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Multi-functional trait-based species selection for regenerating tropical rainforests

ARVID LINDH

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Arvid Lindh
Faculty of Forest Sciences
Department of Forest Ecology and Management
Umeå

SLU
SWEDISH UNIVERSITY
OF AGRICULTURAL
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Cover: Danum Valley after rain.
Photo: Arvid Lindh

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Swedish University of Agricultural Sciences, Department of Forest Ecology and Management, Umeå, Sweden

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Abstract

Forests are key sources of renewable materials needed to transition into a bio-based economy free from fossil-based resources. Tropical forests are especially important due to their large land area and high growth potential. However, tropical forests are under pressure from both climate and land-use changes that reduce ecosystem function. As a response, forest restoration efforts have increased and key aspects to ensure their success include tree species selection and understanding how management alters forested landscapes. In this thesis, I discuss current framing of tropical forest categorization and present a conceptual model that emphasizes management-driven transitions of forests between states (Paper I). Furthermore, I explore how functional-trait variation in tree species native to Borneo correlates with different values and ecosystem services that restoration may need to consider to support a bio-based economy, specifically financial potential (Paper II), conservation of beetle diversity (Paper III), and leaf litter decomposition in a changing climate (Paper IV). Financial potential was found to be linked with low leaf-nutrient content, pH, and specific leaf area, and harvesting of native tree species grown using restoration methods were found to be a potentially viable management option (Paper II). Specific leaf area and leaf area were important in supporting total beetle diversity, but predators and fungivores were related to separate suites of traits (Paper III). Finally, an interactive effect between precipitation frequency (rarely reported) and volume on mass loss was identified, where reductions in either variable lowered mass loss from decomposition (Paper IV). While high nutrient content and pH, and low lignin and tannin content, were correlated with high mass loss, no change in trait-decomposition links between climate scenarios was found. This thesis concludes that while it seems possible to find tree species with disproportionately high ecosystem value, no single trait combination can provide every ecosystem service. Thus, promoting tree species with complementary trait compositions should be prioritized.

Keywords: tropical forests, restoration, functional traits, ecosystem services

Photo: Arvid Lindh

Multifunktionellt och egenskapsbaserat val av trädarter för regnskogsrestaurering i tropikerna

Sammanfattning

Skogar är viktiga källor av förnyelsebara material nödvändiga i omställningen till en biobaserad ekonomi fri från fossila resurser. Tropiska skogar är särskilt viktiga, på grund av deras stora arealer och hög tillväxt. Dock är tropiska skogar utsatta för ändringar i klimat och markanvändning som sänker deras ekosystemfunktion. För att förebygga detta har skogs-restaureringsprojekt blivit vanligare, men för att lyckas kräver de förståelse för hur skötselmetoder påverkar skogliga ekosystem, samt vilka trädarter som bör gynnas. I denna avhandling diskuterar jag den nuvarande kategoriseringen av tropiska skogar, och presenterar en konceptuell modell som understryker hur skötselåtgärder driver övergångar mellan olika tillstånd i skogliga ekosystem (Studie I). Jag undersöker vidare hur variation i funktionella egenskaper hos trädarter inhemska på Borneo är kopplade till ekosystemtjänster och värden som restaurering bör beakta, specifikt ekonomisk potential (Studie II), mångfald bland skalbaggar (Studie III), och nedbrytning av förna i förändrade klimat (Studie IV). Ekonomisk potential var kopplat till lågt näringsinnehåll och pH i löv, samt specifik bladarea. Dessutom visade resultaten att skogsskötsel med restaureringsmetoder kan vara en gångbar skötselmetod (Studie II). Specifik bladarea och bladarea var viktiga för att gynna totala artrikedomen av skalbaggar, men predatorer och svampätande skalbaggar var kopplade till andra egenskaper (Studie III). Slutligen identifierade jag en interaktionseffekt mellan nederbördsfrekvens (sällan rapporterad) och volym för nedbrytning, där en reducering av endera variabel ledde till minskad nedbrytning (Studie IV). Högt näringsinnehåll och pH, samt låga halter lignin och tanniner, var kopplade till hög nedbrytning och klimatbehandlingar påverkade inte denna koppling mellan egenskaper och nedbrytning. Avhandlingen visar att även om det finns trädarter som tillför oproportionerligt höga ekosystemtjänster så finns inga enskilda uppsättningar av egenskaper som tillgodoser alla tjänster. Man behöver därför gynna arter med kompletterande egenskaper.

Nyckelord: tropiska skogar, restaurering, funktionella egenskaper, ekosystemtjänster

Dedication


Photo: U. Ilstedt

"When do people truly die?
When they are shot through the heart? No.
When they are ravaged by an incurable disease? No.
When they consume a deadly mushroom? No.
It's when they are forgotten."

- Eiichiro Oda

In memory of Niles J. Hasselquist (1978-2021)

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. Pain, A.*, Marquardt, K., Lindh, A., Hasselquist, N. J. (2020). What Is Secondary about Secondary Tropical Forest? Rethinking Forest Landscapes. Human Ecology, 49, 239-247. https://doi.org/10.1007/s10745-020-00203-y

II. Lindh, A.*, Sundqvist, M. K., Axelsson, E. P., Hasselquist, N. J., Aguilar, F. X., Alloysius, D., Ilstedt, U. (2024). Functional traits to predict financial value of enrichment planting in degraded tropical forests. New Forests. https://doi.org/10.1007/s11056-024-10030-4

III. Lindh, A.*, Grady, K. C., Abin, J. V., Lardizabal, M. L. T., Ilstedt, U., Sundqvist, M. K., Axelsson, E. P. Physical leaf traits predict foundation status of tropical tree species but enhancing functional diversity of associated communities in restoration still require tree species with complementary trait compositions (manuscript)

IV. Lindh, A.*, Ilstedt, U., Axelsson, E. P., Hasselquist, N. J., Sundqvist, M. K. The role of leaf and litter traits of tropical trees during decomposition under different climate change scenarios (manuscript)

Papers I and II are reproduced with the permission of the publisher and published open access.

* Corresponding author

The contribution of Arvid Lindh to the papers included in this thesis was as follows:

I. AL participated in the writing of the manuscript, which was led by AP.

II. AL is the main author. AL developed the research idea together with UI, NH, MS, and PA. AL conducted trait sampling. AL compiled data and did statistical analyses. AL wrote manuscript in collaboration with the co-authors.

III. AL is the main author. AL developed the research idea together with PA. AL conducted trait sampling. AL compiled data and did statistical analyses. AL wrote manuscript in collaboration with the co-authors.

IV. AL is the main author. AL developed the research idea and experiment design together with MS, UI, NH, and PA. AL conducted trait sampling and led litter collection. AL established and supervised experiment trial. AL compiled data and did statistical analyses. AL wrote the manuscript in collaboration with the co-authors.

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Abbreviations

DBH	Diameter at Breast Height
IRR	Internal Rate of Return
LA	Leaf Area
LDMC	Leaf Dry Matter Content
LEV	Land Expectation Value
LT	Leaf Thickness
OTC	Open-Top Chamber
PLS	Partial Least Square
SLA	Specific Leaf Area
WD	Wood Density

Photo: Ulrik Ilstedt

1. Introduction

1.1 Bio-based economy, tropical rainforests, and forest degradation

Given mounting rises in atmospheric carbon dioxide concentrations, there is a pressing need to develop a sustainable bio-based economy built on renewable energy and materials, decoupled from fossil fuels (European Commission. Directorate-General for Research Innovation 2018). Forests, given their role as a primary source of renewable carbon-based materials, will consequently be subjected to increasing demands as fossil-based raw materials are replaced with renewable ones (Daigneault et al. 2022). At the same time there is a need for restoration of degraded systems to halt species extinctions (Strassburg et al. 2020). Thus, a major challenge of a sustainable bio-based economy is to balance trade-offs between maximizing production of raw materials and minimizing negative impacts to ecosystem services and biodiversity. Globally, much of the bio-based production will be directed towards the humid tropics, because of their expansive land area (Food and Agriculture Organization of the United Nations [FAO] 2020) and great production potential (Running et al. 2004).

Tropical rainforests are among the most iconic and important ecosystems on the planet, supporting immense biodiversity as well as supplying a vast array of services and products. For example, they are greatly important for global carbon stocks, containing 35% of global terrestrial carbon stocks (this includes tropical wet, moist, and montane forests) (Scharlemann et al. 2014). Similarly, tropical forests support at least 40 000 tree species, approximately 60% of all vertebrate species on the planet (with the majority in the humid portion of the biome), ca 6 million arthropod species (also concentrated in the humid tropics), together with thousands of species from other taxa (Hamilton et al. 2010: Basset et al. 2012: Slik et al. 2015: Pillay et al. 2021). Thus, when managing these ecosystems, it is crucial to do so with these values and services in mind.

However, like most biomes on the planet, tropical rainforests are under pressure from human-driven land-use changes and climate change. By the end of the century, tropical forests will experience at least a 1°C increase in mean temperature (Intergovernmental Panel on Climate Change 2021), which also impacts precipitation patterns (Trenberth 2011). Specifically, the frequency and intensity of heavy precipitation events are projected to increase, as is the prevalence of drought periods (Trenberth et al. 2003; Trenberth 2011; Chou et al. 2012; Malhi et al. 2014; Tabari 2020). Such changes will have large-scale and long-term effects on fundamental properties, such as forest community composition, and crucial ecosystem processes, like biomass productivity and decomposition (Malhi et al. 2014). While tropical forests could be a tool for climate change mitigation by sequestering carbon, due to global deforestation and forest degradation, some studies have estimated that they currently emit more carbon than what is absorbed via forest (re)growth (Pan et al. 2011; Baccini et al. 2017). For example, between 1990 and 2010, 6.5% of Southeast Asia's total land area was deforested, mainly due to the growth of cash crop and fast-growing exotic tree plantations, together with unsustainable logging practices (Stibig et al. 2014; Gaveau et al. 2016). In Southeast Asian forest management, the standard approach has been to rely on natural regeneration to recover timber stocks in between selective logging rotations, where a limited number of trees are extracted during each harvest. However, this has historically been ineffective, with timber stocks gradually depleting over multiple logging rotations (Chua et al. 2013; Yamada et al. 2016; Butarbutar et al. 2019). Degraded forests where timber stocks are gradually depleted are in many cases then converted to plantations (Gaveau et al. 2016).

Land-use pressure and biodiversity is especially high on the island of Borneo, which is widely regarded as one of the worlds most imperiled biodiversity hotspots (Myers et al. 2000). Borneo has the highest plant and mammal diversity in Southeast Asia (De Bruyn et al. 2014) and hosts approximately 15 000 vascular plant species, of which a third are endemic (Roos et al. 2004; van Welzen et al. 2005). Lowland rainforests are especially rich in biodiversity, containing ca 10 000 plant species (Kier et al. 2005).

However, almost a fourth of the total land area was deforested between 1973 and 2010 and half of the remaining forest area has been logged to some degree (Gaveau et al. 2014). More than 95% of this logging took place in the biodiverse lowland forests, since they are the easiest to access for logging companies, and are thus more severely exhausted compared to more remote areas (Curran et al. 2004; Gaveau et al. 2014). So far Borneo, and Southeast Asia more generally, has seen a lack of sustainable management, where services and products provided by the region are produced in a renewable manner.

1.2 Current land-use options for management of secondary forests

Traditionally, tropical forests are divided into primary and secondary forests. Primary forests are those who have not been subjected to major disturbances and thus have reached, or are at least close to, a stable climax state. Secondary forests, on the other hand, are defined by the FAO as “forests regenerating, largely through natural processes, after a significant disturbance of the original forests and displaying major differences in forest structure and/or species composition compared to pristine primary forests” (FAO 2003). Traditionally, protection of primary forests has been viewed as the optimal way to protect ecosystem functions and services, and associated biodiversity (Cardinale et al. 2012; Melo et al. 2013). However, given current land-use, secondary tropical forests are becoming increasingly common, and primary forests are becoming rarer. Additionally, increasing demands for forest products increases the opportunity cost of protecting primary forests. Thus, there is an expanding need to consider biodiversity and ecosystem services in the management practices of degraded habitats. Due to this need, the simple dichotomy of “primary vs secondary” forests have been put into question (Pain et al. 2020). Figure 1 shows an alternative conceptual model that emphasizes the many different pathways and actors that can affect tropical forests, and how these can make forests transition between different states (Pain et al. 2020). This model highlights that, depending on the goals and resources available, there are multiple ways a forest can be altered, both in terms of degradation and recovery, which need to be considered in a sustainable management regime.

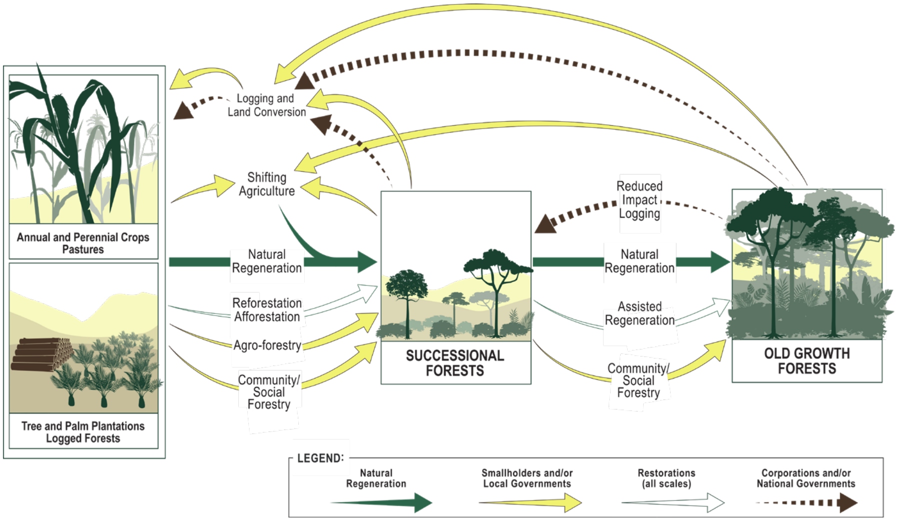


Figure 1. Conceptual model presenting management practices and successional changes that influence tropical forested landscapes. Arrow colors indicate main actors or processes driving forest change. Illustration: Pain et al. 2020.

Forest transitions between states are often guided by financial incentives. Due to a more efficient wood production, the focus has shifted from natural forest management to industrial tree plantations in many areas of the tropics. Management goals of these plantations are high production rates of renewable bio-based materials by planting a small number of the most fast-growing, often non-native, species. For example, *Acacia* and *Eucalyptus* species are common in Southeast Asia, covering about 7 million ha (Harwood and Nambiar 2014b). However, exotic tree plantations, compared to natural forests, often support less biodiversity (Barlow et al. 2007) and soil carbon stocks (Guillaume et al. 2018). Furthermore, many *Acacia mangium* plantations in Southeast Asia are affected by pathogens that heavily reduces production (Harwood and Nambiar 2014a; Nasution et al. 2019) and highlights a need to expand the roster of species used in plantations.

1.3 Potential of native tree species

One possible alternative to exotic tree species could be to harvest the potential of the many hundreds of native tree species occurring naturally at a site. Although it is often assumed that exotic tree species grow faster than native tree species (Piotto et al. 2004; Lamb et al. 2005), many native tree species are still capable of relatively fast growth (Davis et al. 2012; Subiakto et al. 2016), and may offset differences in growth rate by providing more valuable raw materials. Native species could be used over a gradient of land-use types, ranging from intensively managed commercial plantations with native pioneer species to more diversified enrichment plantings, to late successional species for restoration or enhanced natural regeneration projects. Furthermore, native species could also be more resilient to pests and pathogens, and have a higher potential to promote associated biodiversity, given that they share an evolutionary history with native ecosystems (Lamb 1998; Lamb et al. 2005; Crous et al. 2017). Using native species could reduce trade-offs and promote synergies between production of raw material and supply of ecosystem functionality, a crucial aspect of a bio-based economy (Piotto et al. 2004; Lamb et al. 2005; Subiakto et al. 2016; Crous et al. 2017; Bieng et al. 2021). Hence, wider use of native trees for timber production could meet the growing demand for raw materials while simultaneously relieving the negative effects on other ecosystem services resulting from planting exotic species (Lamb et al. 2005; Chazdon 2008; Davis et al. 2012). Thus, in order to maximize ecosystem functionality using a limited number of species that can feasibly be managed within planting projects, there is a need to identify species that reduce trade-offs and enhance synergies among different values and services. However, this task is challenging given the great tree species diversity of tropical forests. A potentially more resource effective approach is to evaluate the provisioning of values and services based on plant functional traits.

1.4 Functional trait approach

Plant functional traits are characteristics that determine the performance of a species in a given environment (Violle et al. 2007). They can be especially useful to study in species-rich areas where sampling the total species community is unfeasible. Functional traits can be morphological, physiological, and phenological in nature, as long as they are linked to the organism’s growth, reproduction, and survival (Violle et al. 2007). Furthermore, plant functional traits can be used to describe a tree species’ location on the “plant economics spectrum”, which spans from traits associated with acquisitive to conservative growth strategies and incorporates a trade-off between the two (Violle et al. 2007; Reich 2014;

Funk et al. 2017). Species with acquisitive traits generally invest relatively little resources in chemical and structural plant defense, such as high phenolic and lignin content or low leaf pH, and instead have traits that enable high growth, such as low wood density, high specific leaf area, and high contents of nutrients like nitrogen, phosphorus, and cations (Cornelissen et al. 2006; Patiño et al. 2012; Reich 2014; Perez-Harguindeguy et al. 2016). Additionally, this growth-defense trade-off may also extend to survival rates (Wright et al. 2010). Many species who invest in high early growth rates also have high mortality rates over the same period (Sterck et al. 2006; Wright et al. 2010; Philipson et al. 2014; Gustafsson et al. 2016). Functional traits are commonly used in ecology to predict ecological functions, such water stress resilience (Harrison and LaForgia 2019). Although less studied, traits could also influence a wide variety of ecosystem services and processes. These may include the interplay with associated communities (Axelsson et al. 2022), where arthropod communities in forest canopies of tropical forests may be particularly important (Godfray et al. 1999). Plant traits can also have after-life effects on important ecosystem processes, such as decomposition, nutrient cycling, and the carbon cycle, the latter being particularly important from a climate-change perspective. Better understanding of trait-ecosystem function relationships for native tropical tree species could potentially help tree species selection in forest management, balancing the supply of the many different values and services required from forests in a sustainable bio-based economy.

1.5 Values and services from tropical forests

Although the full suite of values provided by hyper diverse tropical forests may be elusive due to its exceptional diversity, there are several key values and services that are particularly important for achieving a sustainable bio-based economy, including financial potential, supporting associated biodiversity, and decomposition.

1.5.1 Financial potential

Production of raw material for substitution of fossil fuels is the foundation of a bio-based economy and crucial for economic sustainability and climate change mitigation. Even though functional traits have strong associations with productivity parameters like survival, growth, and wood structure

(Chave et al. 2009; Wright et al. 2010; Kulbat 2016), studies showing connections between financial potential and plant traits are scarce, particularly for species native to the tropics.

1.5.2 Associated biodiversity

Another important function provided by forests and forest trees is the provision of associated biodiversity. Biodiversity is important both for its intrinsic value, and because it can provide, increase and stabilize the provisioning of ecosystem functions, services, and values (Justus et al. 2009; Cardinale et al. 2012; Haines-Young and Potschin 2012). Some examples include pest control, decomposition, and soil generation, but benefits can also be medicinal, spiritual, or educational, etc. (Justus et al. 2009; Haines-Young and Potschin 2012). However, global biodiversity loss is expected to accelerate in coming years, with the tropics being especially vulnerable due to high species richness and a high degree of anthropogenic disturbance (Barlow et al. 2016; Johnson et al. 2017). This is especially true for the immense diversity of tropical insects, which is declining rapidly (Hamilton et al. 2010; Wagner et al. 2021). Beetles (*Coleoptera*) in particular, are incredibly diverse, constituting 40% of all insect species, and fill multiple functional roles crucial for ecosystem functioning (Stork et al. 2015). A simple yet effective way to categorize these different functions is by dividing beetles into feeding guilds, for example based on whether they are predatory or herbivorous. Different guilds fulfill different roles in the ecosystem. Predators can for example regulate prey populations and thus be beneficial from a management perspective (Zhou et al. 2023). Given their broad functional diversity, beetles are a commonly used indicator group for conservation, as it acts as a proxy for several other organism groups and communities. Therefore, it would be valuable to understand how beetles' functional diversity differ between tree species, and if certain tree species are better at promoting certain functional groups of canopy insects. A considerable proportion of insect diversity in tropical forests are made up of tree canopies (Godfray et al. 1999), and since canopy dwelling insects interact directly with plants, they may be distinctly responsive to plant functional trait variation. For example, herbivores are typically more abundant on plants with acquisitive trait compositions, due to high nutrient content and growth rates, together with low defensive investments (Peeters 2002; Wright et al. 2004; Pringle et al. 2010; Njovu et al. 2019; Schön et al.

2023; Bastida et al. 2024). However, there is still a lack of knowledge on to what extent tropical tree species shape the distribution of associated insect communities, particularly for different functional groups where the degree of specialization could vary. Incorporating tree species that maximize associated biodiversity could reduce biodiversity decline (Lamb et al. 2005; Chazdon 2008). However, this requires knowledge on the extent to which different native tree species promote associated biodiversity (Brancalion et al. 2018; Axelsson et al. 2022).

1.5.3 Decomposition under climate change

Finally, decomposition is another key service in a bio-based economy, since it is important for both nutrient cycling and carbon sequestration (Swift et al. 1979; Vitousek and Sanford 1986; Jackson et al. 2017). One key driver of decomposition is climate conditions. Therefore, while climate change will have large repercussions on many services of tropical forests, it is particularly important for decomposition. Some of its effects on decomposition are indirect, like altering trait composition of leaf litter (Heilmeier 2019). However, climate change also directly affect decomposition. For example, higher temperatures increase reaction rates and the activity of soil biota and thus lead to higher decomposition rates (Tang et al. 2019; Wood et al. 2019; Nottingham 2020). However, for aspects like changes in precipitation patterns, consensus is less clear. While drier conditions generally mean slower decomposition (Powers et al. 2009), it is not well understood how precipitation patterns and temperature changes may interact, especially in the tropics where broader conclusions are limited by high species richness. This is especially true for precipitation frequency, where effects are understudied due to the difficulty of accurately analysing it using field-collected data.

Another major driver of decomposition is plant traits, where acquisitive trait values generally are related to fast decompositions rates (Santiago 2007; Cornwell et al. 2008; Bakker et al. 2011; Freschet et al. 2012). However, the effect plant traits have on decomposition have been shown to vary depending on climate scenarios (Liu et al. 2006; Yajun et al. 2016; Petraglia et al. 2019; Fanin et al. 2020; Canessa et al. 2021). However, these interactions are not fully understood and have not been thoroughly tested in experiments, especially under tropical conditions and with precipitation frequency in mind.

1.6 Knowledge gaps

There is an urgent need to improve tropical forest management so that its products and services, e.g. financial and conservation values, can be sustainably supported, and important ecosystem processes, e.g. decomposition, maintained. A key step to achieve this is to improve general understanding of which kinds of actors and management types affect tropical forests, and how forests transition between different states. Another aspect is to acquire understanding of the degree to which native tree species vary in their ability to provide these resources, and to what degree trait composition affect this capacity. Integration of native tree species into forest management practices could reduce trade-offs and result in synergies between commodity production and supply of ecosystem services within a bio-based economy. However, this requires deeper understanding on how differences in functional trait compositions of native tree species are related to the provisioning of different products, services, and processes. If this could be achieved, it would be possible to identify suites of native tree traits that balance these values in species-rich tropical forests.

Photo: Ulrik Ilstedt

2. Research objectives

The overall objective of this thesis was to analyze how native species, and their plant functional trait compositions, can contribute to the supply of goods and services in order to inform species selection in restoration, reforestation, and commercial exploits. It also aims to discuss how common definitions of tropical forest ecosystems can be altered to better mirror the nature of disturbance and regeneration regimes that affect them. This thesis consists of four papers (I-IV). Paper I presents an overview and discussion on the current framing of, and language used to describe, tropical forest management in the literature (Figure 2). The three remaining papers each aim to explore how tree species, based on their trait composition, vary in their ability to supply commodities and ecosystem functionality (Figure 2), information particularly valuable for species selection in assisted natural regeneration efforts. Paper II covers the financial potential of native species in assisted regeneration planting. Paper III explores the relationship between native tree species and their promotion of associated biodiversity and functioning. Paper IV consists of a climate change experiment, identifying to what degree plant traits affect leaf litter decomposition, how projected climate change can be expected to change decomposition rates, and if traits will vary in importance under projected climate change scenarios.

The central research question addressed in each paper of this thesis are:

I. In what sense are primary forests “primary” and secondary forests “secondary”, and are these distinctions useful?
II. Can functional traits predict financial value of enrichment planting in degraded tropical forests?

III. Do functional traits of the host tree species affect beetle species richness in tree canopies, and do these vary depending on beetle feeding guild identity?

IV. How does mass loss from decomposition vary with plant functional traits and future climate change scenarios, and do the importance of traits vary across climate scenarios?

Papers II-IV each present the following main hypotheses (each visualized in a simplified manner in Figure 2) in how plant functional traits affect the provisioning of financial potential, associated beetle biodiversity functionality, and decomposition under climate change:

II. Trees with acquisitive trait values have high financial potential due to their fast growth rates.

III. Plant functional traits associated with the plant economic spectrum can predict variation in beetle richness among tree species, where species richness positively correlates to acquisitive trait values. However, the predictive power of traits will vary depending on the beetle feeding guild considered.

IV. Mass loss from decomposition is altered by both climate change and plant functional traits. Decreased precipitation frequency and volume reduces mass loss, while elevated temperature increases it. Furthermore, leaf litter with conservative traits decompose slower than litter with an acquisitive trait composition. Lastly, the effect plant traits have on decomposition will change depending on the climate change scenario considered.

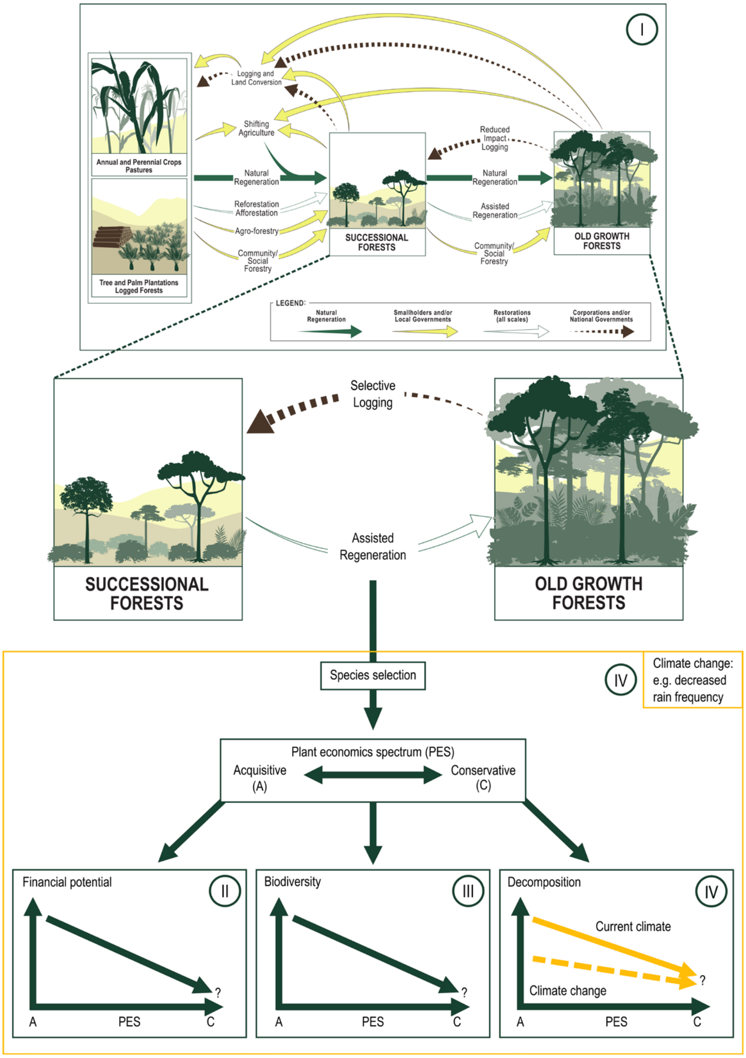


Figure 2. Conceptual model showing how the papers in this thesis are connected, their ties to tropical forest management and the array of services supplied by Bornean rainforests. Paper I discusses the current framing of tropical forest management and presents a conceptual model that emphasises how actors and management types make tropical forests transition between states (Figure 1). The remaining papers hones in on the transition between successional and old growth forests in order to explore how species selection based on plant functional trait compositions of native tree species affect the supply of financial potential (Paper II), conservation value (Paper III), and decomposition, a key ecosystem process (Paper IV). The yellow box illustrates that climate change affect the supply of all of these services, but it is only addressed in paper IV. Illustrations: Adjusted from Pain et al. 2020.

Photo: Ulrik Ilstedt

3. Methods

3.1 Study approach

To determine how forest ecosystems in northern Borneo can be managed to supply a wide array of values and services, I have used a multi-faceted approach including literature reviews, field sampling of plant functional traits and insects, forestry economics, and a climate change and decomposition experiment. To test the hypotheses and research questions outlined for each of the papers, I applied the following study approaches:

- Paper I: Existing literature was used to frame and present a debate within tropical forest management about primary and secondary forests, two categories commonly used to describe tropical forests. I, together with my co-authors, proposed an alternative conceptual model that emphasises the nature of disturbances and forms of regeneration that may alter forest ecology.
- Paper II: I used a tree species field trial established with enrichment planting protocols in northern Borneo to collect functional trait, growth, and survival rate data for tree species native to the region. Data on financial value per cubic meter, allometric equations, and management costs for the region were taken from literature. Financial value, expressed as internal rates of return, based on land expectation value, was then calculated to analyse financial viability of each species. I analysed how internal rates of return varied between species depending on their functional trait values.
- Paper III: The same species field trial utilized in Paper II was used to sample beetle populations from the canopy of native tree

species. Beetles were classified to family level and grouped into five basic feeding guilds. I analyzed how beetle species diversity varied between tree species depending on guilds, and how this was related to plant functional traits sampled in Paper II.

- Paper IV: A climate change experiment was established in order to test how decomposition rates for leaf litter would change under future climate conditions where temperature, precipitation frequency, and precipitation volume are altered. I also included functional trait measurements on fresh leaves from Paper II, together with new measurements on un-decomposed leaf litter, in the analyses to explore what traits were correlated to decomposition, and if these relationships were different under climate change.

3.2 Study site

All data collection in the field took place in Sabah, northern Borneo (Figure 3), inside the 26,880 ha Sungai Tiagau Protection Forest Reserve (4°35′20″N 117°16′19″E). According to the Köppen-Geiger climate classification, the region's climate is humid tropical equatorial (Peel et al. 2007). The mean annual temperature is approximately of 27-28°C (Walsh and Newbery 1999) and the annual average precipitation is 2400–2500 mm (2004–2016, measured at three weather stations close to the study area), with Acrisols as the main soil type (Panagos et al. 2011). The Sungai Tiagau Protection Forest Reserve consists of lowland mixed dipterocarp forest which was logged in the 1970s and burned during a forest fire in 1982–83. The forest reserve is administered by the state government foundation Yayasan Sabah and since 1998, 18,500 ha of the site has been managed by the Sow-A-Seed forest rehabilitation project. This project is a collaboration between Yayasan Sabah, the Swedish University of Agricultural Sciences, and the Swedish company IKEA, with the goal to rehabilitate the forest and its biodiversity (Axelsson et al. 2024).

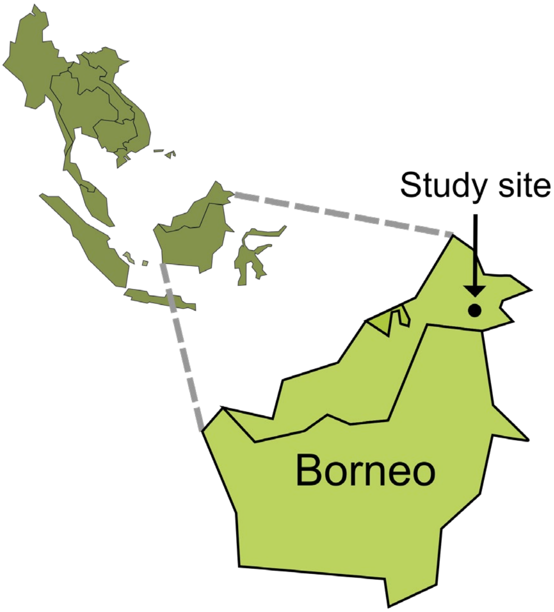


Figure 3. Map of Southeast Asia with the island of Borneo and location of my study site highlighted. Illustration: A. Lindh.

3.2.1 Species trial site (Paper II, III, and IV)

I have made extensive use of a tree species field trial established in a 3-ha plot (at ~ 300 m above sea level) of successional forest within the Sow-A-Seed project area in November 2008 (Figure 1). Seedlings from 34 native tree species were raised from seeds in the project plant nursery and then planted in a random order with one tree every 3 m along 40 linear transects, each approximately 60 m long, with 10 m between the center of transects (Figure 4; Gustafsson et al. 2016). Hence, planting density was approximately 333 trees/ha. No soil preparation was conducted, but each transect was cleared of small pioneer trees and climbers. The planting regime is identical to enrichment planting done in large portions of the Sow-A-Seed project, and similar to methods used in other regional restoration projects (Ruslandi et al. 2017; Philipson et al. 2020).

Figure 4. Species field trial established in November 2008 within the Sow-A-Seed project area, used to sample functional traits (Paper II-IV), growth rates (Paper II), beetles (Paper III), and leaf litter (Paper IV). Photo: A. Lindh.

3.3 Field sampling

3.3.1 Fresh leaf sampling and allometric traits measurement (Paper II – IV)

To create a library of plant functional traits with which to describe my studied tree species, I took leaf samples and measurements of trees in the species field trial (Paper II-IV). Due to resource restraints, only 23 randomly selected species of 34 species present overall in the field trial were sampled and measured (Table 1). I characterized each selected tree species using a combination of plant functional traits, with varying trait selection between papers depending on the specific study question (Table 2). Traits were expressed as average values for each species.

In February-April 2019, ten years and 2-4 months after the establishment of the field trial, I collected five leaves from three different branches (located in the outer canopy whenever possible) from 3-8 individuals of each of the

23 tree species and conducted measurements of tree size and allometry. For each individual tree, I measured diameter at breast height (DBH, 1.3 m), tree height, crown height, as well as crown width. From these measurements I calculated the following tree allometry traits: stem slenderness (tree height/diameter at breast height), relative crown length (crown height/crown width), relative crown depth (crown height/tree height), and relative crown width (crown width/tree height) (Sterck et al. 2001) which were used in Paper II (Table 2).

3.3.2 Litter sampling and preparation (Paper IV)

To address how leaf litter decomposition varies across climate conditions and to what degree this is affected by functional traits, I collected leaf litter from the same trees in the previously mentioned tree species field trial. In February-April 2019, I installed 144 litter traps underneath trees of the 23 species. *Mangifera odorata* and *Sindora irpicina* did not produce enough litter and were excluded from the study (Table 1). Traps measured 1.6 x 1.6 m and consisted of a plastic shade cloth fitted around the stem of the tree, suspended above the ground (Figure 5). Traps were emptied every two to four weeks, and litter was sorted immediately to ensure that only leaf litter from the studied tree species was collected in each trap. Litter was cleaned from hyphae and lichens, oven dried at 70ºC for 72 h, and then stored in a well-ventilated, non-air-conditioned, room until further handling.

Table 1. Tree species sampled, their acronym, and taxonomic family identity.

Scientific name	**Acronym**	**Family**
Canarium sp.	Ca.sp	Burseraceae
Diospyros sp.	Dio.sp	Ebenaceae
Dipterocarpus conformis	Dip.co	Dipterocarpaceae
Dryobalanops keithi	Dr.ke	Dipterocarpaceae
Dryobalanops lanceolata	Dr.la	Dipterocarpaceae
Hopea ferruginea	Ho.fe	Dipterocarpaceae
Mangifera odorata*	Ma.od	Anacardiaceae
Parashorea malaanonan	Pa.ma	Dipterocarpaceae
Parashorea smythiesii	Pa.sy	Dipterocarpaceae
Parashorea tomentella	Pa.to	Dipterocarpaceae
Pentace adenophora	Pe.ad	Malvaceae
Pentace laxiflora	Pe.la	Malvaceae
Rubroshorea beccariana	Ru.be	Dipterocarpaceae
Rubroshorea fallax	Ru.fall	Dipterocarpaceae
Rubroshorea leprosula	Ru.lepr	Dipterocarpaceae
Rubroshorea macrophylla	Ru.map	Dipterocarpaceae
Rubroshorea macroptera	Ru.mat	Dipterocarpaceae
Rubroshorea ovalis	Ru.ov	Dipterocarpaceae
Rubroshorea parvifolia**	Ru.par	Dipterocarpaceae
Rubroshorea pauciflora	Ru.pau	Dipterocarpaceae
Shorea falciferoides	Sh.falc	Dipterocarpaceae
Shorea leptoderma	Sh.lept	Dipterocarpaceae
Sindora irpicina ***	Si.ir	Fabaceae

* Not included in Paper II and IV

** Not included in Paper III

*** Not included in Paper III and IV

3.3.3 Trait measurements and chemical analyses (Paper II, III, and IV)

Physical trait measurements, used in Paper II-IV (Table 2), were performed on fresh leaf samples as soon as they were recovered from the field. For each leaf, I measured leaf thickness (LT) between major veins (Perez-Harguindeguy et al. 2016), scanned them and used resulting images to determine leaf area (LA) using ImageJ (Schneider et al. 2012). Leaves were weighed to determine fresh weight, and then oven dried for 3 days at 70°C to determine dry weight (Perez-Harguindeguy et al. 2016). Fresh and dry weight, along with LA and dry weight, were used to determine leaf dry matter content (LDMC) and specific leaf area (SLA), respectively (Perez-Harguindeguy et al. 2016).

For each of the 23 tree species, a subsample of dried fresh leaves and of un-decomposed leaf litter was sent to the Forest Research Center, Sabah Forestry Department, in Sepilok, Malaysia, for nitrogen (N), phosphorus (P), pH, and total phenolic content analyses. Additionally, each fresh leaf sample was also analyzed for potassium (K), magnesium (Mg), calcium (Ca), sodium (Na), and soluble phenolics content. Fresh leaf values were used in Paper II-IV, while leaf litter values were used only in Paper IV (Table 2).

Additionally, analyses for condensed tannin, total tannin, hemicellulose, cellulose, and lignin content were carried out at Universiti Malaysia Sabah, Kota Kinabalu, Malaysia, on subsamples of both un-decomposed leaf litter and dried fresh leaves of each tree species (included in Paper III and IV, Table 2).

I used the Global Wood Density Database to acquire wood density (WD) values, used in Paper II and III (Table 2), for 17 of the 23 species (Zanne et al. 2009). The remaining six species, *Canarium sp*., *Diospyros sp*., *Pentace adenophora*, *Pentace laxiflora*, and *Sindora irpicina*, were not in the database and in these cases I used average wood densities for species of the same genera growing in tropical Southeast Asia.

3.3.4 Financial calculations (Paper II)

To explore whether functional traits can predict financial value of enrichment planting, I assessed financial viability of 22 of the tree species in the field trial site by estimating their land expectation value, which was used to derive an internal rate of return. To do this I estimated survival and growth rates of each species, used literature to estimate their financial value per cubic meter, and used allometric equations to estimate volume of wood that could be harvested from each tree species at a specific DBH. No data on financial value per cubic meter timber could be obtained for *Mangifera odorata* and it was thus excluded from the study (Table 1).

Internal rate of return (IRR) is the estimated discount rate at which net present value of all cash flows equal zero. It defines the net rate of return you could expect from investing in a specific project. I calculated IRR per hectare for each tree species based on calculations of land expectation value (LEV, USD/ha), an estimate of financial value of a piece of land, assuming the land

Table 2. List of sampled traits, their units of measurement, general relevance, and papers they were included in.

Trait	Unit	Medium*	Relevance	Papers	References
Specific leaf area (SLA)	mm^2/mg	Fresh leaves and litter	Defensive investment, nutrient content, leaf lifespan, growth rate	II, III, IV	Makkonen et al. 2012; Perez-Harguindeguy et al. 2016
Wood density (WD)	mg/mm^3	From literature	Structural strength, pathogen or parasite susceptibility	II, III	Makkonen et al. 2012; Perez-Harguindeguy et al. 2016
Leaf dry matter content (LDMC)	g/g	Fresh leaves and litter	Growth rate, leaf lifespan, leaf toughness	II, III, IV	Makkonen et al. 2012; Perez-Harguindeguy et al. 2016
Leaf thickness (LT)	mm	Fresh leaves	Physical strength, allometry, photosynthetic optimization	II, III, IV	Perez-Harguindeguy et al. 2016; Both et al. 2019
Leaf area (LA)	cm^2	Fresh leaves	Allometry, light interception, temperature regulation	II, III, IV	Perez-Harguindeguy et al. 2016; Both et al. 2019
Nitrogen (N), potassium (K), phosphorus (P) content **	mg/g	Fresh leaves and litter	Essential macronutrients, photosynthetic rate, nutritional quality for herbi- and detrivores, life-history	II, III, IV	Raaimakers et al. 1995; Makkonen et al. 2012; Perez-Harguindeguy et al. 2016
Total and soluble phenolic content **	mg/g	Fresh leaves and litter	Chemical defense against herbivory	II, III, IV	Kulbat 2016; Makkonen et al. 2012

pH	$\mathrm{Log}_{10}(1/a_{H^+})$	Fresh leaves and litter	Leaf digestibility	II, III, IV	Cornelissen et al. 2006; Perez-Harguindeguy et al. 2016
Sodium (Na), calcium (Ca), and magnesium (Mg) content	mg/g	Fresh leaves and litter	Light absorbance, stomatal conductance, nutritional quality for herbivores and detrivores	II, III, IV	Lautner and Fromm, 2010; Makkonen et al. 2012; Jia et al. 2015; Both et al. 2019
Total and condensed tannin content	mg/g	Fresh leaves and litter	Chemical defense against herbivores	III, IV	Coq et al. 2010; Both et al. 2019
Lignin, (hemi)cellulose content	mg/g	Fresh leaves and litter	Leaf physical strength and photodegradation susceptibility	III, IV	Both et al. 2019; Austin and Ballaré, 2010
Relative crown depth	m/m	Stem and canopy	Life-history and allometry	II	Sterck et al. 2001; Osunkoya et al. 2007
Relative crown width	m/m	Stem and canopy	Life-history and allometry	II	Sterck et al. 2001; Osunkoya et al. 2007
Relative crown length	m/m	Stem and canopy	Life-history and allometry	II	Sterck et al. 2001; Gustafsson et al. 2016
Stem slenderness	m/cm	Stem and canopy	Life-history and allometry	II	Sterck et al. 2001; Osunkoya et al. 2007

* Traits measured on leaf litter is only relevant for Paper IV

** K and soluble phenolics content was only measured on fresh leaves (Paper IV) will be under the given forest management indefinitely. I calculated LEV, and subsequently IRR, following Straka and Bullard (1996) in [Eq. 1]:

$$[\text{Eq. 1}] \qquad LEV = \frac{\sum_0^T R_t(1+i)^{T-t} - \sum_0^T C_t(1+i)^{T-t}}{(1+i)^T - 1}$$

where ‘T’ is the rotation length given in years for a certain tree species, ‘t’ is the year of a specific revenue or cost, ‘R_t’ is the revenue received in year t from selling the timber, ‘C_t’ is the cost incurred in year t from management, harvesting, and planting, and ‘i’ is the annualized discount rate, given as a decimal. Finally, IRR is defined as the value of ‘i’ where LEV = 0. I assumed that the planting pattern used to establish the field trial site would be used in each rotation, and thus 333 trees could be grown on a hectare of land. In each calculation I assumed that all 333 trees would be of the same species and that all trees in a hectare would be harvested concurrently when they reached an average of 30 cm DBH, which I defined as one rotation period.

Financial value per cubic meter of timber of each tree species was based on prices of exported round logs (Sabah Forestry Department 2016, 2017). To estimate growth rates for the 22 species, I used DBH measurements collected on all trees planted in the field trial site, starting 3 years after planting and then repeated approximately every 2 years for a total of 7 measurements, with the last measurement taken 14 years and 5 months after the study plot was established. I estimated growth rates for each species using linear mixed effect models, with DBH as the response variable and number of years since planting as the explanatory variable, and used these to extrapolate the average time it would take each species to reach a DBH of 30 cm. Similarly, I estimated tree survival rates for each species, based on their observed survival between planting and the most recent plot survey. I used these survival rates to adjust the number of trees remaining at harvest time, assuming no further mortality after 15 years. To estimate the bole volume for each tree species at the 30 cm DBH harvesting threshold, I used allometric equations from Bertault and Kadir (1998). For management costs I used estimates from Philipson et al. (2020). These costs are based on a separate, nearby, restoration project, and consistent with those incurred at the Sow-A-Seed project (personal communication, David Alloysius, Sow-A-Seed project manager 2003-2022). Logging cost per m^3 estimates were obtained from FRIM and ITTO (2002) and Fisher et al. (2011), which represent costs occurred in conventional logging operations in Peninsular Malaysia.

To capture variation in the dataset and evaluate robustness of my IRR calculations, I performed a sensitivity analysis where I varied management costs and tree growth rates, based on the spread of management costs mentioned in Philipson et al. (2020), and the 80% confidence interval in my mixed effects growth rate models, to produce a high, average and low-value scenario of my IRR estimates.

3.3.5 Insect sampling and classification (Paper III)

To evaluate, how functional traits of the host tree species affect beetle species richness in tree canopies, and whether these vary depending on beetle feeding guild identity, I used a beetle dataset collected in the field trial site using canopy fogging (Axelsson et al. 2022). Two species, *Rubroshorea parvifolia* and *Sindora irpicina*, had a lower sampling effort than the remaining species and were thus excluded, resulting in a dataset containing 21 tree species where each tree species was represented by five individuals (Table 1). To capture seasonal variation, sampling was conducted four times between May 2016 and April 2017. Beetles were categorized to at least family level and grouped into one of five feeding guilds; herbivore, predator, xylophage, saprophage, and fungivore (Lawrence and Newton 1995; Lawrence et al. 2000; Chung, 2003). Morpho-species classification was done if identification to species level was not achievable.

3.3.6 Climate change experiment (Paper IV)

In August 2019, I established an experiment to explore how precipitation (frequency and volume) and warmer temperatures influence leaf litter decomposition for a range of tropical tree species at the seedling nursery for the Sow-A-Seed project. This experiment contained 24 plots (1.2 x 1.2 m) divided into three blocks, where each of the eight plots in each block was assigned a randomized and fully factorial combination of three treatments: ambient or drought watering frequency and volume, and presence/absence of open-top chambers (OTC) (Figure 5). Each plot also included seedlings from 12 tree species, as part of a separate experiment. The entire experiment area (24 x18 m) was covered in shade cloth to reduce direct sunlight, and a roof of transparent plastic film to exclude all-natural precipitation.

Using the collected litter, I prepared 525 litterbags (21 species * 24 plots) with 2-5 g of litter from a single species per bag (litter weight depended on the amount available for each species). I used litterbags with 2 mm mesh size, which excluded macro- and megafauna, but enabled micro- and mesofauna to access the litter (Coleman and Wall 2015). I installed all litterbags in the experiment area on August 30, 2019, with one bag per species in each study plot, resulting in 21 bags in each plot. Immediately after the litterbags were installed, experimental treatments were initiated.

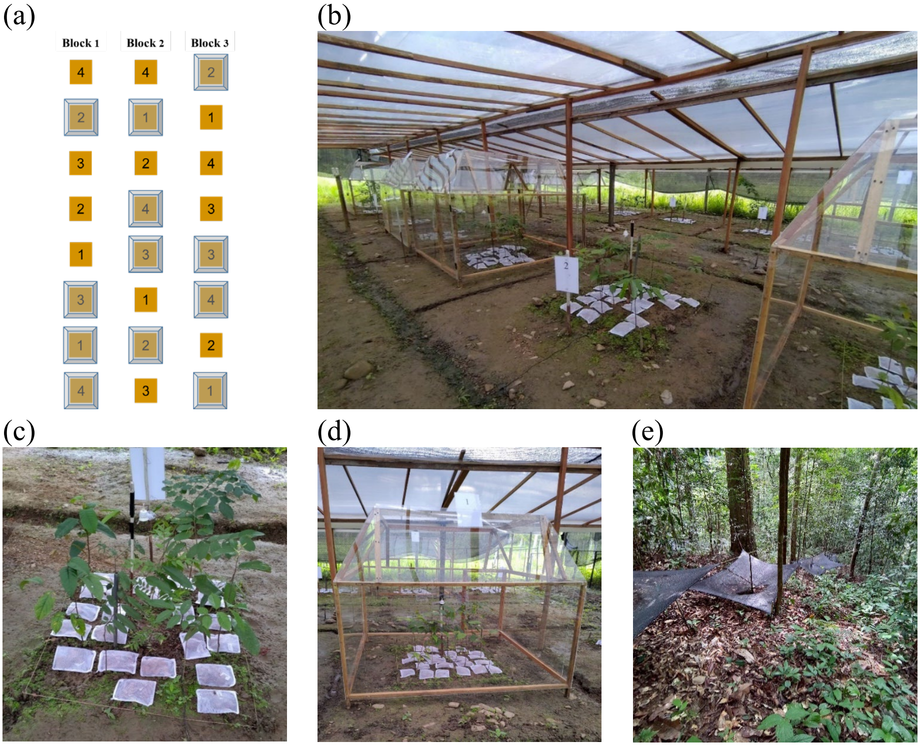


Figure 5. Overview of the experimental setup and data collection in Paper IV. a) shows the experimental design with its block distribution and treatment combinations for each of the 24 plots. Numbers signify watering treatment (1 = ambient water volume and frequency, 2 = lowered watering volume at an ambient frequency, 3 = ambient watering volume at a reduced frequency, 4 = reduced watering volume and frequency). See Table 3 for exact watering treatment specifications. Transparent covers mark the presence of open top chambers used to increase temperature. Each plot contained litterbags with litter from 21 tree species native to Northern Borneo (b-d). e) shows litter traps deployed in species field trial to collect litter used in the decomposition experiment. Photo and illustration: A. Lindh.

3.3.7 Experimental treatments (Paper IV)

To examine how leaf litter decomposition varies under changed climate conditions, I designed two levels (ambient, and a future scenario under climate change) for each of three treatments: temperature, watering frequency, and watering volume. In the ambient level, conditions were designed to match current climatic conditions while in future climate change scenarios, conditions were designed to imitate climate conditions under future climate change, i.e. higher temperature, less frequent precipitation events, and less precipitation volume, for each treatment, respectively. The eight plots within each of the three blocks were randomly assigned one of the eight combinations of the three treatments, resulting in a fully factorial experimental design with three replicates (Figure 5).

Plots assigned the increased temperature treatment were covered with an OTC, made from transparent polycarbonate sheets (Figure 5d). Plots assigned the ambient temperature treatment were left without OTCs.

I initially based decreased watering volume treatment on a precipitation of 50 mm/month, roughly half of the regional soil water deficit threshold (Pramudya et al. 2019). The ambient watering volume was based on precipitation data (2004-2016) from three weather stations located close to the experiment area, which for the study period was 190 mm/month (2300 mm/year). However, once the experiment started, readings indicated that of soil volumetric water content in all plots were considerably higher than reference measurements taken in a nearby successional forest. Thus, the volume of water added was lowered for both treatment levels by 75% on October 9 and by an additional 50% on November 15. After these adjustments the watering volume was 2.3 l and 0.6 l for the ambient and decreased volume treatments, respectively (Table 3), and there was a steep decline in soil volumetric water content.

Plots assigned ambient watering frequency treatment were watered every second day (Table 3), based on the same rainfall data as watering volume (2004-2016). Plots assigned the decreased watering frequency treatment were watered once every 14 days (Table 3), the average yearly maximum of consecutive dry days in the region (Nurlatifah et al. 2023). Number of watering events on each day water was distributed were adjusted so that within the same watering volume treatment, plots with the two frequency treatments received the same volume of water.

After 6.5 months, I harvested the litterbags and the content of each bag was cleaned, dried, and weighed. Litter mass loss (%) was defined as the difference between the initial litter mass and litter mass after incubation.

Table 3. Specifications of watering treatments given to plots in the climate change experiment conducted in Paper IV. Watering volume and frequency were given in an ambient level simulating current climate conditions, and a decreased level simulating projected future conditions under climate change. Watering volume is given after two reductions, made 1.5 and 2.5 months into the experiment, which ran 6.5 months in total.

Volume	Frequency	Water volume per irrigation event (l)	Days between watering	Number of irrigation events during watering days
Ambient	Ambient	2.3	2	1
	Decreased	2.3	14	7
Decreased	Ambient	0.6	2	1
	Decreased	0.6	14	7

3.4 Statistical analyses (Paper II-IV)

Throughout Paper II-IV I have utilized partial least squares (PLS) regressions to analyze relationships between plant functional traits and respective response variables in each study. A PLS regression creates linear components that maximize the degree to which explanatory variables can explain the response variables (Haenlein and Kaplan 2004). Given that my dataset included a large number of traits, PLS regression was a good fit for my research questions. In each study and for each model, I used Q^2, the fraction of total variation of IRR that could be predicted by a component, to determine how many components and which traits to include. I only considered components with Q^2-values above 5%. Variables were considered significant if the 90% (95% in Paper IV) confidence intervals of their loadings obtained by jack-knifing (Quenouille 1949; Efron and Gong 1983) during cross-validation did not overlap with zero. The best-fitting model was determined by backward selection, removing the trait with the confidence interval furthest from zero in each model, one variable at a time until the model only contained significant variables and then compared Q^2

values of resulting models. The model with the highest Q^2 value was deemed best fitting and was kept, while others were discarded.

In Paper II, I used PLS regression to evaluate how variation in plant functional traits related to financial value within the studied species. As the response variable, I used IRR (mid-scenario values from the sensitivity analysis), and as explanatory variables, I used 18 functional traits (Table 2). Furthermore, to evaluate indirect trait effects on IRR, I ran PLS regressions where each of the four variables that influenced IRR, namely growth rate, survival, market value per cubic meter of wood, and volume of wood per tree at the 30 cm DBH threshold, were the response variable, using the same trait selection as explanatory variables as in the trait-IRR model.

Throughout Paper III, I used species richness as the primary measurement of biodiversity since >95% of the species sampled were represented by three individuals or less. Thus, abundance or diversity indices, like Shannon or Simpson, added very little extra information about the beetle community, compared to species richness.

To test if tree species identity were related to beetle richness, I used generalized linear models with beetle richness (total and richness within each feeding guild) as the response variable (expressed either as a Poisson or negative binomial distribution) and with tree species identity as the explanatory variable. I evaluated model results with a type II ANOVA using likelihood ratios for significance testing, and by calculating McFaddens psuedo R^2. Additionally, to test if promotion of functional diversity requires multiple tree species, I compared rank correlations of average species richness between tree species for all possible combinations of feeding guilds using Kendall rank coefficient (Kendall 1938; Kendall 1945). Finally, to evaluate variation in plant functional traits in relation to beetle richness within the 21 species studied, I performed a series of PLS regressions where I included beetle richness, either total beetle richness or for individual feeding guilds, as the response variable in six models. In each model I included the 19 measured traits, as well as canopy volume to account for tree size, as the explanatory variables (Table 2).

In Paper IV, to test whether the three climate treatments and their interactions affected litter mass loss, I used generalized linear models with mass loss as dependent variable together watering volume, frequency, and presence/absence of OTCs as fixed factors, with block as a random factor. In order to find the most appropriate model, I performed backward selection, with a model containing all variables and their interactions as the starting point. A type III ANOVA was used to evaluate each iteration and the variable/interaction with the highest non-significant ($p>0.05$) p-value was removed, until only those that had a statistically significant ($p<0.05$) impact on mass loss remained. For the final model, a post hoc comparison was done on the significant treatment interaction effects.

To explore how traits predicted leaf litter mass loss, regardless of climate treatment, I ran a PLS regression using the mean leaf litter mass loss per tree species over all 24 plots as the response variable, and 24 leaf and litter traits as explanatory variables (Table 2). Additionally, to explore if the trait-decomposition predictions differed under the climate treatments, I ran PLS regressions based on the results of the ANOVA, with one model for each climatic treatment or interaction that had a significant effect on mass loss. For each significant variable, I ran a model where the response variable was the mass loss average for that particular treatment level (e.g. ambient or under a future climate change scenario) with the same fresh leaf and leaf litter traits as explanatory variables.

4. Results and discussion

4.1 Rethinking forest landscapes

The main results of Paper I is that the concepts of primary and secondary forests in most use-cases are too simplistic and limiting since they define secondary forests only as different from primary forests and do not consider causation, degree of disturbance, or human interactions. It also inherently reduces secondary forests to something negative, indicating they are impaired, defective, or flawed compared to primary/old-growth forests. This also invites negative biases, which can cause decision makers to neglect the value of these habitats (Sheil and Meijaard 2010). This enables further transformations, such as agricultural expansion or deforestation. However, a key aspect highlighted in Paper I is that secondary forests can be seen as a compliment to primary forests, since they still retain high species richness and often support alternative species and communities to primary forests (Lawton et al. 1998; Barlow et al. 2007; Berry et al. 2010; Fisher et al. 2011; Hector et al. 2011), which deforested areas or industrial plantations often do not (Sala et al. 2000; Mackey et al. 2015). In terms of carbon sequestration, secondary forests can even be viewed as having a greater potential than primary forests. For example, Poorter et al. (2016) found that carbon uptake rates in Neotropical secondary forests was 11 times higher than that of old growth forests. Thus, secondary forests should not be viewed simply as inferior to primary forests, but as a different type of forest.

In addition to acknowledging the value of secondary forests, Paper I highlights the diversity of drivers of forest change, both for forest restoration and degradation, in order to recognize which actors and forms of governance are relevant in different scenarios. It also emphasizes that forests over time can shift between multiple states depending on the management methods they are exposed to. Thus, Paper I proposes a conceptual model where different types of actors and processes, such as management practices and successional changes, are all recognized as influencing tropical forested landscapes (Figure 1). While natural disturbances are also relevant, this model focuses primarily on the way different management decisions may alter forest states. This conceptual model highlights how governments on different scales, corporations, and smallholders influence forested landscapes via many different management practices. These practices can vary in intensity, extent, and across temporal scales, changing ecosystem and landscape complexity (Chazdon et al. 2016). The same goes for regenerative measures, although these are limited by the growth rates of trees. In this model the terms "secondary and "primary" are replaced with "successional" and "old growth" forest. These definitions are closer to ecological theory, representing successional changes after a disturbance. However, the main take-away is not that these should replace the "secondary" and "primary" epithets, but that more emphasis should be put on the management and actors which put the forest into its current state. This aids more analytical thinking, better explains how human interactions shape forested landscapes, and highlights that these systems are dynamic and varied, with multiple pathways for both disturbances and regeneration.

Paper I highlights the complexity of tropical forest management, and how varied both regeneration and perturbation can be. This paves the way for the remaining papers of the thesis, which evaluate how native species can be used in such contexts to provide both financial and ecosystem services. Although my primary focus has been enrichment planting (Paper II and III), as well as selective logging (Paper II, Figure 2), the topics covered in Paper II-IV could well be applied assisted natural regeneration efforts where planting is absent (like the ones described in Chazdon et al. 2023), informing managers about which naturally occurring tree species should be promoted. The results in Paper II-IV could also apply to other management practices covered in Paper I (Figure 1). For example, the financial potential of native tree species is likely to be of interest in agro- or community forestry, where the tree species with both valuable timber and edible fruits could be of particular interest. Similarly, both associated biodiversity (Paper III), and nutrient cycling and carbon sequestration (Paper IV) is likely to be of relevance in re/af-forestation efforts.

4.2 Financial value and trait variation (Paper II)

In Paper II the aim was to determine whether plant functional traits could predict financial values of native trees in a tropical forest restoration setting, and to identify whether native tree species can be viable options for use. This study shows that for a subset of traits, a plant functional trait approach could be used to predict long-term financial values for 22 tree species native to northern Borneo. Specifically, in conflict with my hypothesis that acquisitive traits would be related to high financial potential, traits associated with a conservative growth strategy were linked to high financial value. Trees with these traits showed a high IRR, partly explained by relatively fast growth and high survival rates.

First, for the 22 tree species, IRR was negatively correlated with leaf Ca, Mg, N content, pH, and SLA (Figure 6). This PLS regression explained 43.6% of the variation in plant functional traits, and 23.3% of the variation in IRR with plant functional traits by one significant component (Q^2, predicted variation of single component = 11.6%). These trait values correspond to species with a conservative growth strategy, that generally have low nutrient content and high content of defensive compounds (Cornelissen et al. 2006; Patiño et al. 2012; Reich 2014; Perez-Harguindeguy et al. 2016). Species with acquisitive traits are generally fast-growing, which could result in higher financial viability, but can also have higher mortality rates compared to species with conservative trait values that are more stress tolerant (Wright et al. 2010; Díaz et al. 2016; Harrison and LaForgia 2019). This applied to this study as well, where the two fastest growing species (*Rubrashorea leprosula* and *parvifolia*) also had lowest survival rates, limiting their IRR.

The moderate amount of predicted variation (11.6%) in the PLS regression is likely due to opposite trait relationships between high survival and growth rate, which was evident when trait relationships were explored for each of the four variables that determined IRR individually (e.g. growth, survival rate, market value per cubic meter of wood, and volume of wood per tree at the 30 cm DBH threshold). Specifically, there seemed to be a tradeoff where traits that were related to a fast growth rate also were negatively related to survival (LT and an array of allometric traits).

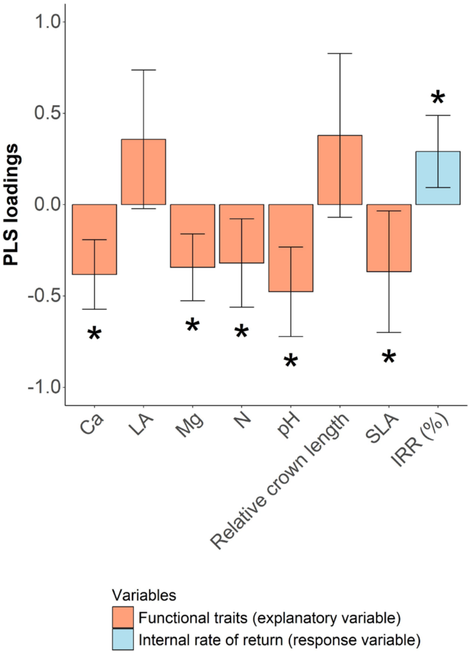
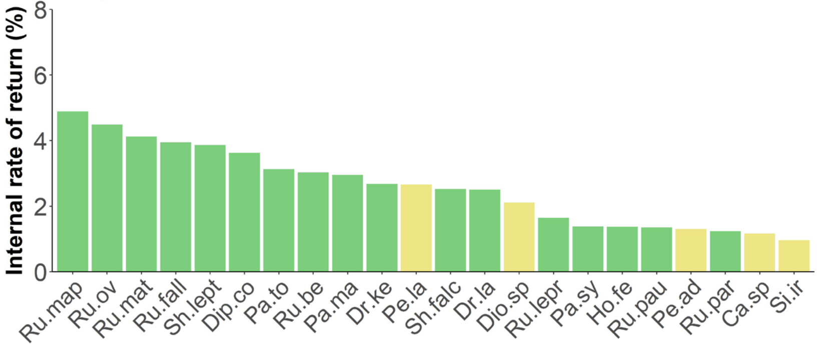


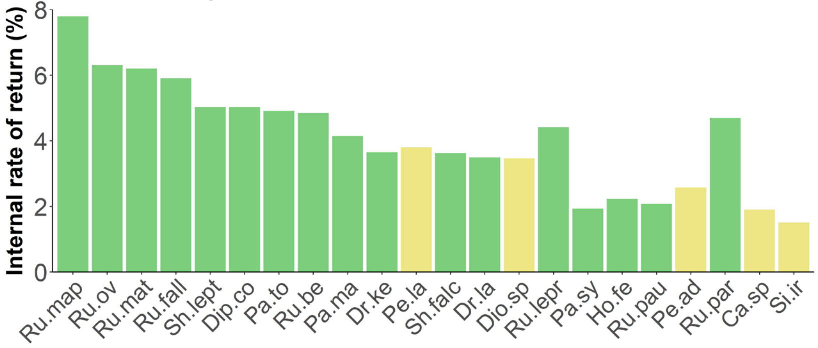
Figure 6. Loadings from a partial least square (PLS) regression based on data from 22 tree species grown in a species trial with active restoration management in Borneo, Malaysia. Orange bars correspond to functional traits measured for each tree species and the blue bar represents internal rate of returns (IRR) based on the land expectation value of the study site. Loadings show the importance and direction of influence for each variable. Error bars represent 90% confidence intervals (CI). A variable was considered to improve model prediction (marked by an asterisk) when its CI did not overlap with zero.

These findings also enabled evaluation of the viability of using native tree species, either in forest landscape restoration or reforestation efforts, as an alternative to exotic tree plantations and selective logging. The potential value of *Rubrashorea macrophylla* (Figure 7), the highest valued species in the mid-(4.9% IRR) and high-value (7.8% IRR) scenarios, were comparable to some hardwood plantations in Australia (6%, Venn, 2005). However, they are overall a less viable choice compared to industrial tree plantations with exotic species like *Acacia* and *Eucalyptus* (up to 14% IRR, Mackensen and Fölster, 2000; Winarni et al. 2018). However, native species are still profitable and could be an alternative in areas where industrial tree plantations are prohibited or impractical, or to decrease pathogen susceptibility by diversifying the species portfolio. In comparison to industrial tree plantations that are mainly grown for pulp and paper, harvesting of native tree species in restoration or reforestation efforts could also fill specific market niches that these industrial plantations cannot. For example, they could supply high-value tropical hardwood (Sarshar 2012), which traditionally have been sourced from natural forests that are now in large part either depleted or protected (Bieng et al. 2021).

a) IRR in mid financial value scenario



b) IRR in highest financial value scenario



c) IRR in lowest financial value scenario

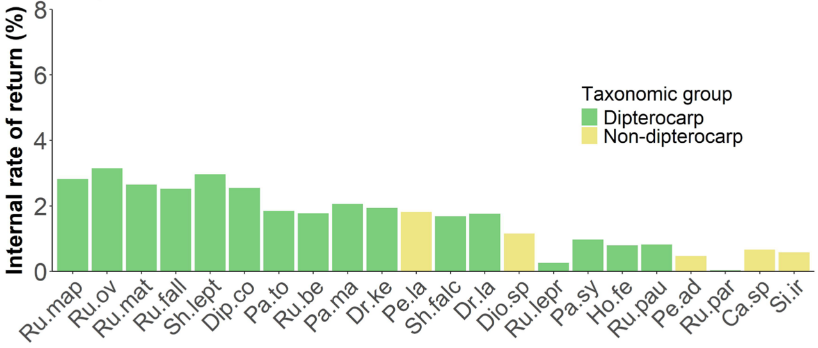


Figure 7. Internal rate of return (IRR) for three scenarios in a sensitivity analysis where assumed growth rates and management costs were varied. Species are denoted using acronyms of their scientific names (Table 1). Species in b) and c) are sorted after values in a).

Due to the extreme diversity of trees in the tropics, most tropical tree species are not well studied. This paper explores some of the variation that exists for such species in terms of functional traits and factors that determine financial viability. Overall, I conclude that enrichment planting, using certain selected native tree species, could be a financially sound and viable alternative to current land management options, such as industrial timber plantations, while also having the potential to improve supply of biodiversity and ecosystem services on degraded lands. I can further conclude that functional traits together with growth and survival rates have potential to be used to screen unexplored native species for financial viability in enrichment planting, but that a tradeoff between growth and survival can be an obstacle when interpreting the results. I found that it is not necessarily the fastest growing species that are the most financially viable, and that species with conservative traits are worth considering during species selection. The paper highlights that the use of native tree species could help produce valuable wood more sustainably, which is an important objective in a sustainable bio-based economy.

4.3 Beetle community composition in relation to tree traits (Paper III)

The objective of this paper was to determine how tropical tree species, currently used in enhanced natural regeneration plantings in northern Borneo, vary in their ability to promote species and functional diversity of associated beetle communities. I analyzed if the functional traits of the host tree species affect beetle species richness in tree canopies, and to what extent the suit of important traits vary depending on beetle feeding guild. I found support for my primary hypothesis, that plant functional traits can predict variation in beetle richness among tree species, and that specific plant traits correlated with beetle richness vary among beetle feeding guilds. However, I only found mixed support for my hypothesis that beetle richness would be correlated to an acquisitive growth strategy.

Overall average beetle richness per tree varied depending on the tree species, but tree species identity was not equally important across beetle feeding guilds (Figure 8). Furthermore, rank distributions between beetle feeding guilds were similar between herbivores and saprophages (Kendall´s $\tau = 0.43$, $p = 0.0098$), and predators and xylophages (Kendall´s $\tau = 0.41$, $p =$

0.023), but no significant correlations were found for remaining feeding guilds. These results suggest that there is no general pattern across tree species and feeding guilds for beetle species richness. While some species exhibit foundation characteristics, i.e. they support a disproportional amount of associated biodiversity (Ellison et al. 2005), multiple tree species with complementary traits compositions are needed to support functional diversity in the associated community. This conclusion was also evident in the trait analyses where two physical traits, LA and SLA, drove species diversity for most of the feeding guilds. Specifically, in the model for total beetle richness, along with the herbivore, xylophage, and saprophage models, beetle richness was positively correlated to SLA and negatively to LA. In addition, herbivore richness was correlated negatively to LT, and xylophage diversity positively associated with leaf Ca content and negatively to canopy volume. Of note is that canopy volume, something that would be expected to positively affect species richness of canopy-dwelling beetles (Campos et al. 2006), and at least partly be tied to fast growth and, thus, the acquisitive side of the plant economic spectrum, did not have a positive association to any of the mentioned guilds. This suggests that beetle diversity among sampled species is driven by specific physical trait associations rather than tree species productivity. High SLA is for example indicative fast growth, high nutrient uptake and fast turnover rates (Reich 2014), which according to the *resource availability hypothesis* (Coley et al. 1985) should incentivise herbivory. On the other hand, small LA can be an adaptation to overcome nutrient or water limitations (Patiño et al. 2012; Perez-Harguindeguy et al. 2016, Wright et al. 2017), but is not a trait limited to only one side of the plant economic spectrum (Lohbeck et al. 2015; Wright et al. 2017). These results suggest that physical leaf traits drive overall beetle diversity, at least partly, by providing generally favourable conditions, like high nutrition plant material to feed on. However, it is likely also influenced by more specific trait interactions that only affect specific parts of the beetle community, like herbivores with certain feeding modes (Caldwell et al. 2016; Bastida et al. 2024).

Two feeding guilds, predators and fungivores, displayed alternate suites of species traits associated with high species richness. For predators, richness was positively correlated with canopy volume and leaf pH, and negatively to LA, and leaf hemicellulose and total phenolics content. In the fungivore community, species richness was positively correlated with leaf K and Mg content, as well as WD, and negatively correlated with leaf total phenolic content. One option for these alternate suites of traits is that, unlike other guilds that utilize plant resources directly for their survival, these groups are more connected to fungal and prey populations upon which they feed, although these in turn could be affected by plant traits. For the fungivore community, I found some limited support for this theory. For instance, similarly to fungivore beetle richness in my study, a study in Panama found that fungal community structure was correlated to leaf K content (Kembel and Mueller 2014), while a literature review on fungal endophyte colonization found that fungi colonization negatively correlated with leaf phenolics and other secondary metabolites (González-Teuber et al. 2021). Thus, there appears to be at least some basic similarities between traits that affect the fungivore beetle richness in this study and traits that drive fungal communities in the literature.

Predators could likely be driven by predator-prey-trait interactions but have also been shown in literature to vary independently of prey populations, and instead vary depending on tree species diversity and structural diversity of the ecosystem (Langellotto and Denno 2004; Moreira et al. 2016; Schuldt et al. 2017; Schuldt et al. 2019). This could for example explain why predators were the only guild with a positive relationship to canopy volume, since larger canopies likely have higher structural diversity.

The trait analyses highlight the conclusion of the correlation analyses. Specifically, tree species with foundation characteristics exists, in this case a large part of beetle diversity was influenced by two physical traits. However, a larger variation in tree trait composition would be necessary to promote functional diversity and a broader species composition within the associated community. This has implications for forest restoration operations, which in Southeast Asia on average only include three tree species historically (Banin et al. 2022). However, Axelsson et al. (2022) estimated that at least 50 tree species would be needed to support most of the beetle community in the species trial plot in the Sow-A-Seed project area. The same conclusion is also supported by my results showing that ranking on tree species in beetle richens depended on feeding guild, clearly indicating that community composition and type of functional diversity differed across different tree species. Therefore, while higher tree species richness likely is advantageous for associated community richness, restoration projects are limited by cost, infrastructure, and managerial know-how, and might not be able to supply a

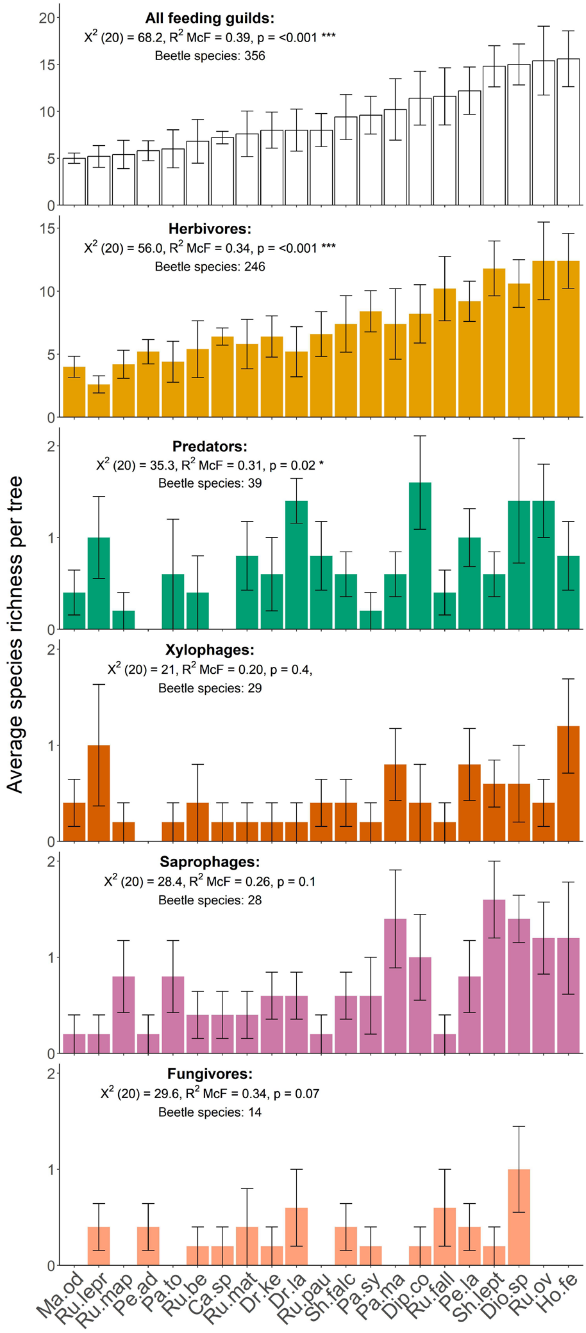


Figure 8. Average beetle (*Coleoptera*) species richness per tree (n=5) for five feeding guilds, and their combined total. Beetles were sampled from 21 tropical tree species (denoted using acronyms found in Table 1) native to Borneo, using four rounds of canopy fogging spanning a year´s time, started eight years after planting. Error bars show standard error of the mean. Number of beetle species of each guild sampled, together with results from generalized linear models (degrees of freedom, chi-square value, McFaddens psuedo R^2, and p-value) to test if species richness varied between tree species, are given under the name of each guild.

wide enough roster of tree species to support associated communities. In such situations my results provide some guidance into which species should be prioritized. Ideally, if conservation is a management objective, then tree species selection should not only be based on the total number of beetle species supported per tree, but should also consider functional diversity.

This study emphasizes that we do not fully understand how tree species characteristics drive associated beetle community diversity and structure. Although the study was conducted exclusively on young trees, and only sampled one part of the total associated community, i.e. beetles, it contributes with insight into how functional groups within beetle communities vary with tree species identity and plant functional traits. While tree diversity can certainly directly drive associated insect community richness (Moreira et al. 2016; Schuldt et al. 2019), tree species clearly differ in the functional diversity they support, driven by differences in tree physical traits. This highlights the complex ecology of biodiversity interactions, where functional diversity can mediate plant-consumer relationships, with knock-on effects on whole communities (Schuldt et al. 2019).

4.4 Role of leaf and litter traits of tropical trees during decomposition under different climate change scenarios (Paper IV)

In my last paper, I conducted a climate change experiment using leaf litter from 21 tree species native to northern Borneo, to explore how changes in temperature, precipitation volume, and precipitation frequency affected liter decomposition, both independently and when combined, and the role of plant functional traits in driving mass loss under different climate change scenarios. I found support for the majority of my hypotheses, with decreased decomposition in plots with lower water availability (both frequency and volume), and increased decomposition in plots with elevated temperature. Similarly, in accordance with my hypothesis, I found that acquisitive trait values were associated with high decomposition rates. However, I did not find that climate scenarios affect the importance of individual traits in driving decomposition, or in the degree to which plant traits explained mass loss overall during decomposition. Altogether, my results demonstrate that both climate change treatments and plant functional traits influenced litter mass loss during decomposition but show little support for traits to shift in importance and function with climate change.

First, I found that, when averaging across all climate treatments, plant functional traits contributed to predicting mass loss of litter from different tree species. Specifically, PLS regression explained 50% of the variation in plant functional traits, and 71% of the variation in leaf litter mass loss (one significant component; $Q^2 = 68\%$). Primarily acquisitive traits, such as high nutrient content and low concentration of chemical and structural defense compounds, were related to high litter mass loss (Figure 9). Specifically, high mass loss was related to high content of Ca, K, and Mg (nutrients), and low concentrations of total tannin and lignin content (plant defense compounds), along with low Na content and high pH. This is generally in line with established theory on the relationship between decomposition and plant traits associated with a rapid versus a conservative plant growth strategy (Santiago 2007; Cornwell et al. 2008; Bakker et al. 2010; Freschet et al. 2012). These results are also consistent with those from a global litter translocation experiment, where Mg and tannin content were highlighted as important drivers of decomposition (Makkonen et al. 2012).

For climate treatments, the primary finding was that precipitation frequency, a variable that is very rarely reported due to the difficulty of accurately measuring it in field trials, interacted with watering volume (a variable that is much more commonly measured) to affect litter mass loss during decomposition ($F(1) = 8.58$, $p = 0.009$; Figure 10a). Specifically, mass loss was highest in the ambient watering regime, while reduced watering frequency only lowered mass loss under ambient watering volume, and similarly, reduced watering volume only decreased mass loss under ambient watering frequency. Thus, average mass loss under ambient conditions was 20.9% ± 3.9% (average ± standard deviation (SD)), and average mass loss when watering frequency and/or volume was reduced, was 14.5 ± 2.8%, i.e. a reduction of 31%. Additionally, litter mass loss was significantly higher in plots with OTCs than in plots without OTCs ($F(1) = 34.42$, $p = <0.001$; Figure 10b); 17.8% ± 4.2% (average ± standard deviation (SD)) compared to 14.5 ± 3.4%, an increase of 23%.

That watering volume and temperature is important for decomposition rates is consistent with previous findings. High soil moisture generally increases mass loss rates and is important for decomposer activity (Powers et al. 2009; Thakur et al. 2017), and temperature similarly has been found to

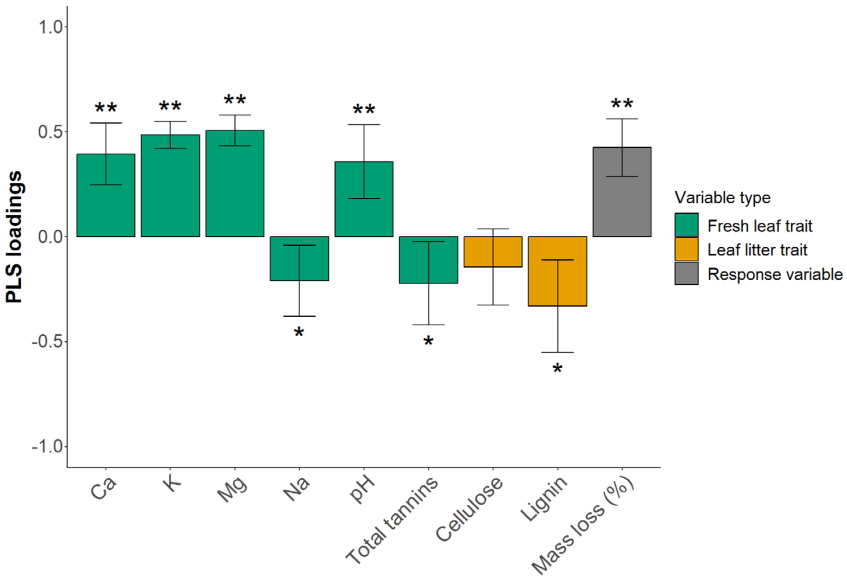


Figure 9. Loadings plot for a partial least squares (PLS) regression testing how plant functional traits correlate to decomposition of leaf litter from 21 tree species native to Borneo, exposed to a climate change experiment for 6.5 months. Green bars correspond to functional traits measured on fresh leaves, orange bars to traits measured on pre-decomposed leaf litter, and the dark grey bar average leaf litter mass lost (%) over the experiment period. Error bars represent 95% confidence intervals (CI). Variables were considered to improve the model's prediction of mass loss if confidence intervals did not overlap with zero. Variables highlighted with an asterisk are significant under 95% CI, while variables significant under a 99% CI (not shown) are signified with two asterisks.

increase soil microbial activity and decomposition rates in the tropics (Salinas et al. 2011; Nottingham et al. 2020). However, precipitation frequency is a very under-researched aspect of climate change, so this study contributes to the field by showing that it can be of similar importance for decomposition as that of lowered precipitation volumes. Additionally, the fact that no further reduction in mass loss occurred when watering frequency and volume was reduced simultaneously suggest that there are threshold values were severely altered precipitation conditions, i.e. under both reduced precipitation frequency and volume, are not likely to further decrease decomposition rates.

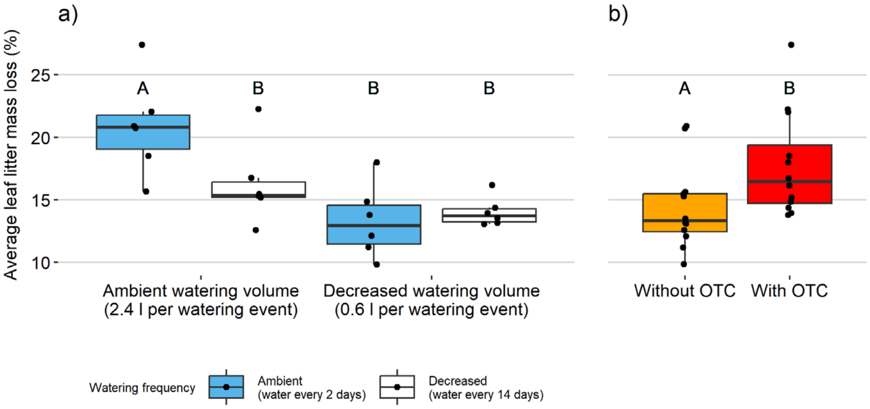


Figure 10. Boxplots showing leaf litter mass loss (%) over 6.5 months in litter from 21 native tree species during a climate change experiment conducted in Borneo, Malaysia. a) illustrates mass loss variation between watering treatments. b) shows mass loss variation for treatments corresponding to presence or absence of an open-top chamber (OTC).

Furthermore, my results also suggest that there is a trade-off between the effects higher temperatures and altered precipitation patterns have on decomposition. That is, they would alter decomposition rates in opposite directions, given that a future climate projection includes both a warmer climate, and reduced precipitation volume and frequency. Thus, depending on the severity of these temperature and precipitation changes, relative to each other and to current conditions, my results suggest that either reductions or increases in decompositions rates could occur under climate change.

Lastly, my results also suggest that leaf and litter trait-decomposition relationships are not altered by warming or changes in precipitation regime in this humid tropical system. Specifically, given the variable and interaction effects of climate treatments on decomposition (Figure 10), I ran six additional PLS regressions to test how functional traits predict mass loss under different climate treatments, with each model only using data from plots with one specific treatment combination (i.e. presence/absence of OTC, ambient volume with reduced or ambient watering frequency, and decreased volume with reduced or ambient watering frequency). All six models were very similar in their ability to predict mass loss (average $Q^2 = 64 \pm 6\%$, average ± SD). While there was some variation in the composition of traits correlated to litter mass loss between climate scenarios, the general trend was similar both between watering treatments, and the presence or absence of OTCs, and the results were similar to the PLS regression that used data from all climate treatments overall.

Hence, while both climate and changes in plant functional traits in response to climate change will be important for driving litter decomposition, my results suggest that these changes act independently of each other to influence litter decomposition. This is in contrast with findings from multiple studies. For example, acquisitive trait values in litter have in several studies been shown to drive decomposition rates only when soil moisture availability is ample (Liu et al. 2005; Yajun et al. 2016; Petraglia et al. 2018). Similarly, one study found that the relative effect of climate depended on litter traits, where soil temperature and moisture was most impactful on mass loss in less well defended and nutrient rich litter, compared to that of recalcitrant and nutrient-poor litter (Fanin et al. 2019). However, none of these studies are from the tropics and thus have different temperature and precipitation regimes, tree species, and decomposer communities compared to the tropical field site used in this study, which might result in different relationships between traits, decomposition, and climate conditions.

5. Conclusions

This thesis contributes to the field of tropical forest ecology and management by exploring how forests are used across the tropics and the different pathways forests can be degraded or restored. Additionally, it examines how plant functional traits affect some of the key services and processes needed to transition to a sustainable bio-economy, and how species selection in various management aspects of forested ecosystems in northern Borneo can be tailored accordingly.

The main result from Paper I is that the categorization of secondary and primary forests can be misleading due to its simplicity. Paper I underlines that it is important to acknowledge the multitude of pathways and actors that affect tropical forested ecosystems, since this emphasizes the dynamic nature of these systems.

The three remaining papers (II-IV) show that functional traits generally predict ecosystem provisioning of goods and services from native trees, although the results are sometimes difficult to interpret. Furthermore, applying these trait-to-ecosystem function relationships to species selection could also potentially improve a number of management approaches listed in Paper I, such as agroforestry or reforestation initiatives (Figure 1).

Paper II provided a novel approach to species selection by analyzing financial viability of tree species in restoration planting using plant functional traits. Overall, high financial potential was not correlated to acquisitive traits values like hypothesized, but to conservative ones. This highlights that the tradeoff between survival and growth rates, which varies greatly between species, is a key determinant of financial potential. This further demonstrates that selective harvesting of trees in restoration plantings for commercial gain could be a viable alternative to traditional land management options.

Paper III showed that species richness in beetle feeding guilds vary across tree species and plant functional traits. Generally, the majority of beetle diversity could be predicted by a few key tree physical traits, but predator and fungivore richness were related to separate suites of traits. The results demonstrate that some tree species support beetle diversity to a higher degree than others, but that complementary tree species diversity is necessary to support the bulk of the beetle community in tropical forests restoration efforts.

Lastly, Paper IV constituted a unique climate change experiment which provided two key findings. First, for decomposition, precipitation frequency is an important aspect of climate change, on par with changing precipitation volumes and temperature changes. Second, traits that that are important for leaf litter decomposition under ambient conditions, mainly nutrient content and chemical defense compounds, are likely to continue to be important under future climate conditions.

6. Final remarks and future perspectives

This thesis provides important insights into a multi-functional approach to tropical species selection in forest restoration projects. It incorporates a wide array of traits, functions, and services to examine how tropical native tree species can be used to fulfill a multitude of management goals in a bio-based economy. It emphasizes that trait-service correlations differed depending on the service considered. In Paper III, beetle diversity was mainly driven by physical traits, in Paper IV, decomposition was associated to nutrient content of the plant material, and in Paper II, a mix of nutrient, physical, and to some extent, allometric traits (in the survival-growth tradeoff) were related to financial potential. The literature discussion in Paper I highlights that at a landscape level, high variation also exists for management options for tropical forest, where a trait-based species selection can be used to promote specific management goals, e.g. associated community diversity in reforestation, and financial value in community forestry. Taken together, the thesis accentuates that no single trait, or particular suite of traits, constitutes a fix-all, and that forest managers will likely need to use multi-functional suites of tree species if they want to promote a balanced array of services.

Throughout papers II-IV I found several synergies and tradeoffs that might be worth consideration in different land-use options outlined in Paper I. Specifically, I can draw some conclusions from the trait relationships between the three studies. Trait values associated with high financial potential (low nutrient content and SLA, Paper II) were similar to those related to low associated beetle diversity (high SLA, Paper III) and slow decomposition (low nutrient content, Paper IV). Furthermore, given that there was a positive relationship between SLA and herbivore richness, and a negative one between IRR and SLA, species that achieved high IRR also exhibit trait values that were related to reduced herbivore richness. This implies that selection of species with high financial potential could equal reduced beetle diversity, suggesting that a tradeoff exists between associated biodiversity and financial potential. It could also mean that the high mortality rate of species with high SLA is at least partly due to a higher herbivore load. This provides an avenue for future research, which could evaluate if this is indeed a tradeoff, and if the presence of herbivores directly reduces survival rates for trees with high SLA values. Similarly, if species with low nutrient content are selected for their high financial value, it will likely have indirect effects on nutrient cycling and carbon sequestration by slowing down decomposition rates.

While the functional trait approach achieved its goals of providing broad ecological context to the species selection process, the results of the functional trait analyses proved varied, and at times, hard to interpret. This is most evident in Paper II, where plant growth rates and survival were correlated to plant traits in opposite ways and thus likely reduced the predictive power of the main traits-financial value model. Additionally, when using a broad library of traits like I have, it can occasionally be difficult to interpret the role each specific trait plays in the results, and why other traits that would be expected to be important are left out. Thus, in some cases, it could be beneficial to limit the number of traits that are included in order to simplify interpretation. Furthermore, it might be valuable to include ecological aspects other than traits in species selection. This could, for example, be a valid approach in follow-up studies to Paper II, where the survival-growth tradeoff might mean it is more viable to screen for financially promising species by testing survival and growth rates directly, for example via seedling performance trials, instead of using traits.

While I could not identify any single trait, or trait suite, associated with the supply of every service considered, I did find tree species that performed particularly well in both Paper II and III. Specifically, *Rubroshorea ovalis* and *Shorea leptoderma* (ranked 2 and 5 in the mid-scenario of Paper II, and 2 and 4 in overall average beetle diversity in Paper III, respectively). Such species, that provide a balanced source of multiple services, would be ideal starting-point options when selecting suites of native tree species.

Furthermore, intraspecific (genetic) trait variation is another aspect of trait composition not considered in this thesis, but which is of considerable importance for ecosystem functionality, in both current and future climates (Christmas et al. 2016; Axelsson et al. 2020; Westerband and Barton 2021, Axelsson et al. 2023; Grady and Axelsson 2023). Such variation could potentially also make native tree species competitive alternatives to exotic tree species in plantation forestry (Grady and Axelsson 2023).

Climate change, even though it was only addressed in Paper IV, is a key aspect of the future of tropical forests that could also affect other functions studied in this thesis (Figure 2). Altered climate conditions, like those introduced in Paper IV, are likely to have large implications for forest degradation and regeneration in the tropics (Malhi et al. 2014), on a landscape level (Paper I), for local tree growth and survival rates (Paper II), and for associated communities (Paper III). Therefore, species selection and management practices will have to be adjusted with climate change in mind. Additionally, furthering the understanding on how trait composition influences the ability of tree species to continue to supply services in future climate scenarios will be essential.

In addition to the future research questions already mentioned, a few other questions that have arisen from this thesis include:

- How much can profitability of enrichment planting be enhanced with improvements to management and plant material that increases growth and survival rates?
- To what extent are species in different feeding guilds specialist or generalists, and do the two categories differ in their responsiveness to trait variation? How does this, for example, vary between herbivores that use different feeding modes?
- To what extent are tropic cascades in complex communities dictated by plant traits?
- How do trait-beetle relationships change as trees age?
- How can the impact of precipitation frequency be validated through field trials?

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Popular science summary

Forests are a key source of sustainable fossil-free materials. Tropical forests are particularly important, due to their large land area and high growth potential. However, native tropical forests are under pressure from climate change, intensive logging, and expansion of industrial plantations. To mitigate these issues, efforts to restore tropical forests have grown more common. One important factor in such efforts is to understand the many ways forested ecosystems can be affected by management decisions, in terms of both forest loss and recovery. Another is to identify which tree species to promote for different purposes. For example, some trees might excel at growing fast and absorbing carbon, while others support more biodiversity. However, tropical forests contain thousands of tree species, making it difficult to research each one individually. A different approach is to measure some key traits, or characteristics, like leaf nutritional levels, for a smaller number of species and see how these relate to the services we hope they can provide. From these traits we can then potentially draw broader conclusions compared to if we looked only at the species themselves. For example, high leaf nutrient levels are generally related to fast growth. In this thesis I have explored the multitude of ways human interventions shape tropical forests, and how tree species native to northern Borneo, a hotspot for both biodiversity and forest loss, vary in their ability to provide key services based on their traits. Specifically, I have looked at their financial potential, ability to support beetle diversity, and litter decomposition rates (decomposition is important for soil carbon storage and nutrient cycling). My results show that while traits can often predict how well trees supply these services, no single combination of traits were able to provide all services, so we need to prioritize promoting tree species with varied characteristics if we want to promote sustainable tropical forests with multiple functions.

Photo: Ulrik Ilstedt

Populärvetenskaplig sammanfattning

Skogar är en viktig källa till förnybara, fossilfria, material. Tropiska skogar är speciellt viktiga eftersom de täcker stora arealer och har hög tillväxt. Tropiska naturskogar är dock utsatta. De påverkas av klimatförändringar, avverkas, och ersätts med industriella plantage. För att motverka detta så har restaurering av tropiska skogar blivit allt vanligare. För att dessa ska lyckas krävs förståelse för hur olika typer av förvaltning påverkar skogliga ekosystem, för både skador och återhämtning. Det är också viktigt att veta vilka trädarter man ska gynna för att uppnå olika mål. Till exempel kan vissa arter vara bra på att växa fort och absorbera koldioxid, medan andra är bättre på att främja biodiversitet. Detta är däremot svårare än vad det låter, då tropikerna är hem till tusentals olika trädarter. Ett alternativ är att istället mäta vissa nyckelegenskaper hos ett mindre antal trädarter, till exempel hur näringsrika löv de har, och se hur dessa är kopplade till de tjänster vi hoppas träden kan bidra med. Via dessa egenskaper kan man då dra bredare slutsatser än om man endast studerat trädarterna i sig. Till exempel så är näringsrika löv ofta kopplade till snabb tillväxt. I denna avhandling har jag undersökt hur val av skötselmetod formar tropiska skogslandskap, och hur egenskaper hos trädarter inhemska på norra Borneo, hem till några av världens artrikaste och mest utsatta skogar, är kopplade till värdefulla tjänster. Specifikt så har jag undersökt trädens ekonomiska potential, hur väl de främjar artrikedom bland skalbaggar, och hur deras löv varierar i nedbrytningshastighet (påverkar hur mycket kol som lagras i marken, och är en viktig del i skogens näringscykel). Mina resultat visar att egenskaper för det mesta kan förutspå hur väl träden bidrar med olika tjänster, men att ingen enskild kombination av egenskaper kan tillgodose alla behov. Därför behöver vi prioritera gynnandet av trädarter med varierade egenskaper, så vi uppnå hållbara skogar som tillhandahåller en mängd olika tjänster.

Photo: Ulrik Ilstedt

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What Is Secondary about Secondary Tropical Forest? Rethinking Forest Landscapes

Adam Pain[1] · **Kristina Marquardt**[1] · **Arvid Lindh**[2] · **Niles J. Hasselquist**[2]

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Abstract

Forests have long been locations of contestation between people and state bureaucracies, and among the knowledge frameworks of local users, foresters, ecologists, and conservationists. An essential framing of the debate has been between the categories of primary and secondary forest. In this introduction to a collection of papers that address the questions of what basis, in what sense, and for whom primary forest is 'primary' and secondary forest is 'secondary,' and whether these are useful distinctions, we outline this debate and propose a new conceptual model that departs from the simple binary of primary and secondary forests. Rather, we propose that attention should be given to the nature of the disturbance that may alter forest ecology, the forms of regeneration that follow, and the governance context within which this takes place.

Keywords Secondary forest · Forest landscapes · Disturbance · Regeneration · Public authority · Subsistence livelihoods

Introduction

There have been two long running but somewhat separate debates concerned with the 'rural' and its transitions that need to be better connected. The older of the two has been concerned with the role of small-scale family farms and their eventual fate. While models of agrarian transition have aspired to and predicted the demise of a peasant economy that has persisted into the twentieth-first century, such that most farms in the global south are small family-operated smallholdings (Wiggins 2006). The majority of these smallholders are poor (Boltvinik and Mann 2016) and are likely to remain so given the evidence of blocked agrarian transitions (Bernstein and Byres 2002). There has also been resistance to the inevitability of incorporation into the legal global commodity markets reflected both in the rise of peasant movements (Borras *et al.* 2008) and in the cultivation of narcotic crops (Pain and Hansen 2019:257). But there is a growing 'surplus' in the landless rural population in some countries with limited futures in either the agrarian or urban economy (Li 2014). While mainstream rural development narratives remain focused around opportunity, competition, entrepreneurship, and value chains (see IFAD 2016), much less visible are rural policies addressing the environment, climate change, and alternative approaches to secure subsistence economies and perhaps something more enduring for rural small-scale farmers.

The second debate has been centred on forests and their management. Historically forest policy has focused on production, conservation, catchment integrity, and revenue (a 'forestry without people' perspective). Over time forest policy has shifted and has given some recognition to rural users and allowed forms of co-management and benefit sharing (e.g., community forestry). Nevertheless, a deep hostility to what are seen to be agricultural land management practice with trees (e.g., swidden agriculture) in tropical forests has persisted. Consequently, the rise of the global environmental agenda has repositioned forestry in a conservation agenda and the need to preserve primary tropical forests for the global good. This in turn has brought notions of forest transition (Mather and Needle 1998) to the fore in policy thinking to justify and legitimate forest management practices including the re-emergence of fortress forestry, albeit married to the commodification of forests through programmes such as REDD+ (Leach and Scoones 2013).

Forestry as a knowledge system and practice in the global south has long been contested. It has its origins in the ways in which European colonisation created a regime of categories of land use that delineated agriculture from forests and defined

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✉ Adam Pain
adamnpain@gmail.com

[1] Department of Urban and Rural Development, Swedish University of Agricultural Science, 750 07 Uppsala, Sweden

[2] Department of Forest Ecology and Management, Swedish University of Agricultural Science, 90183 Umeå, Sweden

what constituted proper management of each. These categories fitted with the colonial imperatives of how things should be ordered, as Bhattacharya (2018) has shown in the case of the conquest of the Punjab in India. Here a priori concepts framed as specific land use types were mapped to a highly filtered vision of what could be seen on the ground even if these categories did not fit with what was actually there. It was only through the coercive power of the colonial state that a new rural landscape could be created. This colonial shaping of the rural world has left deep institutional legacies in terms of organisation and the knowledge frameworks that have structured the agricultural and forestry sectors.

These knowledge frameworks are increasingly challenged, both in agriculture (Sumberg and Thompson 2012) and in forestry. An early marker of the forest debates can be found in questions surrounding who decides what a forest is (Thompson and Warburton 1986). There is also a long history of scholarship questioning the belief in pristine forest landscapes, the notion of foresters as experts, and the limits and deficiencies of forest management practices (Sunseri 2009; Mathews 2011; Hansen and Lund 2017). Although forest policy can be seen as high-modernist and authoritarian (Scott 1998), there are strong grounds to challenge and rethink the ability of normative forestry models (Lund 2018) to address the complexity of the ecological and social life of forests (Hecht *et al.* 2014).

Underlying the long running contention between forestry practices and the populations that live in or near them and make use of their resources (Thompson 1975) are questions of land and the law and the nature of forests as territory and property. As Lund (2016:1199) has argued, the political authority of the state, the primary owner of forests (see Alden Wily this issue), has been constantly challenged 'through the process of successfully defining and enforcing rights to community membership and rights of access to important resources' as seen in the struggle over land rights. For many in the global south, while the state seeks to regulate access and exclusion from land with forests, the ideological power of markets and their framing of environmental services are becoming equally important sources of authority and legitimation (Hall *et al.* 2013). As Thompson (1975) suggests, it is around the rule of law that the future of forest and agrarian practices of the rural poor might be secured.

There are however increasing doubts as to whether the conservation of primary forest (or near-climax forests), if indeed such conservation is possible, will be sufficient to maintain the functioning of tropical forest landscapes (Chazdon 2014). In order to reach the necessary scale of vegetation cover, primary forest conservation will need to be combined with forest restoration efforts by the people who live there. This means that secondary vegetation may well become the main tropical forest cover in the future as primary forest will largely remain only on the steep, uncultivable, and inaccessible areas in the future. This requires a wider acceptance of diversity and complexity in forest forms or types (primary forest, patchy mosaic of secondary forests, and forests in agriculture) and management systems to support this, particularly of secondary growth that re-generates forest. It also brings into question the very meanings of 'primary' and 'secondary' forest as separate categories, and identifies issues of complex temporal or age interactions in forest ecology and the interaction of these with human activities.

It is widely known that large-scale deforestation of tropical forests is strongly associated with agro-capital and the expansionist tendencies of industrialised agriculture (Borras *et al.* 2016). However, there is also increasing evidence suggesting that secondary forest regeneration through smallholder action is contributing to forest recovery. Hecht (2014) describes a re-wooding of some parts of the Amazonian landscape leading to a recovery of forest area and points out that this in turn brings into question whether the agrarian can be so clearly demarcated from the forested. This emphasizes the need to broaden the lens of our understanding of agrarian change. The spread of trees into the agrarian landscape in the mid-hills of Nepal has also been observed (Marquardt *et al.* 2016). Forest regrowth can occur in many ways and there is therefore no reason to think that the variation in these forms of regrowth are any less socially or ecologically complex or independent of land use policies than are other agricultural and forestry land use practices.

Despite secondary successions being a central feature in many tropical landscapes, it is almost invisible in research as well as a low priority in policy agendas on global climate, forestry, and agriculture. Secondary forests are primarily viewed as the by-product of deforestation rather than intrinsic to forest ecology. Additionally, secondary forests are commonly thought of as being degraded, which makes it easier to justify their transformation of these forest into large-scale agriculture as opposed to opportunities to improve the livelihoods of rural people and the important role they play in the ecology of tropical forests. We believe this one-sided perception of secondary forests is problematic and is largely driven by specific expert knowledge systems in forestry, top down management, ideologies of poor farming practices and the perception of smallholders as the major drivers of deforestation. The deforestation and reforestation debates rarely consider smallholders' practices to be based on credible knowledge systems or engage with the messy empirical reality of development where forest change outcomes reflect other complex dynamics with their own logic. As Hecht *et al.* (2014) suggested, it is often policy changes outside the forest that have the greatest effects on forest dynamics.

Yet there is a demonstrated potential in smallholders' forest land use systems to support forest landscapes, provide livelihood security, and expand the forest area (see Alden Wily this issue). Such systems, given the constraints of family labour supply, lack the expansionist tendencies of large-scale market driven land uses. Moreover these practices vary temporally and spatially based on deep contextual knowledge of the forest, which in turn offers the possibility to secure the livelihoods of rural populations and promote forest regeneration (Pokorny 2013).

A workshop was convened in Uppsala in December 2018 to speak across disciplinary interests to these issues and explore the idea of how forest regeneration is both intrinsic to tropical forest ecology as well as an essential smallholder land use category and agricultural practice, and examine the conditions under which both might be supported. We wanted to review what we know about smallholders' active forest regeneration management practices and investments in the landscape by drawing on and developing the notion of landesque capital (Blaikie and Brookfield 1987; Håkansson and Widgren 2014; Börjeson and Ango this issue). This requires a rethinking of what forests are and the role of smallholders in contributing to re-foresting landscapes through critical engagement with concepts of forest transition and different forms of land control. A set of questions guided the selection of papers that were presented at the workshop that this current collection is drawn from.

- What do we mean by 'secondary forest" and how do we manage complex mosaic forest landscapes?
- What do we know about the extent of secondary forest regeneration and to what extent is it complementing and providing additional benefits (ecosystem services) to primary forest conservation?
- What has been the contribution of smallholder practices to secondary forest regeneration and what benefits do they derive from it?
- What are the legal obstacles to smallholder engagement in secondary forests and their regeneration?
- What might be a future research agenda in relation to supporting secondary forest regeneration and supporting the livelihoods of smallholder?

This introductory essay addresses the first of these questions, introduces the papers, and concludes with a discussion of the implications of the debate for future research on secondary forests.

Going beyond the Primary Vs Secondary Dichotomy

The Food and Agriculture Organization of the United Nations (FAO) defines secondary forests as "forests regenerating, largely through natural processes, after a significant disturbance of the original forests and displaying major differences in forest structure and/or species composition compared to pristine primary forests" (FAO 2003). Roughly two thirds of the global forested area are classified as secondary forests (FAO 2010; Mackey *et al.* 2015). In the tropics, secondary forests cover ca. 70% of the entire forested area (FAO 2010) and are thus considerably more common than primary forests. Despite the growing awareness of the extent and importance of secondary forests, these assessments provide little to no information about the causation, human interactions, contribution, and governance of secondary forests. Instead, secondary forests are often all lumped together with the only unifying characteristic being that they are different from pristine, primary forests. This simple dichotomy between primary and secondary forest fails to consider the numerous and diverse natural and anthropogenic drivers influencing and shaping forested ecosystems (Fig. 1).

A consequence of this simple binary between pristine, primary forests and "less" pristine secondary forests is that secondary forests are often thought to be impaired, degraded, flawed, or defective compared to pristine forests, making it easier to justify further transforming them, for example, into plantations. It is well documented that land use changes such as deforestation or agricultural expansion can have a strong negative effect on biodiversity (Sala *et al.* 2000) with species abundance and biodiversity often reduced in secondary compared to primary forests (Mackey *et al.* 2015). However, other studies have shown few differences in total species richness between primary and secondary forests (Lawton *et al.* 1998; Barlow *et al.* 2007; Berry *et al.* 2010; Hector *et al.* 2011). Despite small changes in total species richness, these studies have shown that secondary forests are often characterized by a different range of species compared to primary forests (see Mertz *et al.* this issue). Thus, rather than being viewed as impaired, flawed, or defective in some way, secondary forests are simply a different type of forest with a different suite of species (the issue of what secondary forest should be compared to is addressed by Mertz *et al.* this issue). Nevertheless, it is also important to point out that primary forests provide specific habitat types and characteristics that are not present in secondary forests. Many species are dependent on these unique properties, and thus cannot persist without primary forests (Barlow *et al.* 2007; Gibson *et al.* 2011).

In some respects secondary forests could be viewed as having greater potential than primary forests. For example, it has been shown that secondary forests sequester atmospheric CO_2 ten times greater than primary forests (Poorter *et al.* 2016). Chazdon *et al.* (2016a) estimated that secondary forests in Latin American can sequester 8.5 Pg C in above ground biomass during 40 years, which is equivalent to carbon emissions from fossil fuel use and industrial processes in all of Latin America and the Caribbean from 1993 to 2014. Additionally, Bastin *et al.* (2019) recently mapped the global potential for tree cover and showed that there is room for an extra 0.9 billion hectares of forest cover, which in turn could

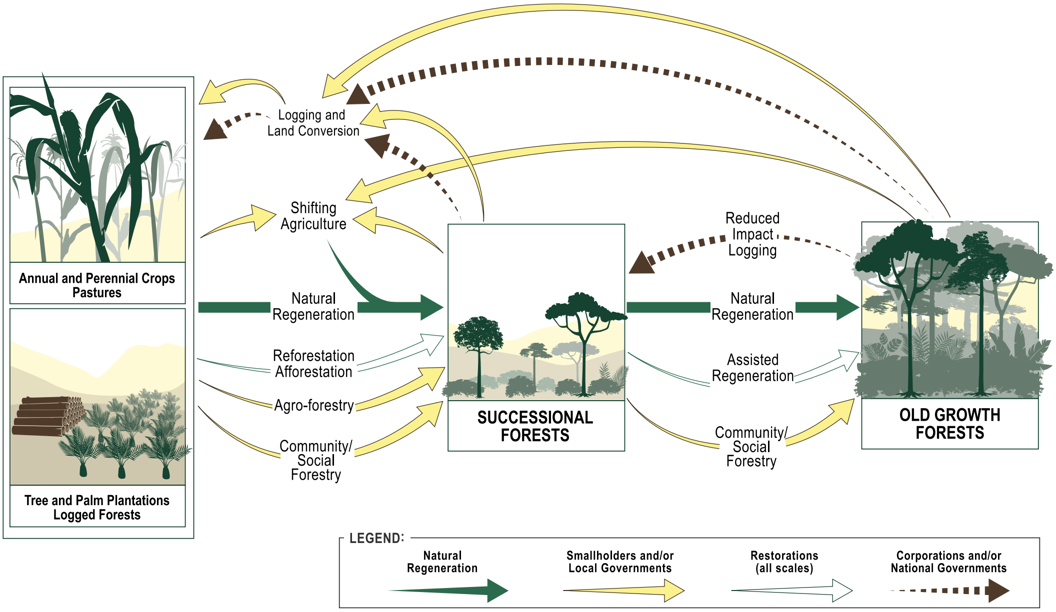

Fig 1 Conceptual model showing how different types of anthropogenic disturbances, management practices and successional changes influence tropical forested landscapes. For each arrow the colours indicate the main actors or processes responsible

sequester 205 gigatonnes of carbon. Thus, secondary forests and global tree restoration efforts (e.g., Bonn Challenge and the New York Declaration on Forest) represent a large and important potential carbon sink for atmospheric CO_2. Thus, the common assumption that secondary forests are impaired, degraded, or defective compared to primary forests appears not to be correct as secondary forests have the potential to play a critical role in climate mitigation.

It is commonly agreed that secondary forests are regenerating from a significant disturbance, yet what constitutes a significant disturbance, especially in terms of the intensity of the disturbance, is debatable. In many ecological textbooks, primary forests are often described as a climax community that is “stable” and thus experiences little to no disturbances (Cain *et al.* 2014; Mackenzie *et al.* 1998). However, this traditional perception of primary forests is being questioned. It is now recognized that disturbances, many of which are anthropogenic, are a core feature of forest ecosystem dynamics (e.g., ‘patch dynamics’ and the ‘non-equilibrium’ view) and thus the distinction between climax (i.e., primary) forests and secondary forests is not as obvious as originally thought (Chokkalingam and De Jong 2001). As Börjeson and Ango (this issue) point out, human disturbance can also be an investment of labour to maintain or enhance productivity and thus the antithesis of degradation. Whittaker and Levin (1977) argue that the vegetation on the Earth’s surface is in constant flux and what we observe is not simply successions and climax communities, but instead a mosaic of plant communities existing in different kinds and degrees of stability and instability. This has led to a growing consensus that the classical definition of primary forests as those that do not experience disturbances and therefore represent a stable climax community may be misleading. Instead, disturbances, especially anthropogenic disturbances, play an important role in both primary and secondary forest dynamics, raising the broader question of causes and consequences of human intervention in forested ecosystems.

In order to go beyond the simple dichotomy of primary vs. secondary forest, it is necessary to identify and understand the main drivers of forest loss leading to secondary forests and the implications of these for forest ecosystems (Chokkalingam and De Jong 2001). It should be remembered that the main drivers of forest loss can be anthropogenic as well as natural disturbances although there are methodological and data challenges in attributing forest loss to specific causes. In temperate and boreal forests Curtis *et al.* (2018) assess the main cause of forest loss to be from natural wildfires and forest management practices. In contrast, in addition to wildfires they consider the biggest threat to tropical forests to be human intervention through commodity-driven deforestation, row crop agriculture, and cattle grazing in South America, oil palm plantations in Southeast Asia, and shifting and subsistence agriculture by indigenous people in Africa (ibid.). It is important to recognize and understand the numerous drivers leading to secondary forests as they highlight the range of different ways in which humans interact with forests. These in turn are strongly coupled to people's livelihoods, financial incentives, and the tenure regimes in which forests are embedded.

Central to understanding forest dynamics is the question of who has control over forest land and how that control is exercised, crucially, how territory is defined and by whom, who regulates the use of that territory, and the property or ownership rules that are imposed (individual, community, state). As Alden Wily (this issue) makes clear, the assumption that the state is the best defender of forests is under critical attack and she proposes a different vision for the future of tropical forests in which the emerging trend of community-owned forest land provides both use values and protection. In the global south, local forest user groups' views on what constitutes territory and who has authority over territory have often been at variance with forest department or state views, leading to a long history of contestation (as in Nepal and Peru, see Pain *et al.* 2020). Moreover, where the state has less regulatory authority for reasons of weakness and/or collusion with powerful national or regional forest companies or agribusinesses and where forest boundaries are not clearly defined, deforestation may be aggressive and destructive.

There is also a need to recognise the drivers outside forests linked to agrarian transitions that have impacts on forest cover and use. There are diverse routes to forest transition (the determination of the forest boundary and forest recovery) and their relation to agrarian transitions are likely have a strong influence on tropical forest landscapes. Intensification and market engagement can result in greater deforestation. Securing household subsistence can also follow a tree management intensification route, as has been observed in Nepal (Pain *et al.* 2020), but equally plantation agriculture can lead to forest substitution. Lastly, global policies in relation to forest conservation can impact tree management practices both within and outside forests (ibid.). These diverse processes can all be operating at the same time leading to contradictory impacts and sometimes perverse outcomes.

In summary, when characterizing secondary forests, it is essential to account for the regulatory framework surrounding secondary forest, the security of property rights, and the diverse drivers of agrarian and forest change.

Rethinking the Forest Landscape

The Schema

Given inconsistencies in definitions as well as increasing human pressure on forest ecosystems we do not see any value in continuing to characterize forests simply as either primary or secondary. We argue that there is a need to rethink how forested landscapes are characterized and propose a new conceptual model to do this.

Figure 1 presents our schema, an approach that takes a more discriminating approach than a simple primary-secondary binary classification of forests. It directs attention to how governments on different scales, corporations, and smallholders influence the forested landscape through different types of anthropogenic disturbances and management practices. Reading from left to right the figure represents successional changes after a disturbance, with logged forests or deforested landscapes on the left and old-growth, more mature forests on the right. The various line colours highlight the main actors or processes active in the landscapes and each arrow is tied to a certain kind of anthropogenic disturbance or management practice observed in tropical forests. Restoration can be done on all scales and by all actors, and natural regeneration occurs automatically when no actors are present. This aids more analytical thinking about the diversity of secondary forest formations and their implications for future forests.

Disturbances

In our conceptual model, we acknowledge the importance of both natural and anthropogenic disturbances in forested landscapes but mainly focus on the importance of anthropogenic disturbance. As is the case with natural disturbances, anthropogenic disturbances vary in their causation and severity, ranging from small, local disturbances to larger scale deforestation and land degradation that can occur across a range of temporal scales. We must also remember that such disturbances by design can contribute to long-term land productivity enhancement (see Börjeson and Ango this issue). We further suggest that there is a correlation between land-tenure and financial incentives and the severity of the disturbance. For example, many indigenous people, who often lack land-tenure, practice shifting and subsistence agriculture to sustain their livelihoods. Although these practices represent a disturbance to forest landscapes, these disturbances are often for subsistence living, occur at small spatial scales, and do not necessarily cause large-scale degradation. However, if the frequency of these small-scale disturbances is high, forests may not be able to recover, resulting in cumulative and potentially large and negative effects on forest landscapes. In contrast, government agencies and/or large private companies, which often own large amounts of land, tend to manage the land in a way to maximize their financial gains. In doing so, forested landscapes are often drastically altered at large spatial scales, as can be seen in the conversion of tropical forest to tree plantations. Not surprisingly, financial incentives and the nature of land-tenure regimes (see Alden Wily this issue) are the main drivers shaping tropical forested landscapes.

Regeneration

It is commonly assumed that, if secondary forests are undisturbed by recurrent disturbances, with enough time they will revert to pristine, primary forests (Brown and Lugo 1990; Corlett 1994). But this assumption ignores the investment of human labor to support regeneration processes (see Börjeson and Ango this issue), which is often the case when the disturbance is relatively small scale (see Pain *et al.* 2020). This human intervention can serve to selectively enrich natural secondary forest (see Peru, ibid.) or lead to significant change in forest species composition (see Nepal, ibid., and the coffee plantations in Ethiopia, Börjeson and Ango this issue). Large-scale disturbance may also result in an entirely different floristic composition, as is the case of the secondary babassu forests in Maranhão, Brazil (Porro and Porro 2014).

In many places, forest restoration may be needed to recreate the original structure and biodiversity associated with primary forests (Chazdon 2008). The possibility of restoration greatly depends on the initial state of the forest and the intensity of disturbance and degradation and can be extremely timely and costly. Moreover, there has recently been a growing number of afforestation initiatives (e.g., Bonn Challenge, Regreening Africa, and the New York Declaration on Forest) with the goal of curbing land degradation and assisting in climate mitigation. Consequently, human intervention is now playing a critical role in the recovery of forested landscapes, although differences in law and governance practices are likely to strongly influence outcomes.

Public Authority and Secondary Forests

The control over forest land is ultimately what determines how forests are managed (the management regime) and by whom. Central to land control is how territory is defined (Hall 2013), who regulates the use of that territory and the property or ownership rules that regulate land use. Territory is land that is considered as belonging to a particular person, people or country. In the global south there is rarely one single source of authority over the regulatory control of forest land and consequently forest territory is often contested. In such cases, there is a need to better understand the processes of mobilisation of territorial control and authority over its use (see Arora-Jonsson *et al.* this issue).

In many contexts governments have limited control over its territory and authority and legitimacy are often questioned (see Peru, Pain *et al.* 2020). This creates a disjuncture between a state's 'de jure' sovereignty – which establishes the state's boundaries and the state's authority to control society within these borders through international law – and its 'empirical' sovereignty, which is its ability to actually impose its authority over territory (Lund 2011). In many tropical countries there is often 'fragmented' sovereignty and attempts to establish territorial control, not least over the forests and people, are not simply the result of extending formal government structures. Rather, the extent and degree of control are shaped by forms of competition and coalition between a wide range of formal and non-formal actors, including government departments, private companies, non-government organisations, distinct social groups, and possibly, armed groups.

A central question then with respect to secondary forest landscapes is how public authority is established and contested and how this is reflected in the ways that the forest economies are managed and regulated. Analysing the nature of public authority can further understanding of the composite and partial forms of governance, the spatial control and territorialisation of the forests, and the nature of secondary forest formation and regeneration. Thus, shifting agriculture is more likely to take place at a small scale where government authority is limited. Conversely, large-scale timber plantations may reflect stronger government presence while large-scale commercial crop plantations that result from forest clearance may reflect private companies' influence over government authority.

Central to the issue of public authority and its exercise are those of rights (Lund 2016). The key struggles are those over the ability of forest-based populations to secure property rights (see Alden Wily this issue) and the inability of states to guarantee property rights, either collectively or individually, reflecting their lack of authority and legitimacy. As Lund (2016:1) notes: 'rights do not simply flow from authority but also constitute it. Authority and rights are conceptually tied together by recognition.'

Review of Papers in Collection

The five papers that follow this introduction develop and elaborate on specific aspects of our schema. Pain *et al.*, through an analytical contrast of the role and contribution of secondary forest in the Nepalese mid-hills and Peruvian Amazon, provide an empirical foundation to the schema and to the papers that follow. They draw attention to the diverse forms of secondary forest in the two countries, the conditions under which they arose and the interplay between forest dynamics, governance regimes, and wider agrarian processes. While Nepal is primarily an account of the significance of secondary forest and the role of community forestry, since most primary forest is long gone, the Peruvian Amazon clearly illustrates diverse forms of secondary forests, how they are created, and the consequences of a forestry agenda that favours primary forest and conservation over secondary forest formations.

Börjeson and Ango build on Pain *et al.*, speaking to the contribution of smallholders to secondary forest regeneration, and show the investment of human labour needs to be taken into account during the creation of secondary forest landscapes. Conceptually they draw on the notion of landesque capital (Blaikie and Brookfield 1987), and specifically "green" landesque capital to emphasize the co-work of nature and labour in the regeneration of tropical forests. They illustrate Landesque capital, conceptualised as an investment of site specific resources and labour for future production, and the relative contribution of human labour and nature through a case study of different forest mosaic landscapes in South-Western Ethiopia where coffee is an important cash crop.

Arora-Jonsson *et al.* move beyond the dominant narrative of forests being about trees and unpack the social life of forests to explore, in particular, issues of gender and violence in forests. Forests have long been framed as sites of men's work and values neglecting both the work in kind and directly that women do in forest management. Violence is an element of daily life in the Peruvian forest (see Pain *et al.*) and, like forest change processes, can only be understood by reference to wider agrarian processes of change. Site specific violence within the forest and forest families has to be understood as being shaped by wider frames of violence, both in terms of the structure of power, as in the denial of indigenous rights accorded by law in the case of Peru, and deep seated norms of masculinity.

As was noted by Pain *et al.*, the official forestry discourse in Peru is that the swidden agriculture practiced by rural people in the Amazon is the main cause of forest degradation and loss. But, returning us to the first two research questions that connect these papers, Mertz *et al.* review ecosystem services (ES) from secondary forests in shifting cultivation. They find that the body of evidence that robustly compared ES provision from secondary forest with comparable land uses is surprisingly thin and limited. Moreover, much of the evidence they review is equivocal, based on contrasts of a very restricted number of ES. They also raise issues of how comparable ES are between secondary and primary forests. A more inclusive perspective on ES, including food provisioning and cultural ecosystem services would probably place secondary forest in a more favourable light.

Finally, Alden Wily addresses the central issue of the legal framework and territorial rights accorded to forest users. She makes a strong case, in many ways backed by current trends in giving communities tenure rights over their forests, that giving communities secure property rights through forms of collective tenure is necessary to secure forest futures. Neither state ownership nor commercial capital have shown themselves to be interested or competent guardians of the forests and there is increasing recognition community based governance has more to offer.

Towards a Future Research Agenda

Most research on "secondary forests" has been from an ecological perspective, focussing primarily on a restricted range of environmental services, notably biodiversity and carbon sequestration. However, our new conceptual model highlights the importance of human intervention in shaping tropical forest landscapes, and thus we believe a key question that needs to be further addressed is how different types of human intervention and the various scales at which they act influence forested ecosystems. It is also crucial to better understand how these altered forested landscapes affect humans and societies (e.g., health, gender equality, migration). Despite previous studies comparing biodiversity and carbon sequestration between primary and secondary forests, we know less about how ES services vary among different types of secondary forests, not only with respect to biodiversity and carbon sequestration, but also other less studied ES. One forest ES service that may be particularly important and linked to biodiversity, as the current Covid 19 pandemic illustrates in terms of the rising risks of pandemics (Tolleson 2020), is effects (or disservices) on human health and how that varies among different forested ecosystems. A further dimension to this might be the risk of human diseases (e.g., malaria) among different forest landscapes. A better understanding of how ES vary among forested landscapes is essential as many rural people in the tropics rely on forests for their livelihoods. This would also move the relations on ecosystem services and forests into more of a landscape perspective that contains diverse land uses rather than confining it to forest ecosystems alone (Chazdon *et al.* 2016b).

But central to a future research agenda is learning more about what drives the shaping of authority and rights in forest and land practices (policies, programmes, land tenure arrangements) and the management of disturbance in forests. More needs to be known of the links between disturbance regimes and the consequences of these at different scales for the various types of successional forests as well as the people who use them for their livelihoods. Given the diverse and gender-based interests of different categories of smallholders, groups, and other interested parties, more understanding is needed as to how they perceive and interpret policies regarding land use, land ownership, and preservation of forests areas: what their forms of resistance and tactics of engagement with the state are, particularly with regard to territorial rights and how do they differ among different successional forests. This will have consequences in terms of how people interact with forests and how they influence the form and complexities of forest landscapes, particularly where successional and managed forests replace previous old growth rainforests. In turn, all the above processes will not only strongly influence the regeneration of tropical forests but will have consequences in shaping the wellbeing of individuals relying on tropical forests for the livelihoods.

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Compliance with Ethical Standards

Conflict of Interest The authors declare they have no conflict of interest.

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II

New Forests
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Functional traits to predict financial value of enrichment planting in degraded tropical forests

Arvid Lindh[1] · Maja K. Sundqvist[1] · E. Petter Axelsson[2] · Niles J. Hasselquist[1] · Francisco X. Aguilar[3] · David Alloysius[4] · Ulrik Ilstedt[1]

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Abstract

Demand for tropical timber is expected to rise due to an increased global need for sustainable renewable materials. However, sustainable tropical timber production remains a challenge for the global wood product supply chain, especially for high-value tropical hardwoods. Restoration of degraded lands through enrichment planting of native hardwood species could provide a solution, but the financial viability of using native tropical tree species remains largely unknown. We evaluated the financial viability of 22 hardwood tree species native to northern Borneo in enrichment plantings of a degraded forest in Sabah, Malaysia. We investigated how the species' financial value, expressed as an internal rate of return (IRR) based on land expectation value, varied with their functional trait composition. We found that high financial value was positively correlated with trait values associated with a conservative growth strategy, i.e., financial value was negatively correlated with leaf calcium, magnesium, and nitrogen content, as well as with leaf pH and specific leaf area. Trees with these traits showed a high IRR, partly explained by relatively fast growth and high survival rates. For the most economically promising species, *Shorea macrophylla*, we estimated that enrichment planting for forest restoration could reach IRRs up to 7.8%. Our results showed that enrichment planting for high-value hardwood production in degraded forests can be financially viable, with variation among species, and that various traits associated with a more conservative growth strategy were linked to high financial value.

Keywords Tropical forests · Borneo · Functional traits · Forest restoration · Financial value

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Niles J. Hasselquist is Deceased.

✉ Arvid Lindh
Arvid.Lindh@slu.se

[1] Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden

[2] Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden

[3] Department of Forest Economics, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden

[4] Conservation and Environmental Management Division, Yayasan Sabah Group, Kota Kinabalu, P.O. Box 11623, 88817 Sabah, Malaysia

Introduction

There is a pressing need to develop environmentally and ecologically sustainable economic systems based on renewable energy and materials, as well as for restoration of degraded systems to halt species extinctions. Forests are a primary source of renewable carbon (C)-based materials needed to support the emerging bio-based economy that is decoupled from fossil fuels (WWF 2012b; European Commission. Directorate-General for Research Innovation 2018). Therefore, annual global wood removals from forests will likely need to increase three-fold by 2050 compared to 2010, to meet the future demand for solid wood, paper, and bioenergy products (WWF 2012a). Global wood production is currently dominated by countries in boreal and temperate zones (FAO 2018), but much of the increase in future demand will need to be met by tropical forests (FSC 2012) because of their vast land area (FAO 2020) and high production potential (Running et al. 2004). Southeast Asian forests will be subject to particularly high demand because of their proximity to the world's largest consumer of wood products, China, and other growing markets like India (Ajani 2011; Malhi et al. 2014).

Historic ineffectiveness of natural regeneration of tropical forests by regrowth after logging (Chua et al. 2013; Yamada et al. 2016; Butarbutar et al. 2019) has switched focus from natural forest management towards tree plantations. Management practices in these plantations are intended to maximize production of renewable bio-based materials by nutrient optimization (achieved by fertilization) and by selectively planting often non-native fast-growing species (Putz et al. 2000; Sist et al. 2003; Curran et al. 2004; Hansen et al. 2008). Tree plantations in Southeast Asia are dominated by exotic *Acacia* and *Eucalyptus* species that are intensively managed and optimized for fast growth (Fah et al. 2008; Hardiyanto and Nambiar 2014; Harwood and Nambiar 2014a, b). Compared to natural forests, exotic tree plantations can have negative effects on local biodiversity (Barlow et al. 2007) and soil C stocks (Guillaume et al. 2018). Some could turn into invasive species, thereby leading to negative effects on biodiversity within, as well as outside plantations (Osunkoya et al. 2005). Furthermore, many second and third generation *Acacia mangium* plantations in Malaysia and Indonesia are suffering from severe pathogen attacks, resulting in heavily reduced outputs (Harwood and Nambiar 2014a; Nasution et al. 2019) and highligting a great need to diversify the portfolio of plantation species.

An alternative to exotic plantations is to use native tree species. Their adoption can reduce trade-offs and achieve synergies between raw material production and supply of ecosystem services within a bio-based economy (Piotto et al. 2004; Lamb et al. 2005; Subiakto et al. 2016; Crous et al. 2017; Bieng et al. 2021). Although it is often assumed that native tree species tend to be slower growing than many exotic tree species (Piotto et al. 2004; Lamb et al. 2005), native tree species may provide raw materials that are more valuable. As native species also share an evolutionary history with native ecosystems, they may be better adapted to pests and pathogens, and have a higher value for promoting native flora and fauna (Lamb 1998; Lamb et al. 2005; Crous et al. 2017), all while maintaining relatively high growth rates (Davis et al. 2012; Subiakto et al. 2016). Hence, it has been proposed that wider use of native trees for timber production could sustainably meet the growing demand for raw materials while ameliorating negative effects on other ecosystem services resulting from planting exotic species (Lamb et al. 2005; Davis et al. 2012). However, more research is needed to identify suitable native species for this purpose and to further determine whether they are financially viable alternatives (Lamb et al. 2005; Bieng et al. 2021).

Developing native tree species as economically viable options could also enable forest landscape restoration approaches that provide conservation benefits while simultaneously supporting social and economic objectives in accordance with the twin objectives of the Bonn challenge. Native species could be used over a gradient of land-use types ranging from intensively managed commercial plantations to enrichment plantings for restoration. However, there is little documented knowledge on growth potential and form, wood characteristics, correct management (Haggar et al. 1998; Piotto et al. 2004; Lamb et al. 2005), and genetic potential of native species (Thomas et al. 2014; Axelsson et al. 2020). Therefore, if native tree species are to be widely used for timber production, it is necessary to first identify which species are most suitable (Lamb et al. 2005). This is a challenging task given that the Indo-Pacific region, including Southeast Asia, has been estimated to contain between 19,000 and 25,000 tree species (Slik et al. 2015), each with unique adaptations that are not well known. Understanding of tree species' adaptations to different environments can be derived from their traits, which could allow predicting function of a broad set of species from their composition of "functional traits".

Plant functional traits are morphological, physiological, and phenological qualities that affect the organism's growth, reproduction, and survival, thereby determining performance across variations in environmental conditions (Violle et al. 2007). For trees, commonly measured traits include specific leaf area, wood density, and leaf nitrogen content (Perez-Harguindeguy et al. 2016), all of which correspond to plant functions important for fitness.

Plant functional traits can be used to describe a tree species' characteristics, ecosystem niche, and location in the "plant economics spectrum", the latter which spans from traits associated with acquisitive to conservative growth strategies and incorporates a trade-off between the two (Violle et al. 2007; Reich 2014; Funk et al. 2017). Acquisitive traits include a high specific leaf area, pH, and high contents of nitrogen, phosphorus, and cations (Cornelissen et al. 2006; Patiño et al. 2012; Reich 2014; Perez-Harguindeguy et al. 2016). For example, specific leaf area is a proxy for resource investment per leaf area, whereby a high specific leaf area is associated with a high rate of resource capture and growth at the expense of leaf defense (Kurokawa and Nakashizuka 2008; Reich 2014).

A tradeoff between plant investments in defense versus growth can occur across different ecosystems, driven by gradients of resource availability (Endara and Coley 2011). Species adapted to low resource environments might thus invest relatively more resources in chemical and structural defense, such as high phenolic content, than in growth, compared to species in more resource rich environments (Jones and Hartley 1999; Endara and Coley 2011). Additionally, many species who invest in high growth rates early also have higher early life mortality (Sterck et al. 2006; Philipson et al. 2014; Gustafsson et al. 2016).

The allometry of the tree, here defined in terms of the relationships between stem diameter, tree height, and crown size, are life-history traits that also affect plant performance. Allometry can be strongly associated with a species' resource capture strategy and early growth rates. Young trees with wide, flat crowns and thick stems that can support this crown shape may effectively capture light entering vertically through the canopy, and often have higher growth rates than trees with thinner crowns and more leaf layers (Sterck et al. 2001).

Functional traits are widely used in ecology to predict diverse ecological functions, including growth and survival (Wright 2010; Wills et al. 2018), drought tolerance (Harrison and LaForgia 2019), and interactions with associated communities (Kraft et al. 2008; Wright 2010; Wills et al. 2018; Harrison and LaForgia 2019; Axelsson et al. 2022). However, despite showing a strong correlation to productivity parameters such as growth and survival, functional traits have rarely been combined with estimates of financial value, especially for tropically indigenous tree species. Yet, there are many possible relationships and tradeoffs between financial value and traits, for example, variables capturing growth are consistently associated with financial performance. For instance, Lopez et al. (2010) found that mean annual increment explained most of the variation in financial performance of pine plantations in Colombia. Similarly, survival rates directly affect financial value by determining the quantity of resources needed for planting, re-planting, and other managerial adaptions to avoid high mortality of the planted material. Additionally, defensive compounds, such as phenolics, along with structural traits, such as wood density, are related to timber properties like resistance to decay, mechanical strength, and general durability, which in turn could contribute to define the market price of timber per unit volume (Chave et al. 2009; Kulbat 2016).

While reports on financial performance exist (for example Cubbage et al. 2007; Cuong et al. 2020), few comparisons between plant traits and financial relationships across species are available. Such an approach could potentially be used to identify suites of native tree traits that provide favorable balances between timber production and other ecosystem functions and services in species-rich tropical forests. In this study, we evaluated functional traits, estimated financial values, and calculated their associations for different species under similar ecological conditions.

We used a unique field trial with a range of native tree species in the Malaysian state of Sabah, northern Borneo (Gustafsson et al. 2016)—a global biodiversity hotspot with around 3000 native tree species (MacKinnon 1996; Myers et al. 2000). In this common garden, we measured 18 functional traits of 22 native tree species, examining the functional diversity within the group. We assessed the financial viability of each tree species in enrichment planting in a secondary forest by estimating their land expectation value, which was used to derive an internal rate of return under restoration treatment in the field trial site. Additionally, we conducted a sensitivity analysis to assess the robustness of these estimates, and to determine whether native tree species can be financially viable under different scenarios of restoration management.

We hypothesized that the financial value of trees could be predicted from a suite of functional traits. Specifically, we hypothesized that trees expressing high-value traits on the acquisitive side of the plant economics spectrum would have high financial value due to their higher growth rates. According to this hypothesis, high financial value was expected to be associated with a high specific leaf area and pH, high contents of nitrogen, phosphorus, and cations, and low wood density, leaf dry matter content, phenolic content, and leaf thickness (Cornelissen et al. 2006; Patiño et al. 2012; Reich 2014; Perez-Harguindeguy et al. 2016). High growth rates of species with these traits were expected to outweigh the potentially greater market value of timber from slow-growing conservative species with denser and more durable wood. Furthermore, with respect to tree allometry, we hypothesized that tree species that maximize capture of sunlight penetrating the canopy vertically would have the highest growth rates (Sterck et al. 2001). Such trees have crowns that are broad relative to the crown height (meaning a low relative crown length), but are also thin and short relative to the tree's total height, meaning that they have a low relative crown width and relative crown depth (Sterck et al. 2001). In addition, since the crown is small and concentrated at the top of the tree, they have stems that are thin relative to the tree height (i.e., high stem slenderness). We tested these hypotheses and used the results obtained to analyze relationships between plant traits associated with financial value in the studied native tree species and ecosystem processes and functions.

Methods

Study site

This study was conducted within the 26,880 ha Sungai Tiagau Protection Forest Reserve in Sabah, Borneo, Malaysia (4°35′20″N 117°16′19″E). According to the Köppen-Geiger climate classification, the region's climate is humid tropical equatorial (Peel et al. 2007), with a mean annual temperature of 27.6 °C (Walsh and Newbery 1999). The annual average precipitation (2004–2016) is 2400–2500 mm, based on data from three weather stations within a 15 km radius of the study location. The Sungai Tiagau Protection Forest Reserve consists of lowland mixed dipterocarp forest, dominated by Acrisols (Panagos et al. 2011). It was logged in the 1970s and burned during a forest fire in 1982–83. The forest reserve is managed by the state government foundation Yayasan Sabah. Since 1998, 18,500 ha of the site has been managed by the Innoprise-IKEA (INIKEA) Forest Rehabilitation Project, a collaboration between Yayasan Sabah, the Swedish University of Agricultural Sciences, and the Swedish company IKEA. The goals of the INIKEA Forest Rehabilitation Project are to rehabilitate the forest and to increase biodiversity, and efforts to achieve these goals have resulted in the planting of more than 90 native tree species and 4 million seedlings since its inception.

In November 2008, we established a tree species field trial with 34 different trees species within the INIKEA project area by raising 680 seedlings from seeds in the project plant nursery. These seedlings were then acclimatized to forest conditions in a second nursery close to the forest field site (Gustafsson et al. 2016) before being planted in the 3 ha forest site, located at ~ 300 m a.s.l. Within species, seedlings were of approximately the same size at the time of plantation (Gustafsson et al. 2016). Between species, the average height varied between 30 cm (*Hopea ferruginea*) and 105 cm (*Pentace laxiflora*) at the time of planting. The tree species were planted in a random order with one tree every 3 m along a total of 40 linear transects. Planting was conducted to avoid rocks, streams, and slopes exceeding 15% inclination, extending the transects when needed. Each transect was 2 m wide, 60–100 m long, and the distance between the center of transects was 10 m (Gustafsson et al. 2016), hence, the planting density was ca. 333 trees/ha. All transects are positioned perpendicularly to a stream and most of the study site was located on a south-facing slope, rising approximately 100 m above stream elevation (Gustafsson et al. 2016). Before planting, transects were cleared of bushes, small pioneer trees and climbers. No prior soil preparation was conducted; seedlings were planted directly into the forest soil. Four years after planting, climbers were removed and a few pioneer trees growing at the edges of the transects were girdled to promote growth of the planted seedlings (Gustafsson et al. 2016). The planting regime used for the study site is identical to enrichment planting done in large swathes of the INIKEA-project, and similar to methods in other regional restoration projects (Philipson et al. 2020; Ruslandi et al. 2017). Ideally, natural mortality rates among seedlings and clearing of nearby climbers and pioneer trees limit competition and enable growth of the surviving planted material.

Sampling and trait measurement

Due to resource restraints, not all 34 species present in the common garden were sampled and measured. The 22 species sampled were selected randomly out of the pool of 34 total species. We characterized each selected tree species (n = 3–8 individuals per species) using a combination of 18 physical, chemical, and tree allometry traits (Table 1). Physical traits included specific leaf area (SLA), leaf dry matter content (LDMC), leaf area (LA), leaf thickness (LT), and wood density (WD). Chemical traits constituted concentrations of leaf nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na), and total and soluable phenolics, as well as pH. Tree allometry traits were stem slenderness, and relative crown length, depth, and width (Table 1). Traits are expressed as average values for each species. For physical and allometric traits, this value constitutes the arithmetic mean of measurements from all sampled individuals of the species. For chemical traits, leaves from all sampled individuals of a species were pooled and homogenized into one sample prior to analysis. Hence, the final sample size for each individual trait was 22.

During February–April 2019, 10 years and 2–4 four months after the planting of the trees, leaves were collected from 3 to 8 individuals of each of the 22 tree species, and allometric traits were measured (studied species are listed in Table 2; short descriptions of the silvicultural and ecological relevance of major taxonomic groups are presented in Box 1). Of these 22 species, 17 belonged to the Dipterocarpaceae family, which is the region's dominant tree family (Symington et al. 2004; Ghazoul 2016). All 22 tree species were classified into local timber groups; trade names used to group closely related timbers with similar properties and appearance since the high number of tree species in the region would make it impractical to trade each on a per-species basis (Wong 1982). For each individual tree, we measured diameter at breast height (dbh, 1.3 m), tree height, and crown height, together with two perpendicular measurements of crown width, using measurement tape and a laser rangefinder (Nikon Forestry Pro). From these measurements we calculated the following tree allometry traits: tree height: diameter at breast height ratio (stem slenderness), crown height: crown width ratio (relative crown length), crown height: tree height ratio (relative crown depth), and crown width: tree height ratio (relative crown width) (Sterck et al. 2001). Leaf sampling was conducted by using ladders (approximately 10 m) and cutting or twisting branches or leaves off using a telescopic branch cutter or an approximately 5 m long stick with a forked ending. Sampling was performed between 8:00 AM and 1:00 PM. For each tree, leaves were collected (n = 5) from three different branches located in the outer canopy whenever possible. For very large trees where the outer canopy could not be reached, leaves from the inner canopy were collected instead. In cases where trees had compound leaves, we instead collected one leaflet per branch. Where possible, we sampled leaves that were undamaged by herbivores and not covered by lichen. If it was impossible to obtain enough material satisfying these criteria, the least damaged leaves were sampled. Immediately after sampling, leaves were wrapped in wet napkins and placed in plastic bags. Before sealing the bags, we exhaled into them to increase their CO_2 concentration and moisture (Perez-Harguindeguy et al. 2016). Bags were then stored in an ice-cooled plastic box until trait measurements were taken later on the same day (Perez-Harguindeguy et al. 2016). Where necessary, lichen and dirt were removed from leaves before measuring traits (Perez-Harguindeguy et al. 2016). Physical trait measurements were performed as soon as the samples were retrieved from the field. First, LT was measured between major veins in the bottom, middle, and top thirds of each leaf (Perez-Harguindeguy et al. 2016) using a digital micrometer (RS Components Ltd., Corby, UK). Leaves were then scanned (Canon E410 series, Canon Inc., Tokyo, Japan) and LA determined by image analysis using the ImageJ software package (Schneider et al. 2012). Fresh and dry weight (after oven drying for 3 days at 70 °C) was determined for

Table 1 List of trait categories, associated sampled traits, their units of measurement, and the biological relevance of each trait

Trait category	Trait	Unit	Relevance	References
Physical	Specific leaf area (SLA)	mm^2/mg	Defensive investment, nutrient content, leaf lifespan, and growth rate	Makkonen et al. (2012) and Perez-Harguindeguy et al. (2016)
	Wood density (WD; from literature)	mg/mm^3	Structural strenght, pathogen or parasite susceptibility, resistance to breakage	Makkonen et al. (2012) and Perez-Harguindeguy et al. (2016)
	Leaf dry matter content (LDMC)	g/g	Growth rate and leaf lifespan	Kattge et al. (2011), Makkonen et al. (2012) and Perez-Harguindeguy et al. (2016)
	Leaf thickness (LT)	mm	Physical strength of leaf	Makkonen et al. (2012) and Both et al. (2019)
	Leaf area (LA)	cm^2	Light interception area and temperature regulation	Perez-Harguindeguy et al. (2016) and Both et al. (2019)
Chemical	Leaf nitrogen (N), potassium (K), and phosphorus (P) concentration	mg/g	Essential macronutrients, photosynthetic rate, nutritional quality for herbivores, and life-history	Kattge et al. (2011), Makkonen et al. (2012), Gustafsson et al. (2016) and Perez-Harguindeguy et al. (2016)
	Total and soluble phenolic concentration	mg/g	Chemical defense against herbivory	Kattge et al. (2011), Kulbat, (2016) and Makkonen et al. (2012)
	Leaf pH	$Log_{10}(1/a_H^+)$	Leaf digestability	Makkonen et al. (2012) and Perez-Harguindeguy et al. (2016)
	Leaf sodium (Na), calcium (Ca), and magnesium (Mg) concentration	mg/g	Light absorbance, stomatal conductance, response to environmental stress, nutritional quality for herbivores	Makkonen et al. (2012) and Both et al. (2019)
Tree allometry	Relative crown depth (crown depth: tree height ratio)	m/m	Life-history and allometry	Sterck et al. (2001), Osunkoya et al. (2007) and Gustafsson et al. (2016)
	Relative crown width (crown width: tree height ratio)	m/m	Life-history and allometry	Sterck et al. (2001) and Osunkoya et al. (2007)
	Relative crown length (crown depth: crown width ratio)	m/m	Life-history and allometry	Sterck et al. (2001) and Gustafsson et al. (2016)
	Stem slenderness (tree height: diameter at breast height ratio)	m/cm	Life-history and allometry	Sterck et al. (2001) and Osunkoya et al. (2007)

Table 2 Data for 22 tree species that either contributed to or constitute our estimates of financial value

Scientific name	Acronym	Timber group[a]	Price per m^3		Survival (%)	Volume per stem at 30 cm dbh (m^3)	Time needed to reach 30 cm dbh (years): average (low–high)	IRR: average (low–high)
			MYR[b]	USD[c]				
Canarium sp.	**Ca.sp**	**Genus specific**	**445**	**115**	**55**	**0.76**	**100 (77–140)**	**1.17 (0.67–1.90)**
Diospyros sp.	**Dio.sp**	**Genus specific**	**494**	**123**	**65**	**0.76**	**71 (52–108)**	**2.11 (1.16–3.47)**
Dipterocarpus conformis	Dip.co	Species specific	838	209	60	0.78	65 (53–83)	3.63 (2.55–5.04)
Dryobalanops keithi	Dr.ke	Kapur	661	165	68	0.76	78 (66–95)	2.68 (1.94–3.65)
Dryobalanops lanceolata	Dr.la	Kapur	661	165	70	0.76	84 (69–106)	2.51 (1.76–3.49)
Hopea ferruginea	Ho.fe	Merawan	493	123	40	0.76	72 (58–95)	1.37 (0.79–2.23)
Parashorea malaanonan	Pa.ma	White Seraya	581	145	75	0.81	69 (57–87)	2.96 (2.06–4.14)
Parashorea smythiesii	Pa.sy	White Seraya	581	145	57	0.81	125 (105–154)	1.38 (0.97–1.93)
Parashorea tomentella	Pa.to	White Seraya	581	145	55	0.81	55 (42–80)	3.13 (1.85–4.91)
Pentace adenophora	**Pe.ad**	**Takalis**	**478**	**119**	**53**	**0.76**	**92 (59–205)**	**1.30 (0.47–2.58)**
Pentace laxiflora	**Pe.la**	**Takalis**	**478**	**119**	**95**	**0.76**	**68 (56–87)**	**2.66 (1.82–3.80)**
Shorea beccariana	Sh.be	Red Seraya	550	137	45	0.82	47 (36–66)	3.03 (1.78–4.85)
Shorea falciferoides	Sh.falc	Selangan Batu	712	178	65	0.82	88 (70–118)	2.53 (1.68–3.63)
Shorea fallax	Sh.fall	Red Seraya	550	137	70	0.79	47 (37–63)	3.95 (2.52–5.91)
Shorea leprosula	Sh.lepr	Red Seraya	550	137	15	0.83	19 (14–26)	1.64 (0.26–4.42)
Shorea leptoderma	Sh.lept	Selangan Batu	712	178	75	0.82	62 (54–73)	3.87 (2.96–5.04)
Shorea macrophylla	Sh.map	Red Seraya	550	137	70	0.82	39 (29–58)	4.89 (2.82–7.80)
Shorea macroptera	Sh.mat	Red Seraya	550	137	55	0.82	40 (32–53)	4.12 (2.65–6.20)
Shorea ovalis	Sh.ov	Red Seraya	550	137	70	0.79	41 (35–51)	4.49 (3.15–6.31)
Shorea parvifolia	Sh.par	Red Seraya	550	137	15	0.79	20 (12–45)	1.24 (0.03–4.70)
Shorea pauciflora	Sh.pau	Species specific	543	136	60	0.89	129 (99–185)	1.35 (0.82–2.07)
Sindora irpicina	**Si.ir**	**Species specific**	**494**	**123**	**50**	**0.76**	**126 (100–169)**	**0.96 (0.58–1.51)**

Species in bold are not part of the *Dipterocarpaceae* family

[a] Retrieved from Soepadmo and Wong (1995), Soepadmo et al. (1996, 2002, 2004, 2007), Soepadmo and Saw (2000), and Lee (2003)

[b] Malaysian Ringgit per cubic meter of exported round logs, free on board, reported by the Sabah Forestry Department (2016, 2017)

[c] Adjusted for inflation and converted to spring 2023 USD via consumer price index (CPI) and exchange rates (MYR CPI mid 2016/2017 – spring 2023 = 1:1.13/1.09 = 0.229 USD)

Box 1 Relevance of studied tree species' taxonomic groups

Dipterocarpaceae (family)

Dipterocarpaceae contains about 500 species, many of which are both ecologically and economically significant in Southeast Asia and are considered important for the timber industry (Ghazoul 2016). They are primarily canopy trees, and many exceed 50 m in height (Ghazoul 2016). In dipterocarp lowland forests, they make up 20–50% of the forest basal area, and comprise the majority of canopy trees (Ghazoul 2016). Additionally, some members of the *Shorea* genus, especially *Shorea macrophylla*, produce edible fruits (Soepadmo et al. 2004)

Canarium (genus)

The *Canarium* genus consists of light hardwoods sold under the name Kedondong (Wong 1982) and is distributed throughout Africa, Asia, and Oceania; in Sabah, it is commonly found in lowland mixed dipterocarp forests (Soepadmo and Wong 1995). Additionally, some members have edible fruit and nuts (Soepadmo and Wong 1995)

Diospyros (genus)

The *Diospyros* genus, sold locally under the name Kayu Malam, consists of heavy hardwoods (Wong 1982) and is distributed across Africa, Asia, and Oceania over a wide spectrum of habitat types (Soepadmo et al. 2002). Despite having wood with very desirable characteristics, members of this genus have been overlooked as timber species due to their relatively small dimensions when compared to dipterocarps (Soepadmo et al. 2002). Several members have edible fruits (Soepadmo et al. 2002)

Pentace (genus)

Pentace laxiflora is endemic to Borneo, while *Pentace adenophora* is found in Sumatra, Peninsular Malaysia, and Borneo (POWO 2022). Both species belong to the Melunak timber group and are categorized as light hardwoods (Wong 1982). However, very little is known about their ecology

Sindora irpicina (species)

Sindora irpicina is a legume endemic to Borneo (Soepadmo and Saw 2000) that belongs to the Sepetir timber group of light hardwoods (Wong 1982)

all samples (Perez-Harguindeguy et al. 2016). For each sample, fresh and dry weight measurements were used to determine LDMC, and SLA was calculated from the LA and dry weight (Perez-Harguindeguy et al. 2016).

Dried leaf samples were transported to the Forest Research Center of the Sabah Forestry Department in Sepilok, Malaysia, for all chemical trait analyses, where they were bulked by species, air dried to a constant weight, and ground using a Wiley Mill ED-5 (Thomas Scientific, US). A subset of each sample was dried at 105 °C, weighed, and used to convert all data to oven-dry values. Bulk samples were then analyzed for pH, soluble phenolics, total phenolics, as well as total contents of N, P, Mg, K, Ca, and Na. Specifically, for each ground sample, leaf tissue pH was analyzed by mixing a subsample in distilled water (volume ratio 1:8) and measuring the resulting pH using a Mettler Toledo inLab pH electrode (Greifensee, Switzerland) connected to a Corning pH meter 240 (Corning Life Sciences, Texas, US) (Cornelissen et al. 2006). Another subsample was used to measure total and soluble phenolics by extraction in methanol and deionized-water, respectively, both at a ratio of 1:50 (Gundale et al. 2010), and extracts were analysed by the Folin-Ciocalteu assay at 765 nm on a Hitachi U-2900 UV/Vis Spectrophotometer (Tokyo, Japan) (Singleton and Rossi 1965). Total N contents were determined by dry combustion at 900 °C on Vario Max CN Elemental Analyzer (Elementar Analysensysteme, Germany). To determine P, Mg, K, Ca, and Na contents of each sample, subsamples were digested using the sulfuric acid-hydrogen peroxide method (Allen 1989). Additionally, Mg, K, Ca, and Na content was measured on a Spectro Arcos ICP-OES (Spectro Analytical Instruments, Kleve, Germany), and P content was determined using the molybdenum-blue method (Anderson and Ingram 1993) at 880 nm with a Hitachi U-2900 UV/Vis Spectrophotometer (Tokyo, Japan). For *Hopea ferruginea, Pentace laxiflora, Shorea parvifolia* and *Sindora irpicina,* bulked samples were too small to perform all analyses. In these cases, additional leaves were collected, weighed, and dried on 29 March 2019 and analyzed as described above.

We used the Global Wood Density Database to acquire wood density values for 16 of the 22 species (Zanne et al. 2009). The remaining six species, *Canarium sp*., *Diospyros sp*., *Pentace adenophora*, *Pentace laxiflora*, and *Sindora irpicina*, were not in the database. In these cases we instead used average wood densities for species of the same genera growing in tropical Southeast Asia.

Growth rate estimation

To estimate growth rates for the 22 species, we used dbh measurements collected on all planted trees growing at the study site. These measurements were taken on seven occasions, starting 3 years after planting, and then repeated roughly every second year, up to 14 years and 5 months after planting. For each species, we generated linear mixed effect models with dbh as the response variable and number of years since planting as the explanatory variable, with random intercepts and slopes based on tree identity (i.e., replicate). Using the coefficients from the generated models, we extrapolated the average time it would take each species to reach a dbh of 30 cm and defined this as one rotation period. This dbh value is below the lower dbh limit of 60 cm stipulated by the current regulations concerning logging in natural forests in Sabah (Berry et al. 2010; Reynolds et al. 2011; Bryan et al. 2013) but was chosen because the volumes extracted under this cutting limit would better match logging intensities seen in the region. Harvesting up to 333 trees at 60 cm dbh, after adjusting for survival rates presented in Table 2, would result in average wood extractions of 783 m^3/ha. This greatly exceed the average volume of 152 m^3/ha extracted by conventional logging in the region (Fisher et al. 2011), and those extracted from timber plantations, which rarely exceed 400 m^3/ha (Cuong et al. 2020). Using 30 cm as the cutting limit gave average wood extractions of 154 m^3/ha, thus enabling a more realistic comparison to conventional logging and plantation practices.

Internal rates of return

Internal rate of return (IRR) corresponds to the estimated discount rate at which net present value of all cash flows equal zero, and helps define the total rate of return from investment in a project and compare it against the opportunity cost of capital. It is commonly used to rank different investment alternatives where the higher the IRR, the more profitable the investment. Here, IRR is given per hectare for each tree species and was estimated based on calculations of land expectation value (LEV, USD/ha), a standard discounted cash flow technique in timberland appraisal, used to determine financial value of a patch of land, assuming the land will be under this forest management indefinitely. The LEV, and subsequently IRR, was calculated following Straka and Bullard (1996) in (1):

$$LEV = \frac{\sum_0^T R_t(1+i)^{T-t} - \sum_0^T C_t(1+i)^{T-t}}{(1+i)^T - 1}. \tag{1}$$

where ‘R_t’ is the revenue received in year t, ‘C_t’ is the cost incurred in year t, ‘T’ is the rotation length in years, ‘t’ is the year of a particular revenue or cost, and ‘i’ is the annualized discount rate, expressed as a decimal. The internal rate of return is defined as the value of ‘i’ where LEV = 0.

Assuming that the planting pattern does not change between rotations, 333 trees could be grown on a hectare of land. Additionally, in each calculation we assumed that all 333 trees would be of the same species. Lastly, we assumed that all trees in a hectare could be harvested simultaneously when they reach an average of 30 cm dbh. Tree survival rates were calculated for each species based on their observed survival between planting and the most recent plot survey (a 15-year period), and were used to adjust the number of trees remaining at harvest time, assuming no further mortality after 15 years.

Financial value of each species per unit volume of timber was based on the price per cubic meter of exported round logs, free on board, reported by the Sabah Forestry Department (2016, 2017). Price per cubic meter is reported for timber groups used in the local region based on similarities in timber properties and phylogenetic relatedness. Timber group identities for the 22 tree species were retrieved from Soepadmo and Wong (1995), Soepadmo et al. (1996), Soepadmo and Saw (2000), Soepadmo et al. (2002), Lee (2003), Soepadmo et al. (2004), and Soepadmo et al. (2007). All price data were taken from the Sabah Forestry Department 2017 report except in the case of *Canarium* sp., which were only mentioned in the 2016 report. Values from the reports were adjusted for inflation and converted to spring 2023 USD via consumer price index (CPI) and exchange rates (MYR CPI mid 2016/2017 − spring 2023 = 1:1.13/1.09 = 0.229 USD).

We used allometric volume equations obtained from the Indonesian STREK-project (Bertault and Kadir 1998) to calculate tree volume at the 30 cm dbh threshold for each tree species. Volume was calculated in (2):

$$V = A + B * dbh + C * dbh^2 \tag{2}$$

where ‘V’ is the volume given in m^3, ‘dbh’ is the diameter at breast height (1.3 m, cm), and ‘A’, ‘B’, and ‘C’ are constants estimated through field measurements from the STREK-project (Bertault and Kadir 1998). The STREK-project produced species- and genera-specific constants, together with an “others”-category based on measurements on species for which specific equations could not be made due to a lack of measurements. For the 17 dipterocarp species in this study, we used species- or genera-specific constants. However, no such constants were available for the five non-dipterocarp species, so the non-specific equation constants were used in these cases. The complete list of equation constants can be found in Lussetti et al. (2016).

Management costs were taken from Philipson et al. (2020), which includes expenditures from site preparation, seed collection, seedling raising, planting, post site management, and replanting. These costs are based on a separate restoration project consistent with those incurred during the INIKEA project (personal communication, David Alloysius, manager of INIKEA). Logging costs were taken from FRIM and ITTO (2002) and Fisher et al. (2011), and represent average logging costs per m^3 timber in conventional logging operations in Peninsular Malaysia. Logging costs include operations such as road construction, felling, skidding, as well as transport to the mill, taxation, administration, and other expenditures (FRIM and ITTO 2002; Fisher et al. 2011). Cost estimates for each activity is avaliable in Table 3. All costs were adjusted for inflation and converted to USD (MYR CPI mid 2001 − spring 2023 = 1:1.59 = 0.229 USD).

To capture variation in our data and evaluate robustness of our IRR values, we performed a sensitivity analysis by varying management costs and tree growth rates. For each of these variables we used a high, average, and low value, and produced three scenarios representing the upper, middle, and lower limit of our IRR estimates. Philipson et al. (2020) estimated management costs between 1500 and 2500 USD/ha, depending on the intensity of site preparation. For the sensitivity analysis, we used management costs of 1500, 2000, and 2500 USD/ha for the high, mid, and low-value scenarios, respectively. These values where then adjusted for inflation, which gave management costs of 1742, 2323, and 2903 USD/ha for each respective scenario (MYR CPI mid 2020 – spring 2023 = 1:1.16). We assumed that 80% of these costs would be used in the first year to cover field preparation and seedling planting, and that the remaining 20% would be spread out during the following nine years, covering site maintenance, for a total management period of 10 years. To account for variation in tree growth rates, we used the bounds of the 80% confidence interval in our mixed effects models. The lower bound of the confidence interval represents the shortest growth time needed to reach the cutting limit and was thus used in the high-value scenario, while the average growth rate and the upper bound of the interval were used in the mid and low-value scenarios, respectively.

A full list of species names, species acronyms, timber group identity, wood market value, growth rate, survival, volume of wood per tree, and time needed to reach 30 cm dbh, for each species and scenario from the sensitivity analysis is available in Table 2.

Statistical analyses

To evaluate variation in plant functional traits in relation to financial value within the studied species, we performed a multivariate partial least squares (PLS) regression in Simca (version 17.0.0.24543 (64-bit), Sartorius Stedim Data Analytics AB 2021). We included the mid-scenario estimate of IRR as the response variable and the 18 measured traits as explanatory variables for all 22 species. To determine how many components to include we used the Q^2 value, the fraction of the total variation of IRR that could be predicted by a component, produced by cross-validation. We only considered components with Q^2 values above 5%. Variables were considered significant if the 90% confidence intervals of their loadings obtained by jack-knifing (Quenouille 1949; Efron and Gong 1983) during cross-validation did not overlap with zero. The best-fitting model was determined by backward selection, removing the trait with the confidence interval furthest from zero in each model, one variable at the time. We continued this way until the model only contained significant variables and then compared Q^2 values of the resulting models. The model with the highest Q^2 value was deemed the best fitting and was kept while others were discarded.

In addition, to distinguish between direct and indirect effects traits had on IRR, we ran four additional PLS models, following the same procedure as in the trait-IRR model. Each model was run with the same traits as explanatory variables, but one of the four variables that determined IRR as the response variable (e.g., time needed to reach 30 cm dbh, survival rate, market value per cubic meter of wood, and volume of wood per tree at the 30 cm dbh threshold).

To test which variables in the IRR equation were the most influential, we used simple linear regression models with IRR as the response variable. Explanatory variables were survival rate, time needed to reach 30 cm dbh, i.e., the reverse of growth rate, market price for a cubic meter of wood, and volume of wood per tree at the given cutting limit of 30 cm dbh. Additionally, to improve the model assumption of normally distributed data, survival rate was logit transformed and time needed to reach 30 cm dbh was log transformed. In order to find the most appropriate model we performed a backward selection, starting with a model containing all four variables and their interactions, excluding three- or four-way interactions. We removed one variable at a time and evaluated model fit using AIC values adjusted for small sample sizes, AICc (Hurvich and Tsai 1989), with the model with the lowest value being retained. This continued until the AICc was no longer improved by removing additional variables. We interpreted models using a type III anova, using Kenward–Rogers "F" tests with Satterthwaite's degrees of freedom and restricted maximum likelihood estimation, which are especially appropriate for small sample sizes (Fox and Weisberg 2019; Kenward and Rogers 1997; Satterthwaite 1941). We validated the final model via visual inspection of residuals distribution and linearity assumption for the variables and interactions. While the model for low levels of survival showed signs of non-linearity in the interaction term with the time needed to reach the set cutting limit of 30 cm dbh, this was likely due to a few species having very low survival rates compared to the rest. However, the R^2-value for the overall model remained above 95% without including non-linear terms. Therefore, we did not include any quadratic terms in the model.

Results

Tree species' functional traits associated with financial viability

Our first PLS model, including 22 tree species, explained 43.6% of the variation in plant functional traits, and 23.3% of the variation in IRR with plant functional traits by one significant component (Q^2, predicted variation by the single component = 11.6%, Fig. 1a). According to the model, IRR was negatively correlated with leaf Ca, Mg, N content, pH, and SLA (Fig. 1b). Leaf area and relative crown length were also included in the model but did not significantly contribute to explained variance, i.e., the loading 90% confidence interval overlapped with zero.

Our four additional models that each includes one of the four variables used to calculate IRR, could all explain their respective response variable with one significant component (Table 4; Figure 4a, c, e, and g). In the first model, high values in time needed to reach the cutting limit of 30 cm dbh was positively correlated with LT, LDMC, relative crown width, and stem slenderness, and negatively correlated with leaf N (Fig. 4b). In the second model, survival rate was positively correlated with LT, relative crown depth, relative crown length, and relative crown width (Fig. 4d). In the third model, market price per cubic meter of wood was positively correlated with stem slenderness, soluble phenolics, and WD, and negatively correlated with leaf Ca, Mg, K, and N content (Fig. 4f). Lastly, in the fourth model, volume of wood per tree at the 30 cm dbh threshold was negatively correlated with leaf K and Mg content, as well as LT (Fig. 4h). In all four models additional traits were included, but these did not significantly contribute to the explained variance (Fig. 4b, d, f, and h).

Distribution of financial value in sensitivity analysis

In our mid financial value scenario (for which moderate growth rates and management costs were assumed), the average IRR was 2.58%. *Shorea macrophylla* had the highest IRR (4.89%), and *Sindora irpicina* the lowest (0.96%) (Table 2; Fig. 2a).

In the high financial value scenario (high growth rates and low management costs), the average IRR was 4.07%. As for the mid financial scenario, the species with the highest IRR was *Shorea macrophylla* (7.8%) while *Sindora irpicina* had the lowest IRR (1.51%) (Table 2; Fig. 2b).

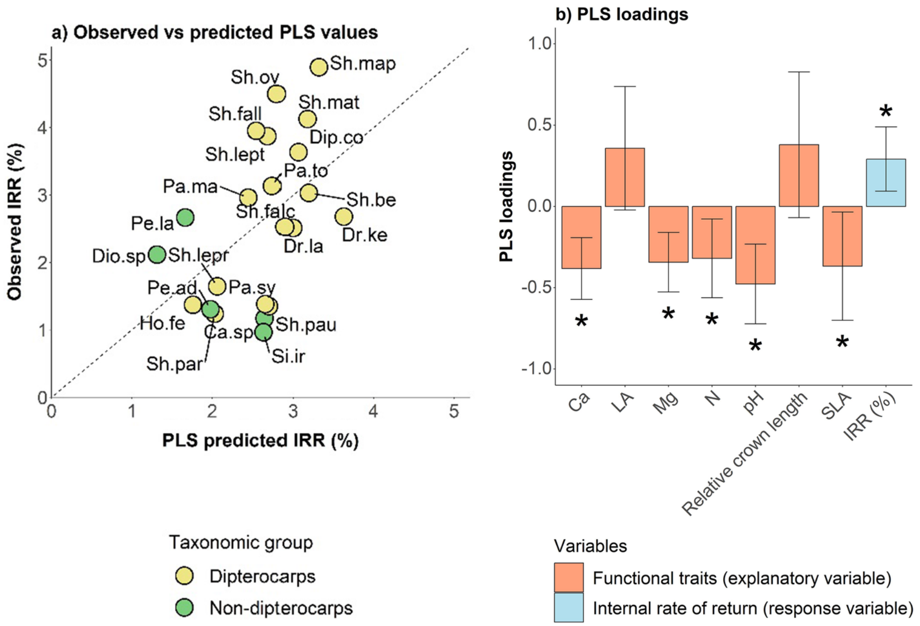


Fig. 1 Results from a partial least square model (PLS) including data for 17 *Dipterocarpaceae* species, and 5 non-dipterocarp species grown in a common garden experiment with active restoration management in Sabah, Malaysia. Plot **a** shows observed and predicted internal rate of returns (IRR) based on the land expectation value of the study system. Observed values represent mid-scenario IRR values obtained from a sensitivity analysis of costs and revenue from managing trees planted as part of the restoration effort. Predicted IRR values are based on values of functional traits included in each model after backward selection, taken from a pool of 18 traits measured for each tree species (n = 22 per trait). The dotted line represents a 1:1 correspondence between measured and predicted values. Tree species are denoted using acronyms of their scientific names (Table 2). Plot **b** shows PLS loadings. Orange bars correspond to functional traits measured for each tree species, chosen via backwards selection from a pool of 18 traits. The blue bar represents the same IRR values as the observed IRR in plot **a**, i.e., the mid-scenario values obtained in a sensitivity analysis of financial viability of the restoration planting. Loadings indicate the importance and direction of influence of variables contributing to the component in question; large loadings, either positive or negative, indicate substantial influence on the model. Error bars represent 90% confidence intervals. A variable was considered to significantly improve the model's prediction if its confidence interval did not overlap with zero. Significant variables are highlighted with an asterisk

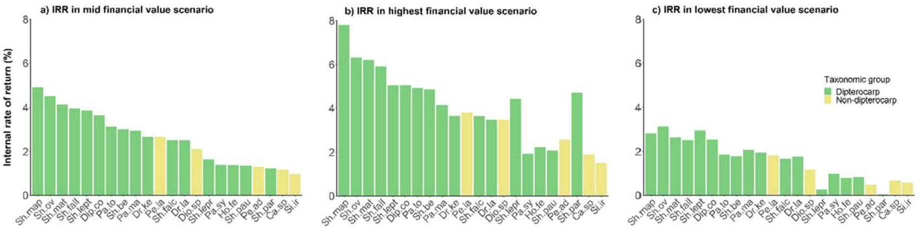


Fig. 2 Internal rate of return (IRR) for each tree species and each scenario included in the sensitivity analysis, in which the assumed growth rate and management costs were varied. Green bars indicate species in the *Dipterocarpaceae* family; yellow bars indicate non-dipterocarp species. Components contributing to IRR and their exact values are listed in Table 2. Tree species are denoted using acronyms of their scientific names (Table 2). Species in **b**, **c** are sorted after IRR values in **a**

Finally, in the low financial value scenario (low growth rates and high management costs), the average IRR was 1.6%. The highest IRR was obtained for *Shorea ovalis* (3.15%) and the lowest for *Shorea parvifolia* (0.03%), (Table 2; Fig. 2c).

A simple linear regression model with survival rate, time needed to reach the set cutting limit of 30 cm dbh, market price per cubic meter, and number of cubic meters of wood per tree as explaining variables could explain 97% of the variation in IRR (F (5, 16) = 158, $p < 0.0001$). Internal rate of return was positively related to the survival rate (F = 305, $p < 0.0001$), the market price per cubic meter of wood (F = 71, $p < 0.0001$), and the number of cubic meters of wood per tree at time of harvest (F = 20, $p = 0.0004$). Additionally, IRR was negatively related to the time needed to reach the set cutting limit of 30 cm dbh (F = 445, $p < 0.0001$), i.e., the shorter the rotation time, the higher the IRR. Furthermore, there was an interaction effect between survival and growth rate (F = 230, $p < 0.0001$). Each additional unit of survival rate increased the negative relationship between IRR and time needed to reach the cutting limit of 30 cm dbh, and vice versa, i.e., decreasing time needed to reach the cutting limit of 30 cm dbh increased the positive relationship between IRR and survival rate (Fig. 3). For example, an increase in survival rate of one standard deviation, while time needed to reach the cutting limit was fixed at 33 years (ln = 3.5), would increase IRR by approximately 1.3% (Fig. 3).

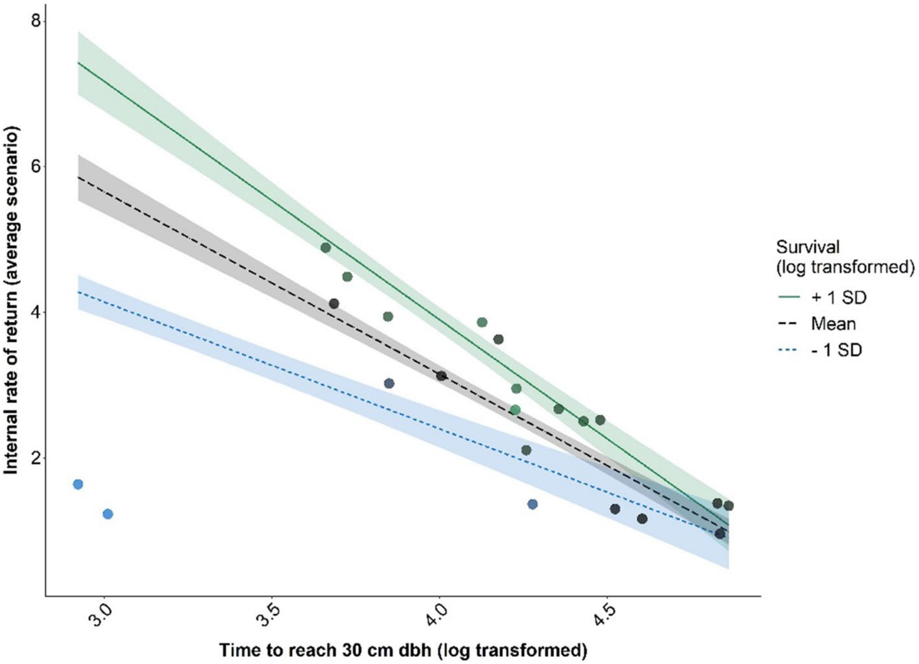


Fig. 3 Linear regression analysis, showing the relationship between internal rate of return (IRR) and numbers of years needed to reach the size threshold for when harvest would take place in our model (30 cm dbh), for 22 tree species. Each dot represents a species, and lines represent the relationship between IRR and the time needed to reach the harvesting threshold, when the survival rate for each tree species 15 years after planting is varied around the mean ± one standard deviation. Both predictor variables are log transformed. Colored bands represent the 80% confidence interval

Discussion

The aim of this study was to determine whether plant functional traits could predict financial values of native trees in a forest restoration setting by enrichment planting in tropical rainforests and to identify tree species as economically viable options for use in such settings. Our results show that for a subset of traits, a plant functional trait approach could be used to predict long-term financial values for tree species native to northern Borneo, but that the predictions where opposite to our expectations. We hypothesized that acquisitive traits indicative of high growth rates would be related to high financial value. However, we instead found an opposite pattern; high financial value was correlated to conservative trait values such as low SLA and low N content.

We found that a subset of five traits (Ca, Mg, N, pH, and SLA) was useful for predicting IRR of tree species. Hence, of the 18 traits we measured, thirteen were not significantly related to IRR in the model. In order to support our hypothesis that acquisitive trait values would be related to high IRR, the traits included in the PLS model would all have been positively related to IRR (i.e., high Ca, Mg, N, pH, and SLA would be accompanied by high IRR). This would indicate high nutrient content and low content of defensive compounds, which is typical for a plant species with an acquisitive strategy. However, the tree species exhibited the opposite relationship between their traits and IRR, meaning that species with trait values in ranges normally associated with more conservative growth strategies had higher IRR than species with more acquisitive values. The most likely reason is that the fastest-growing species with acquisitive traits also tended to have lower survival rates, which reduces overall income. This is in line with other studies showing that species with conservative traits are more robust and can endure environmental stress in a better way than species with more acquisitive traits (Wright 2010; Díaz et al. 2016; Harrison and LaForgia 2019).

We also found a potential tradeoff between growth rate (i.e., time needed to reach 30 cm dbh) and survival. Specifically, our results revealed that traits positively correlated with time needed to reach the cutting limit (i.e., traits related to low growth rates) were similar to traits that were positively correlated with survival rate (Fig. 4b, d). In the growth-rate and survival models, LT along with an array of allometric traits were positively correlated to the time needed to reach 30 cm dbh (i.e., low growth rate) and survival rate, respectively. We hypothesize that the contrasting pattern by which traits related to high growth versus survival rates is a plausible explanation for our finding that neither architectural traits nor LT were correlated to IRR. This tradeoff where the two main variables, growth and survival rate, associated with plant traits in opposite ways, might also explain why the traits-IRR model only accounted for a modest part of the observed variance.

Aside from its effects on financial value, species selection could be used to promote other services to increase utility of enrichment plantings. Species' traits can affect ecosystem functionally through a multitude of pathways, and are not limited to one trophic level (de Bello et al. 2010). For example, the *Diospyros*, *Canarium,* and *Shorea* genera all include species with edible fruits. Identifying financially viable fruit tree species could support biodiversity and provide additional food security to local communities. Additionally, leaf pH, and by extension cation content, which influence pH levels, has been shown to slow down decomposition, affecting nutrient cycling and soil carbon sequestration (Cornelissen et al. 2006). Furthermore, traits that were not related to IRR in our study could promote other services independently of financial value. In the case of decomposition, tropical forests generally have very poor litter quality and decomposition rates that are slower than expected given the climate conditions that are excellent for fast decomposition (Makkonen et al. 2012). This poor litter quality is driven partly by traits we found related to IRR, but also by others, such as lignin content.

Our study design, which focused on financial value of different tree species, grown within a secondary forest setting, could be expanded upon by considering other management goals, such as forest ecosystems' ability to supply a multitude of services and respond to disturbances of various kinds, i.e., functional resilience (Messier et al. 2019). Recovery of functional resilience is often one of the main goals of forest restoration efforts (Lamb et al. 2005). For example, the original purpose of the INIKEA project was to promote recovery of tree biodiversity after heavy disturbance in the forest reserve. Further, a different restoration project in Sabah showed that enrichment planting can accelerate recovery of carbon stocks after human disturbance (Philipson et al. 2020). Selecting suites of multiple species, based on plant functional traits, that increase the likelihood of survival and form a functional network that cover a wide array of management goals, may improve forest resilience and versatility in the enrichment planting approach (Aquilué et al. 2021).

Survival rates among the tree species ranged from 95% to, in some cases, as low as 15% and this variation was highly influential in predicting IRR of the species. There are several possible reasons for why we saw such a large variation among species. For example, low seedling survival may simply be common for some species, particularly on the acquisitive side of the trait spectrum, or because the site conditions poorly matched the species' niche. Regardless, low survival rates reduced IRR, to the point where the two fastest growing species, *Shorea leprosula* and *Sh. parvifolia*, had some of the lowest IRR values in two out of three scenarios of our sensitivity analysis, due to their very low survival rate of 15% (Figs. 2a, 3; Table 2). If survival rates for these species could be raised to the mean of our 22 species, then their IRR in the mid scenario of our sensitivity analysis would be around 6% (Fig. 3), surpassing the 4.89% of *Shorea macrophylla*, currently the highest valued species in the scenario. Therefore, management efforts to improve survival, selection of species with higher survival rates, or increased planting to compensate for low survival could be used in conjunction with selection for fast early growth to maximize IRR. The last option might be necessary, given that there likely are tradeoffs between fast growth and survival for some species, as seen for *Shorea leprosula* and *Sh. parvifolia*. However, species like *Shorea macrophylla* show that this growth-survival trade-off can be tapered, achieving both a relatively high survival rate (70%) and growth rate (40 years to achieve cutting limit dbh in mid-scenario). Yields could probably also be improved by a range of management interventions outside the scope of this study. Potentially useful interventions could for example include optimizing the planting regime and harvesting dimensions, applying additional canopy, and/or climber treatments to improve light conditions (Gustafsson et al. 2016), limited selective logging of trees not included in the enrichment plantings, and acquiring deeper knowledge of species-specific site adaptations and genetic variability (Axelsson et al. 2020).

Shorea leprosula and *Sh. parvifolia* also stood out as the two species that varied most in our sensitivity analysis (Fig. 2). While a few species swapped rankings between different scenarios, e.g., *Sh. macrophylla* and *Sh. ovalis*, for most species, variation between scenarios were relatively minor. In comparison, for *Sh. leprosula* and *Sh. parvifolia*, the relative change between different scenarios was much larger. For example *Sh. parvifolia* was ranked 19/22 in the mid-IRR-scenario (Fig. 2a), 9/22 in the highest value scenario (Fig. 2b), and 22/22 in the low-value scenario (Fig. 2c). This fluctuation is likely explained by the fact that the two parameters that vary in the sensitivity analysis, management cost and growth rate, interact with survival and growth characteristics (i.e., very high growth rate and very low survival rate; Table 2) of the two species differently across scenarios compared the other 20 species.

In our methodology, we used growth rate estimations based on the first 15 years of growth in our plots, and assumed linear growth throughout the tree's lifespan. However, the growth rate of tropical trees normally accelerates as trees grow larger in diameter and height, and gain access to more sunlight (Appanah and Turnbull 1998; King et al. 2006). Thus, our growth rates should be viewed as conservative estimates. For example, in plantation trials by the Forest Research Institute of Malaysia (FRIM), *Shorea macrophylla* reached 48 cm dbh in 23 years, which is a much higher growth rate than in our study, where the species reached 30 cm dbh in 29 years in our most optimistic scenario (Appanah and Weinland 1993). The exception would be *Shorea leprosula* and *Sh. parvifolia*, which exhibited very rapid growth (Table 2), matching values in literature. For example, the same FRIM trials included *Sh. leprosula* that achieved 33.6 cm dbh in 30 years, and *Sh. parvifolia* that achieved 30.9 cm dbh in 23 years, which is similar to our results (Appanah and Weinland 1993). Generally, our species outpaced growth rates from trees under canopy shade in primary forests, where the mean annual increment can be as low as 0.1 mm/year (Manokaran and Kochummen 1994), at which rate it would take 300 years to reach 30 cm dbh for the average tree. However, in logged forests, mean growth rates are generally higher than most of our estimates. A traditionally used assumption for growth rate in logged forests is 0.8 cm/year, i.e., 30 cm would be reached in 37.5 years (Appanah and Turnbull 1998). While this assumed growth rate is likely higher than realized growth, it would need to be cut approximately in half in order to match the average species growth rate in our mid-scenario, and that is with our study plot receiving liberation and thinning treatments designed to improve growth, that a logged forest does not.

Our findings also allowed us to evaluate viability of native tree species in forest landscape restoration or reforestation efforts as an alternative to exotic tree plantations and selective logging. For example, the IRR for *Shorea macrophylla* was 4.89% in the average scenario and ranged from 2.82% in the low-value scenario to 7.8% in the high-value scenario. Even in the average-value scenario, its IRR is comparable to that for hardwood plantations in Australia, where the average IRR is 6% (Venn 2005). However, the IRR in the high-value scenario is lower than the 13–14% estimated for rubber plantations (Winarni et al. 2018) as well as the 9–14% estimated for *Acacia* and *Eucalyptus* (Mackensen and Fölster 2000). It is also considerably lower than another estimate for plantation forestry using exotic tree species in Vietnam, for which IRRs of 26–34% were obtained (Cuong et al. 2020). Finally, IRR in the high-value scenario was lower than low-end estimates of profits from oil palm plantations, which are around 15% (Svatoňová et al. 2015). However, it should be noted that other sources suggest that oil palm plantations have higher IRR values of 21–27% (Latif et al. 2003), 68% (Noormahayu et al. 2009), or 58–74% (Wildayana 2016). The financial potential of restoration plantings thus seems to be lower than that of most alternative and comparable land-use types. Nevertheless, it is still profitable and could be viable in areas where other land uses are prohibited or are marginal for practical reasons. Alternatively, it could find viability by filling market niches that other land-use types cannot.

One challenge in the global wood value chain is meeting the demand for high-value tropical hardwood used in furniture and décor (Sarshar 2012). These demands have traditionally been met by harvesting natural forests that have now largely been depleted or are being protected (Bieng et al. 2021). While hardwood plantations with *Acacia* and *Eucalyptus* are common, these species are mainly used for pulpwood and are poor options for the production of high-value hardwoods (Sarshar 2012). If enrichment planting with native hardwood species in successional lowland dipterocarp forests can be made financially viable, it could be an attractive alternative to both conventional logging and forest plantations, neither of which have historically been able to provide a sustainable supply of hardwoods. Combining selective logging with enrichment planting has been proposed to address this issue at various times in recent decades (Schulze et al. 1994; Rimbawanto 2006) and is actively being implemented in Indonesia (Rimbawanto 2006; Izuno et al. 2013; Ruslandi et al. 2017). There, the four main species used in enrichment plantings are *Shorea leprosula, Sh. johorensis, Sh. parvifolia* and *Sh. macrophylla* (Ruslandi et al. 2017). Our study included all of these species except *Sh. johorensis* and our results suggest that *Sh. macrophylla* has the highest financial value in this context.

The trait approach applied in this study could potentially be used to select for specific purposes in the wood industry, although this would require future studies to be verified. For example, species with large investment in defense compounds such as phenolics could be expected to be more resistant to fungi and insect attacks (Kulbat 2016). Similarly, high wood density is sometimes used as a proxy for mechanical stability, and is further correlated to other important attributes like elasticity to bending and resistance to breakage (Chave et al. 2009). Furthermore, trait composition is also likely to influence species' ability to adapt to climate change. While long-term forest resilience to increased temperatures may be higher than previously thought, higher temperatures are projected to reduce forest productivity, especially in ecosystems with high mean annual temperatures (Sullivan et al. 2020). Species with a conservative growth strategy are generally more resilient to environmental stress and might thus to some extent be better adapted to rapidly changing abiotic conditions (Wright 2010; Díaz et al. 2016; Harrison and LaForgia 2019). For example, the abundance of moisture-demanding species on Barro Colorado Island have been shown to decline due to climate change, even in a relatively short time frame (Condit et al. 1996). Additionally, within-species genetic variation might also be a source of considerable trait variation, which can be used to improve seed source selection by identifying beneficial local adaptations (Axelsson et al. 2023). As global wood demand is only expected to increase, in order to secure the supply of wood in the tropics, selecting species for climate resilience, along with other properties, will be an important part of all enrichment planting programs moving forward (WWF 2012a).

Conclusions

Our results showed that a subset of functional traits could be used to predict financial values of native tree species. Financial value was negatively correlated with Ca, Mg, and N content, along with pH and specific leaf area. Thus, financial value was highest when values for these traits corresponded to those associated with the more conservative side of the plant economics spectrum. This is likely due to tradeoffs between survival and growth rates, which vary heavily among the studied species. On the financial side, enrichment plantings generally seem to be profitable, although not to the same degree as the most common competing land-use types. Overall, we conclude that enrichment planting using selected native tree species could be a financially sound and viable alternative to traditional land management strategies that possibly improves biodiversity and ecosystem services on degraded lands. We further conclude that functional traits together with growth and survival rates have potential to be used to screen unexplored native species for financial viability in enrichment planting.

Appendix A: Supplementary material

See Box 1, Tables 3, 4 and Fig. 4.

Fig. 4 Results from four partial least square models (PLS) with different response variables; time needed to reach 30 cm dbh, survival rate, market price per cubic meter of wood, and volume per tree at the 30 cm dbh threshold. Each model includes data from 17 *Dipterocarpaceae* species, and 5 non-dipterocarp species grown in a common garden experiment with active restoration management in Sabah, Malaysia. Plots **a**, **c**, **e**, and **g** show observed and predicted values of each response variable. Dotted lines represent a 1:1 correspondence between measured and predicted values. Tree species are denoted using acronyms of their scientific names (Table 2). Plots **b**, **d**, **f**, and **h** show PLS loadings. Orange bars correspond to functional traits measured for each tree species, chosen via backwards selection from a pool of 18 traits (n = 22 per trait). Blue bars represent response variables. Loadings indicate the importance and direction of influence for variables contributing to the component in question; large loadings, either positive or negative, indicate substantial influence on the model. Error bars represent 90% confidence intervals. A variable was considered to significantly improve the model's prediction if its confidence interval did not overlap with zero. Significant variables are highlighted ▶

Table 3 Logging costs for conventional logging practices

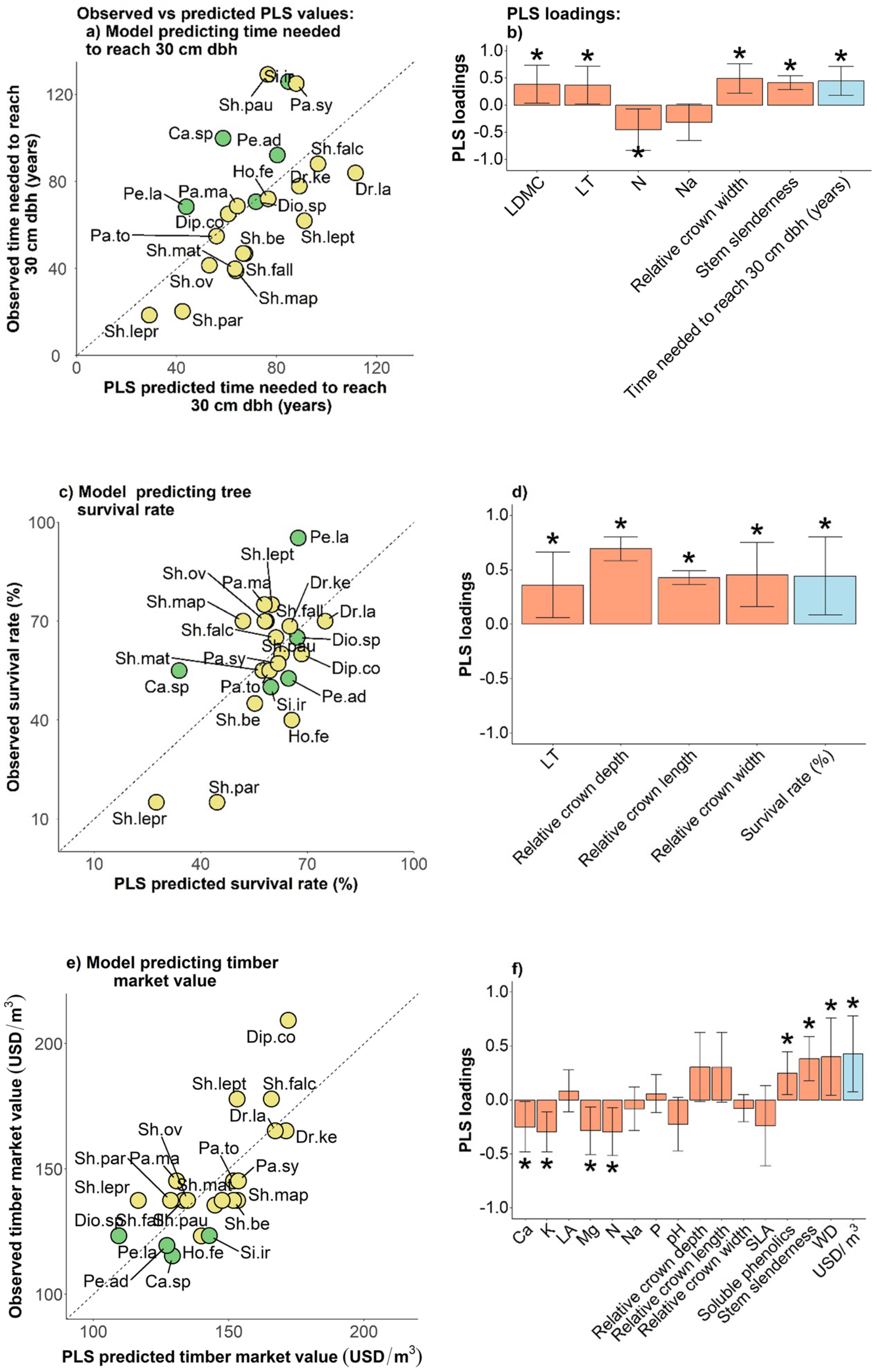
Activity	Costs	
	MYR[a]	USD[b]
Management plan	0.24	0.09
Pre-felling inventory	0.88	0.32
Boundary demarcation	0.87	0.32
Proposed road plan	0.52	0.19
Tree marking and mapping	2.4	0.88
Road construction	3.86	1.41
Felling and bucking	5.52	2.02
Skidding	20.71	7.57
Log loading	2.02	0.74
Short distance haulage	10.98	4.01
Monitor (supervision and inspection)	2.51	0.92
Other expenditures (e.g., administration)	13.26	4.84
Taxation	53.18	19.43
Closing reports	0.1	0.04
Long distance haulage	54.9	20.06
Total	**171.95**	**62.82**

[a] Malaysian Ringgit (MYR) 2001; [b] adjusted for inflation to spring-2023 value, assuming original values are from mid-2001 (ratio 1.59) and converted to USD (1 MYR = 0.229 USD, spring-2023 exchange rate). Adapted from FRIM and ITTO (2002), and Fisher et al. (2011)

Table 4 Descriptive statistics for four partial least square (PLS) models using data from 17 *Dipterocarpaceae* species, and 5 non-dipterocarp species grown in a common garden experiment with active restoration management in Sabah, Malaysia

Response variable	Explained variance in functional traits (%)	Explained variance in response variable (%)	Predictive accuracy of model (Q^2) (%)
Time needed to reach 30 cm dbh	33	38	23
Survival rate	47	36	21
Market price per cubic meter	23	56	32
Volume of wood per tree	63	24	18

Each model has the same 18 functional traits as the explanatory variables, but a different response variable


Observed vs predicted PLS values:
a) Model predicting time needed to reach 30 cm dbh
Observed time needed to reach 30 cm dbh (years)
PLS predicted time needed to reach 30 cm dbh (years)
0
40
80
120
Si.ir
Sh.pau
Pa.sy
Ca.sp
Pe.ad
Sh.falc
Ho.fe
Dr.ke
Dr.la
Pe.la
Pa.ma
Dio.sp
Dip.co
Pa.to
Sh.be
Sh.lept
Sh.mat
Sh.fall
Sh.ov
Sh.map
Sh.par
Sh.lepr
PLS loadings:
b)
PLS loadings
1.0
0.5
0.0
-0.5
-1.0
*
LDMC
LT
N
Na
Relative crown width
Stem slenderness
Time needed to reach 30 cm dbh (years)
c) Model predicting tree survival rate
Observed survival rate (%)
PLS predicted survival rate (%)
10
40
70
100
Pe.la
Sh.lept
Sh.ov
Pa.ma
Dr.ke
Sh.map
Sh.fall
Dr.la
Sh.falc
Dio.sp
Sh.pau
Sh.mat
Pa.sy
Dip.co
Ca.sp
Pa.to
Pe.ad
Si.ir
Sh.be
Ho.fe
Sh.par
Sh.lepr
d)
PLS loadings
LT
Relative crown depth
Relative crown length
Relative crown width
Survival rate (%)
e) Model predicting timber market value
Observed timber market value (USD/m^3)
PLS predicted timber market value (USD/m^3)
100
150
200
Dip.co
Sh.lept
Sh.falc
Dr.la
Dr.ke
Sh.ov
Pa.to
Sh.par
Pa.ma
Pa.sy
Sh.lepr
Sh.mat
Sh.map
Dio.sp
Sh.fall
Sh.pau
Sh.be
Pe.la
Ho.fe
Si.ir
Pe.ad
Ca.sp
f)
PLS loadings
Ca
K
LA
Mg
N
Na
P
pH
Relative crown depth
Relative crown length
Relative crown width
SLA
Soluble phenolics
Stem slenderness
WD
USD/ m^3

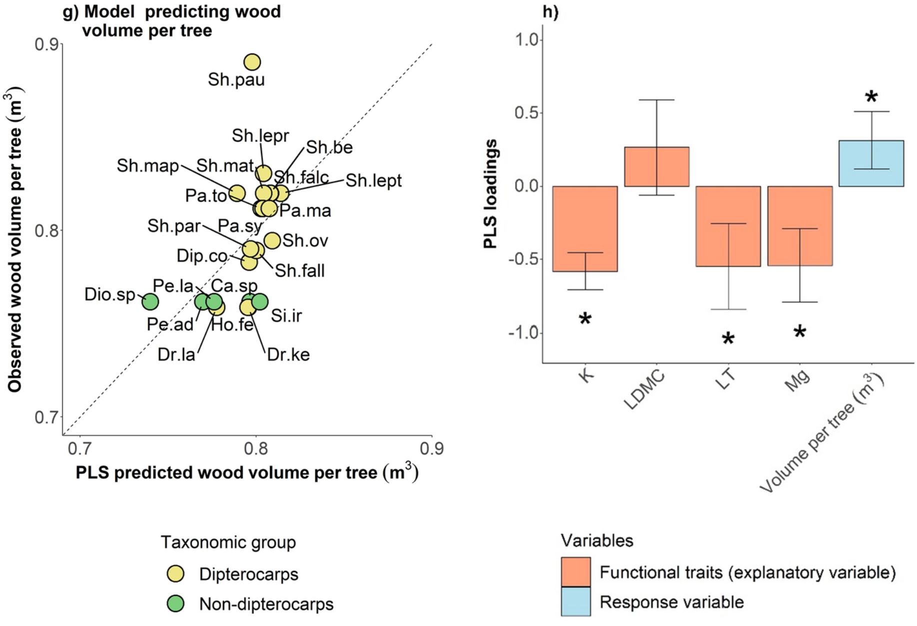


Fig. 4 (continued)

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Declarations

Conflict of interest David Alloysius worked for the Conservation & Environmental Management Division at the Yayasan Sabah Group during the study period. All other authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Tropical forests are a key source of renewable materials needed to transition to a bio-based economy free from fossil-based resources. This thesis explores how functional traits correlate to ecosystem services in tree species native to northern Borneo, specifically financial potential, ability to support associated communities, and leaf litter decomposition. It also discusses how forest management drives forests transitions between different states. The results highlight that, to support multi-functional forests, promoting tree species with complementary trait compositions should be prioritized.

Arvid Lindh received his doctoral education at the Department of Forest Ecology and Management, SLU, Umeå. He holds a Master of Science degree in Conservation Biology from Lund University.

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