Pitman, N.C.A., Poorter, L., Poulsen, A.D., Poulsen, J., Powers, J., Prasad, R.C., Puyravaud, J.-P., Razafimahaimodison, J.-C., Reitsma, J., dos Santos, J.R., Roberto Spironello, W., Romero-Saltos, H., Rovero, F., Rozak, A.H., Ruokolainen, K., Rutishauser, E., Saiter, F., Saner, P., Santos, B.A., Santos, F., Sarker, S.K., Satdichanh, M., Schmitt, C.B., Schöngart, J., Schulze, M., Suganuma, M.S., Sheil, D., da Silva Pinheiro, E., Sist, P., Stevart, T., Sukumar, R., Sun, I.F., Sunderand, T., Suresh, H.S., Suzuki, E., Tabarelli, M., Tang, J., Targhetta, N., Theilade, I., Thomas, D.W., Tchouto, P., Hurtado, J., Valencia, R., van Valkenburg, J.L.C.H., Van Do, T., Vasquez, R., Verbeeck, H., Adekunle, V., Vieira, S.A., Webb, C.O., Whitfeld, T., Wich, S.A., Williams, J., Wittmann, F., Wöll, H., Yang, X., Adou Yao, C.Y., Yap, S.L., Yoneda, T., Zahawi, R.A., Zakaria, R., Zang, R., de Assis, R.L., Garcia Luize, B. & Venticinque, E.M. (2015). An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences,* 112(24), pp. 201423147-201423147.

Slik, J.W.F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J.-L., Eler, E., Ferreira, L., Forshed, O., Fredriksson, G., Gillet, J.-F., Harris, D., Leal, M., Laumonier, Y., Malhi, Y., Mansor, A., Martin, E., Miyamoto, K., Araujo-Murakami, A., Nagamasu, H., Nilus, R., Nurtjahya, E., Oliveira, Á., Onrizal, O., Parada-Gutierrez, A., Permana, A., Poorter, L., Poulsen, J., Ramirez-Angulo, H., Reitsma, J., Rovero, F., Rozak, A., Sheil, D., Silva-Espejo, J., Silveira, M., Spironelo, W., ter Steege, H., Stevart, T., Navarro-Aguilar, G.E., Sunderland, T., Suzuki, E., Tang, J., Theilade, I., van der Heijden, G., van Valkenburg, J., Van Do, T., Vilanova, E., Vos, V., Wich, S., Wöll, H., Yoneda, T., Zang, R., Zhang, M.-G. & Zweifel, N. (2013). Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography,* 22(12), pp. 1261-1271.

Sterck, F.J., Bongers, F. & Newbery, D.M. (2001). Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. *Plant Ecology,* 153(1/2), pp. 279-292.

Swaine, M.D. & Whitmore, T.C. (1988). On the definition of ecological species groups in tropical rain forests. *Plant Ecology,* 75(1), pp. 81-86.

Thomas, E., Jalonen, R., Loo, J., Boshier, D., Gallo, L., Cavers, S., Bordács, S., Smith, P. & Bozzano, M. (2014). Genetic considerations in ecosystem restoration using native tree species. *Forest Ecology and Management,* 333, pp. 66-75.

Tripler, C.E., Kaushal, S.S., Likens, G.E. & Walter, M.T. (2006). Patterns in potassium dynamics in forest ecosystems. *Ecology Letters,* 9(4), pp. 451-66.

Walker, L.R. & Wardle, D.A. (2014). Plant succession as an integrator of contrasting ecological time scales. *Trends in Ecology & Evolution,* 29(9), pp. 504-510.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002). Plant Ecological Strategies: Some Leading Dimensions of Variation between Species. *Annual Review of Ecology and Systematics,* 33(ArticleType: research-article / Full publication date: 2002 / Copyright © 2002 Annual Reviews), pp. 125-159.

Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., LeRoy, C.J., Lonsdorf, E.V., Allan, G.J., DiFazio, S.P., Potts, B.M., Fischer, D.G., Gehring, C.A., Lindroth, R.L., Marks, J.C., Hart, S.C., Wimp, G.M. & Wooley, S.C. (2006). A framework for community and ecosystem genetics: from genes to ecosystems. *Nat Rev Genet,* 7(7), pp. 510-523.

Whitmore, T.C. & Brown, N.D. (1996). Dipterocarp Seedling Growth in Rain Forest Canopy Gaps during Six and a Half Years. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 351(1344), pp. 1195-1203.

Woods, P. (1989). Effects of Logging, Drought, and Fire on Structure and Composition of Tropical Forests in Sabah, Malaysia on JSTOR.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004). The worldwide leaf economics spectrum. *Nature,* 428(6985), pp. 821-827.

Wright, I.J. & Westoby, M. (1999). Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology,* 87(1), pp. 85-97.

Wright, J. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia,* 130(1), pp. 1-14.

Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J., Díaz, S., Engelbrecht, B.M.J., Harms, K.E., Hubbell, S.P., Marks, C.O., Ruiz-Jaen, M.C., Salvador, C.M. & Zanne, A.E. (2010). Functional traits and the growth–mortality trade-off in tropical trees. *Ecology,* 91(12), pp. 3664-3674.

Wright, S.J., Muller-Landau, H.C., Condit, R. & Hubbell, S.P. (2003). Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology,* 84(12), pp. 3174-3185.

Yeong, K.L., Reynolds, G. & Hill, J.K. (2016). Enrichment planting to improve habitat quality and conservation value of tropical rainforest fragments. *Biodiversity and Conservation,* 25(5), pp. 957-973.

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