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

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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.

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## 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 highlighting 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 m³ | | Survival (%) | Volume per stem at 30 cm dbh (m³) | 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

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*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)

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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 m³/ha. This greatly exceed the average volume of 152 m³/ha extracted by conventional logging in the region (Fisher et al. 2011), and those extracted from timber plantations, which rarely exceed 400 m³/ha (Cuong et al. 2020). Using 30 cm as the cutting limit gave average wood extractions of 154 m³/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):

$$V = A + B * dbh + C * dbh^2 \qquad (2)$$

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).
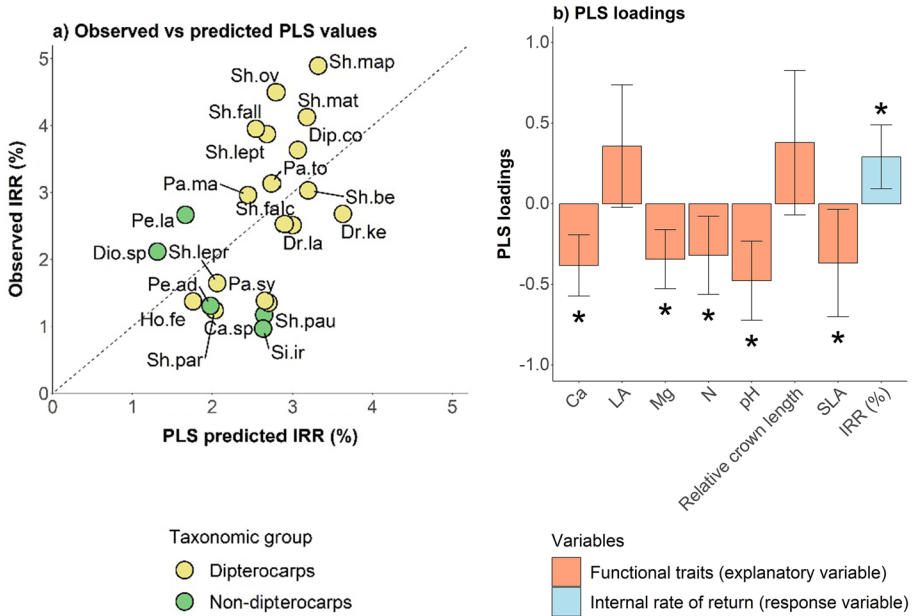
**Fig. 1** Results from a partial least square model (PLS) including data for 17 *Dipterocarpaceae* species, and 5 non-dipterocarp species grown in a common garden experiment with active restoration management in Sabah, Malaysia. Plot **a** shows observed and predicted internal rate of returns (IRR) 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
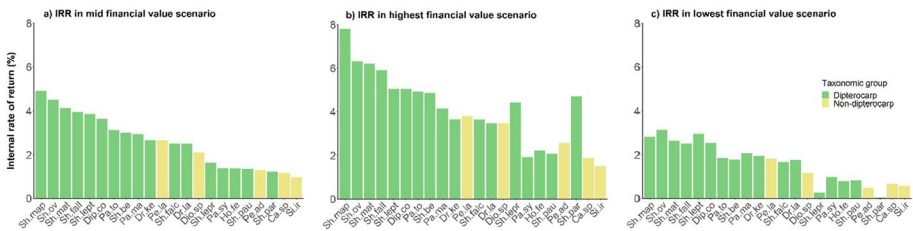


**Fig. 2** Internal rate of return (IRR) for each tree species and each scenario included in the sensitivity analysis, in which the assumed growth rate and management costs were varied. Green bars indicate species in the *Dipterocarpaceae* family; yellow bars indicate non-dipterocarp species. Components 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).
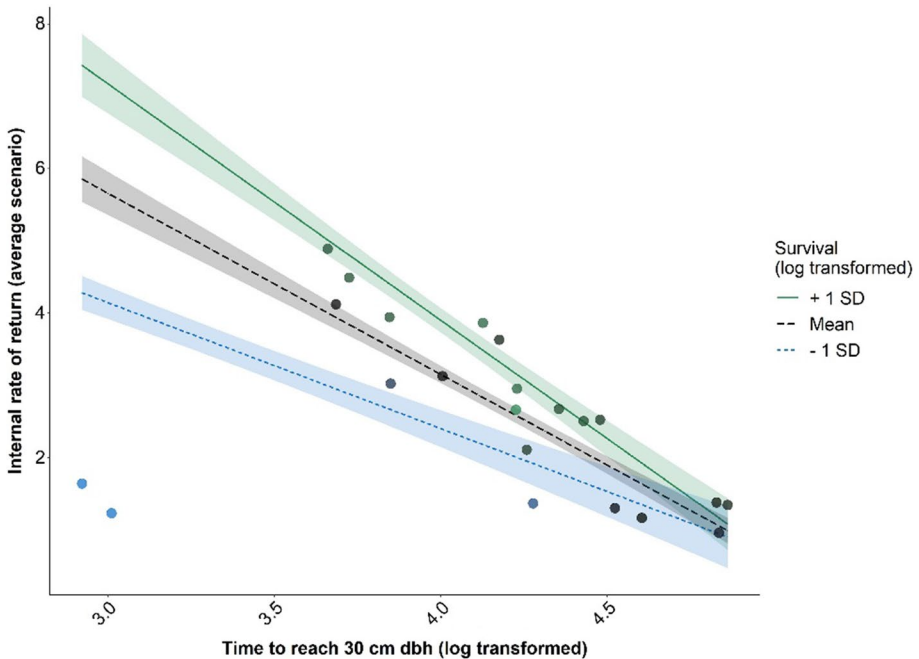


**Fig. 3** Linear regression analysis, showing the relationship between internal rate of return (IRR) and numbers of years needed to reach the size threshold for when harvest would take place in our model (30 cm dbh), for 22 tree species. Each dot represents a species, and lines represent the relationship 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
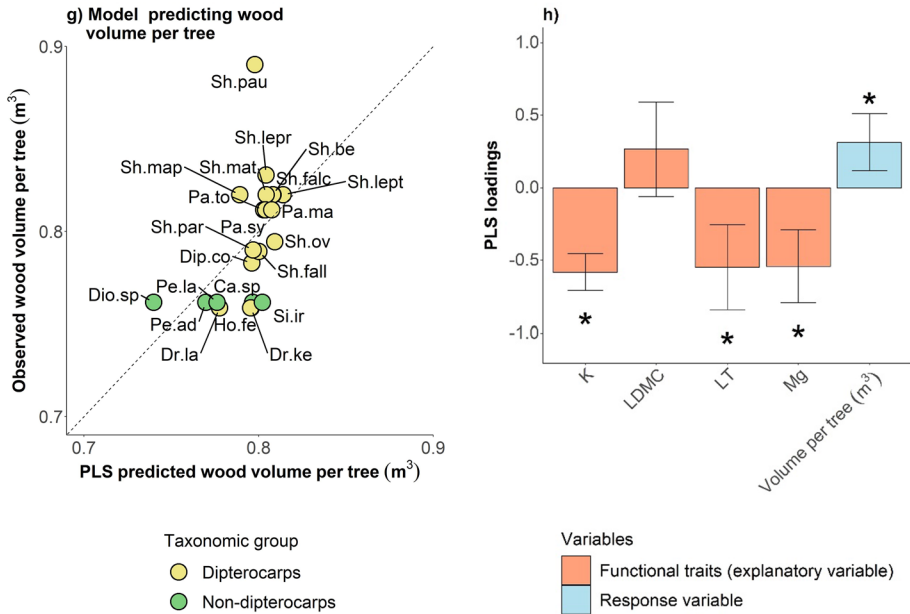
Observed vs predicted PLS values:
a) Model predicting time needed to reach 30 cm dbh

b) PLS loadings:

c) Model predicting tree survival rate

d)

e) Model predicting timber market value

f)

**Fig. 4** (continued)

## Declarations

# References

Ajani J (2011) The global wood market, wood resource productivity and price trends: an examination with special attention to China. Environ Conserv 38:53–63. https://doi.org/10.1017/S037689291 0000895

Allen SE (1989) Analysis of vegetation and organic materials. In: Allen SE (ed) Chemical analysis of ecological materials, 2nd edn. Blackwell Scientific Publications, Hoboken

Anderson J, Ingram J (1993) A handbook of methods, vol 221. CAB International, Wallingford, pp 62–65

Appanah S, Weinland G (1993) Planting quality timber trees in peninsular Malaysia—a review. Malaysian Forest Records No. 38. Forest. Research Institute Malaysia, Kepong, Kuala Lumpur

Appanah S, Turnbull JM (1998) A review of dipterocarps: taxonomy, ecology and silviculture. CIFOR, Bogor

Aquilué N, Messier C, Martins KT, Dumais-Lalonde V, Mina M (2021) A simple-to-use management approach to boost adaptive capacity of forests to global uncertainty. For Ecol Manag 481:118692. https://doi.org/10.1016/j.foreco.2020.118692

Axelsson EP, Grady KC, Lardizabal ML, Nair IB, Rinus D, Ilstedt U (2020) A pre-adaptive approach for tropical forest restoration during climate change using naturally occurring genetic variation in response to water limitation. Restor Ecol 28:156–165. https://doi.org/10.1111/rec.13030

Axelsson EP, Abin JV, Lardizabal MLT, Ilstedt U, Grady KC (2022) A trait-based plant economic framework can help increase the value of reforestation for conservation. Ecol Evol 12:e8855. https://doi.org/10.1002/ece3.8855

Axelsson EP, Ilstedt U, Alloysius D, Grady KC (2023) Elevational clines predict genetically determined variation in tropical forest seedling performance in Borneo: implications for seed sourcing to support reforestation. Restor Ecol 31:e14038. https://doi.org/10.1111/rec.14038

Barlow J, Gardner TA, Araujo IS, Ávila-Pires TC, Bonaldo AB, Costa JE, Esposito MC, Ferreira LV, Hawes J, Hernandez MIM, Hoogmoed MS, Leite RN, Lo-Man-Hung NF, Malcolm JR, Martins MB, Mestre LAM, Miranda-Santos R, Nunes-Gutjahr AL, Overal WL, Parry L, Peters SL, Ribeiro-Junior MA, da Silva MNF, da Silva Motta C, Peres CA (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc Natl Acad Sci 104:18555–18560. https://doi.org/10.1073/pnas.0703333104

Berry NJ, Phillips OL, Lewis SL, Hill JK, Edwards DP, Tawatao NB, Ahmad N, Magintan D, Khen CV, Maryati M, Ong RC, Hamer KC (2010) The high value of logged tropical forests: lessons from northern Borneo. Biodivers Conserv 19:985–997. https://doi.org/10.1007/s10531-010-9779-z

Bertault JG, Kadir K (1998) Silvicultural research in a lowland mixed dipterocarp forest of East Kalimantan: the contribution of STREK Project. Cirad-foret, Montpellier

Bieng MAN, Oliveira MS, Roda J-M, Boissière M, Herault B, Guizol P, Villalobos R, Sist P (2021) Relevance of secondary tropical forest for landscape restoration. For Ecol Manag 493:119265. https://doi.org/10.1016/j.foreco.2021.119265

Both S, Riutta T, Paine CT, Elias DM, Cruz R, Jain A, Johnson D, Kritzler UH, Kuntz M, Majalap-Lee N (2019) Logging and soil nutrients independently explain plant trait expression in tropical forests. New Phytol 221:1853–1865. https://doi.org/10.1111/nph.15444

Bryan JE, Shearman PL, Asner GP, Knapp DE, Aoro G, Lokes B (2013) Extreme differences in forest degradation in Borneo: comparing practices in Sarawak, Sabah, and Brunei. PLoS ONE 8:e69679. https://doi.org/10.1371/journal.pone.0069679

Butarbutar T, Soedirman S, Neupane PR, Köhl M (2019) Carbon recovery following selective logging in tropical rainforests in Kalimantan, Indonesia. For Ecosyst 6:36. https://doi.org/10.1186/s40663-019-0195-x

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. Ecol Lett 12:351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Chua SC, Ramage BS, Ngo KM, Potts MD, Lum SKY (2013) Slow recovery of a secondary tropical forest in Southeast Asia. For Ecol Manag 308:153–160. https://doi.org/10.1016/j.foreco.2013.07.053

Condit R, Hubbell SP, Foster RB (1996) Assessing the response of plant functional types to climatic change in tropical forests. J Veg Sci 7:405–416. https://doi.org/10.2307/3236284

Cornelissen JH, Quested H, Van Logtestijn R, Pérez-Harguindeguy N, Gwynn-Jones D, Díaz S, Callaghan TV, Press M, Aerts R (2006) Foliar pH as a new plant trait: can it explain variation in foliar chemistry and carbon cycling processes among subarctic plant species and types? Oecologia 147:315–326. https://doi.org/10.1007/s00442-005-0269-z

Crous CJ, Burgess TI, Le Roux JJ, Richardson DM, Slippers B, Wingfield MJ (2017) Ecological disequilibrium drives insect pest and pathogen accumulation in non-native trees. AoB Plants 9:plw081. https://doi.org/10.1093/aobpla/plw081

Cubbage F, Mac Donagh P, Sawinski Júnior J et al (2007) Timber investment returns for selected plantations and native forests in South America and the Southern United States. New for 33:237–255. https://doi.org/10.1007/s11056-006-9025-4

Cuong T, Chinh TTQ, Zhang Y, Xie Y (2020) Economic performance of forest plantations in Vietnam: eucalyptus, *Acacia mangium*, and *Manglietia conifera*. Forests 11:284. https://doi.org/10.3390/f11030284

Curran LM, Trigg SN, McDonald AK, Astiani D, Hardiono YM, Siregar P, Caniago I, Kasischke E (2004) Lowland forest loss in protected areas of Indonesian Borneo. Science 303:1000–1003. https://doi.org/10.1126/science.1091714

Davis AS, Jacobs DF, Dumroese RK (2012) Challenging a paradigm: toward integrating indigenous species into tropical plantation forestry. In: Stanturf J, Lamb D, Madsen P (eds) Forest landscape restoration. Springer, Berlin, pp 293–308

de Bello F, Lavorel S, Díaz S, Harrington R, Cornelissen JH, Bardgett RD, Berg MP, Cipriotti P, Feld CK, Hering D, da Silva PM, Potts SG, Sandin L, Sousa JP, Storkey J, Wardle DA, Harrison PA (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. Biodivers Conserv 19:2873–2893. https://doi.org/10.1007/s10531-010-9850-9

Díaz S, Kattge J, Cornelissen JH, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I (2016) The global spectrum of plant form and function. Nature 529:167–171. https://doi.org/10.1038/nature16489

Efron B, Gong G (1983) A leisurely look at the bootstrap, the jackknife, and cross-validation. Am Stat 37:36–48

Endara M-J, Coley PD (2011) The resource availability hypothesis revisited: a meta-analysis. Funct Ecol 25:389–398. https://doi.org/10.1111/j.1365-2435.2010.01803.x

European Commission. Directorate-General for Research Innovation (2018) Bioeconomy: the European way to use our natural resources: action plan 2018. Publications Office of the European Union

Fah LY, Mohammad A, Chung AY (2008) A guide to plantation forestry in Sabah. Sabah Forest Record, Malaysia

FAO (2018) Global forest products, facts and figures. UN Food and Agriculture Organization, Rome

FAO (2020) Global Forest Resources Assessment 2020: main report. UN Food and Agriculture Organization, Rome

Fisher B, Edwards DP, Giam X, Wilcove DS (2011) The high costs of conserving Southeast Asia's lowland rainforests. Front Ecol Environ 9:329–334. https://doi.org/10.1890/100079

Fox J, Weisberg S (2019) An R companion to applied regression, 3rd edn. Sage, Thousand Oaks. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

FRIM (Forest Research Institute Malaysia) and ITTO (International Tropical Timber Organization) (2002) A model project for cost analysis to achieve sustainable forest management: volume 2 main report. FRIM and ITTO, Kepong

FSC (Forest Stewardship Council) (2012) Strategic review on the future of forest plantations, Helsinki, Finland

Funk JL, Larson JE, Ames GM, Butterfield BJ, Cavender-Bares J, Firn J, Laughlin DC, Sutton-Grier AE, Williams L, Wright J (2017) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biol Rev 92:1156–1173. https://doi.org/10.1111/brv.12275

Ghazoul J (2016) Dipterocarp biology, ecology, and conservation. Oxford University Press, Oxford

Guillaume T, Kotowska MM, Hertel D, Knohl A, Krashevska V, Murtilaksono K, Scheu S, Kuzyakov Y (2018) Carbon costs and benefits of Indonesian rainforest conversion to plantations. Nat Commun 9:2388. https://doi.org/10.1038/s41467-018-04755-y

Gundale MJ, Sverker J, Albrectsen BR, Nilsson M-C, Wardle DA (2010) Variation in protein complexation capacity among and within six plant species across a boreal forest chronosequence. Plant Ecol 211:253–266. https://doi.org/10.1007/s11258-010-9787-9

Gustafsson M, Gustafsson L, Alloysius D, Falck J, Yap S, Karlsson A, Ilstedt U (2016) Life history traits predict the response to increased light among 33 tropical rainforest tree species. For Ecol Manag 362:20–28. https://doi.org/10.1016/j.foreco.2015.11.017

Haggar JP, Briscoe CB, Butterfield RP (1998) Native species: a resource for the diversification of forestry production in the lowland humid tropics. For Ecol Manag 106:195–203. https://doi.org/10.1016/S0378-1127(97)00311-3

Hansen MC, Stehman SV, Potapov PV, Loveland TR, Townshend JRG, DeFries RS, Pittman KW, Arunarwati B, Stolle F, Steininger MK, Carroll M, DiMiceli C (2008) Humid tropical forest clearing from 2000 to 2005 quantified by using multitemporal and multiresolution remotely sensed data. Proc Natl Acad Sci 105:9439–9444. https://doi.org/10.1073/pnas.0804042105

Hardiyanto EB, Nambiar ES (2014) Productivity of successive rotations of *Acacia mangium* plantations in Sumatra, Indonesia: impacts of harvest and inter-rotation site management. New for 45:557–575. https://doi.org/10.1007/s11056-014-9418-8

Harrison S, LaForgia M (2019) Seedling traits predict drought-induced mortality linked to diversity loss. Proc Natl Acad Sci 116:5576–5581. https://doi.org/10.1073/pnas.1818543116

Harwood CE, Nambiar EKS (2014a) Productivity of acacia and eucalypt plantations in Southeast Asia. 2. trends and variations. Int for Rev 16:249–260. https://doi.org/10.1505/146554814811724766

Harwood CE, Nambiar EKS (2014b) Sustainable plantation forestry in South-East Asia. ACIAR Technical Reports Series 84

Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples. Biometrika 76:297–307. https://doi.org/10.1093/biomet/76.2.297

Izuno A, Indrioko S, Widiyatno W, Prasetyo E, Kasmujiono K, Isagi Y (2013) Current plantation practices have negligible genetic effects on planted dipterocarps in the tropical rainforest. Silvae Genet 62:292–299. https://doi.org/10.1515/sg-2013-0035

Jones CG, Hartley SE (1999) A protein competition model of phenolic allocation. Oikos 86:27–44. https://doi.org/10.2307/3546567

Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G, Garnier E, Westoby M, Reich PB, Wright IJ, Cornelissen JHC, Violle C, Harrison SP, Van Bodegom PM, Reichstein M, Enquist BJ, Soudzilovskaia NA, Ackerly DD, Anand M, Atkin O, Bahn M, Baker TR, Baldocchi D, Bekker R, Blanco CC, Blonder B, Bond WJ, Bradstock R, Bunker DE, Casanoves F, Cavender-Bares J, Chambers JQ, Chapin FS III, Chave J, Coomes D, Cornwell WK, Craine JM, Dobrin BH, Duarte L, Durka W, Elser J, Esser G, Estiarte M, Fagan WF, Fang J, Fernández-Méndez F, Fidelis A, Finegan B, Flores O, Ford H, Frank D, Freschet GT, Fyllas NM, Gallagher RV, Green WA, Gutierrez AG, Hickler T, Higgins SI, Hodgson JG, Jalili A, Jansen S, Joly CA, Kerkhoff AJ, Kirkup D, Kitajima K, Kleyer M, Klotz S, Knops JMH, Kramer K, Kühn I, Kurokawa H, Laughlin D, Lee TD, Leishman M, Lens F, Lenz T, Lewis SL, Lloyd J, Llusià J, Louault F, Ma S, Mahecha MD, Manning P, Massad T, Medlyn BE, Messier J, Moles AT, Müller SC, Nadrowski K, Naeem S, Niinemets Ü, Nöllert S, Nüske A, Ogaya R, Oleksyn J, Onipchenko VG, Onoda Y, Ordoñez J, Overbeck G, Ozinga WA, Patiño S, Paula S, Pausas JG, Peñuelas J, Phillips OL, Pillar V, Poorter H, Poorter L, Poschlod P, Prinzing A, Proulx R, Rammig A, Reinsch S, Reu B, Sack L, Salgado-Negret B, Sardans J, Shiodera S, Shipley B, Siefert A, Sosinski E, Soussana J-F, Swaine E, Swenson N, Thompson K, Thornton P, Waldram M, Weiher E, White M, White S, Wright SJ, Yguel B, Zaehle S, Zanne AE, Wirth C (2011) TRY—a global database of plant traits. Glob Change Biol 17:2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Kenward MG, Roger JH (1997) Small sample inference for fixed effects from restricted maximum likelihood. Biometrics. https://doi.org/10.2307/2533558

King DA, Davies SJ, Noor NSM (2006) Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. For Ecol Manag 223:152–158. https://doi.org/10.1016/j.foreco.2005.10.066

Kraft NJB, Valencia R, Ackerly DD (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. Science 322:580–582. https://doi.org/10.1126/science.1160662

Kulbat K (2016) The role of phenolic compounds in plant resistance. Biotechnol Food Sci 80:97–108. https://doi.org/10.34658/bfs.2016.80.2.97-108

Kurokawa H, Nakashizuka T (2008) Leaf herbivory and decomposability in a Malaysian tropical rain forest. Ecology 89:2645–2656. https://doi.org/10.1890/07-1352.1

Lamb D (1998) Large-scale ecological restoration of degraded tropical forest lands: the potential role of timber plantations. Restor Ecol 6:271–279. https://doi.org/10.1046/j.1526-100X.1998.00632.x

Lamb D, Erskine PD, Parrotta JA (2005) Restoration of degraded tropical forest landscapes. Science 310:1628–1632. https://doi.org/10.1126/science.1111773

Latif J, Mohd N, Tayeb D, Kushairi D (2003) Economics of higher planting density in oil palm plantations. Oil Palm Ind Econ J 3:32–39

Lee Y (2003) Preferred check-list of Sabah trees. Natural History Pub. (Borneo) in association with Sabah Forestry Dept

Lopez J, De La Torre R, Cubbage F (2010) Effect of land prices, transportation costs, and site productivity on timber investment returns for pine plantations in Colombia. New for 39:313–328. https://doi.org/10.1007/s11056-009-9173-4

Lussetti D, Axelsson EP, Ilstedt U, Falck J, Karlsson A (2016) Supervised logging and climber cutting improves stand development: 18 years of post-logging data in a tropical rain forest in Borneo. For Ecol Manag 381:335–346. https://doi.org/10.1016/j.foreco.2016.09.025

Mackensen J, Fölster H (2000) Cost-analysis for a sustainable nutrient management of fast growing-tree plantations in East-Kalimantan, Indonesia. For Ecol Manag 131:239–253. https://doi.org/10.1016/S0378-1127(99)00217-0

MacKinnon K (1996) The ecology of Kalimantan. Periplus Editions, Hong Kong

Makkonen M, Berg MP, Handa IT, Hättenschwiler S, van Ruijven J, van Bodegom PM, Aerts R (2012) Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. Ecol Lett 15:1033–1041. https://doi.org/10.1111/j.1461-0248.2012.01826.x

Malhi Y, Gardner TA, Goldsmith GR, Silman MR, Zelazowski P (2014) Tropical Forests in the Anthropocene. Annu Rev Environ Resour 39:125–159. https://doi.org/10.1146/annurev-environ-030713-155141

Manokaran N, Kochummen, KM (1994) Tree growth in primary lowland and hill dipterocarp forests. J Trop For Sci 6:332–345

Messier C, Bauhus J, Doyon F, Maure F, Sousa-Silva R, Nolet P, Mina M, Aquilué N, Fortin M-J, Puettmann K (2019) The functional complex network approach to foster forest resilience to global changes. For Ecosyst 6:1–16. https://doi.org/10.1186/s40663-019-0166-2

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853. https://doi.org/10.1038/35002501

Nasution A, Glen M, Beadle C, Mohammed C (2019) Ceratocystis wilt and canker—a disease that compromises the growing of commercial Acacia-based plantations in the tropics. Aust for 82:80–93. https://doi.org/10.1080/00049158.2019.1595347

Noormahayu M, Khalid A, Elsadig M (2009) Financial assessment of oil palm cultivation on peatland in Selangor, Malaysia. Mires Peat 5:1–18

Osunkoya OO, Othman FE, Kahar RS (2005) Growth and competition between seedlings of an invasive plantation tree, *Acacia mangium*, and those of a native Borneo heath-forest species, *Melastoma beccarianum*. Ecol Res 20:205–214. https://doi.org/10.1007/s11284-004-0027-4

Osunkoya OO, Omar-Ali K, Amit N, Dayan J, Daud DS, Sheng TK (2007) Comparative height–crown allometry and mechanical design in 22 tree species of Kuala Belalong rainforest, Brunei, Borneo. Am J Bot 94:1951–1962. https://doi.org/10.3732/ajb.94.12.1951

Panagos P, Jones A, Bosco C, Senthil Kumar PS (2011) European digital archive on soil maps (EuDASM): preserving important soil data for public free access. Int J Digit Earth 4:434–443. https://doi.org/10.1080/17538947.2011.596580

Patiño S, Fyllas NM, Baker TR, Paiva R, Quesada CA, Santos AJB, Schwarz M, ter Steege H, Phillips OL, Lloyd J (2012) Coordination of physiological and structural traits in Amazon forest trees. Biogeosciences 9:775–801. https://doi.org/10.5194/bg-9-775-2012

Peel MC, Finlayson BL, McMahon TA (2007) Updated world map of the Köppen-Geiger climate classification. Hydrol Earth Syst Sci 11:1633–1644. https://doi.org/10.5194/hess-11-1633-2007

Perez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE (2016) Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 64:715–716. https://doi.org/10.1071/BT12225_CO

Philipson CD, Dent DH, O'Brien MJ, Chamagne J, Dzulkifli D, Nilus R, Philips S, Reynolds G, Saner P, Hector A (2014) A trait-based trade-off between growth and mortality: evidence from 15 tropical tree species using size-specific relative growth rates. Ecol Evol 4:3675–3688. https://doi.org/10.1002/ece3.1186

Philipson CD, Cutler ME, Brodrick PG, Asner GP, Boyd DS, Costa PM, Fiddes J, Foody GM, Van Der Heijden GM, Ledo A (2020) Active restoration accelerates the carbon recovery of human-modified tropical forests. Science 369:838–841. https://doi.org/10.1126/science.aay4490

Piotto D, Vıquez E, Montagnini F, Kanninen M (2004) Pure and mixed forest plantations with native species of the dry tropics of Costa Rica: a comparison of growth and productivity. For Ecol Manag 190:359–372. https://doi.org/10.1016/j.foreco.2003.11.005

POWO (2022) Plants of the world online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet. http://www.plantsoftheworldonline.org/. Retrieved 08 April 2022

Putz FE, Dykstra DP, Heinrich R (2000) Why poor logging practices persist in the tropics. Conserv Biol 14:951–956. https://doi.org/10.1046/j.1523-1739.2000.99137.x

Quenouille MH (1949) Approximate tests of correlation in time-series 3. Math Proc Camb Philos Soc 45(3):483–484. https://doi.org/10.1017/S0305004100025123

Reich PB (2014) The world-wide 'fast–slow'plant economics spectrum: a traits manifesto. J Ecol 102:275–301. https://doi.org/10.1111/1365-2745.12211

Reynolds G, Payne J, Sinun W, Mosigil G, Walsh RP (2011) Changes in forest land use and management in Sabah, Malaysian Borneo, 1990–2010, with a focus on the Danum Valley region. Philos Trans R Soc Lond B Biol Sci 366:3168–3176. https://doi.org/10.1098/rstb.2011.0154

Rimbawanto A (2006) Silviculture systems of Indonesia´s dipterocarps forest management: a lesson learned. Fakultas Kehutanan Universitas Gadjah Mada, Yogyakarta

Running SW, Nemani RR, Heinsch FA, Zhao M, Reeves M, Hashimoto H (2004) A continuous satellite-derived measure of global terrestrial primary production. Bioscience 54:547–560. https://doi.org/10.1641/0006-3568(2004)054[0547:ACSMOG]2.0.CO;2

Ruslandi, Romero C, Putz FE (2017) Financial viability and carbon payment potential of large-scale silvicultural intensification in logged dipterocarp forests in Indonesia. For Policy Econ 85:95–102. https://doi.org/10.1016/j.forpol.2017.09.005

Sabah Forestry Department (2016) Production & export statistics of forest products 2016. Economy, Industry & Statistics Division, Sabah Forestry Department, Sandakan

Sabah Forestry Department (2017) Production & export statistics of forest products 2017. Economy, Industry & Statistics Division, Sabah Forestry Department, Sandakan

Sarshar D (2012) Hardwood timber supply & demand in Asia: an opportunity for Hardwood plantation investment. New Forests, Singapore

Satterthwaite FE (1941) Synthesis of variance. Psychometrika 6:309–316. https://doi.org/10.1007/BF02288586

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675. https://doi.org/10.1038/nmeth.2089

Schulze PC, Leighton M, Peart DR (1994) Enrichment planting in selectively logged rain forest: a combined ecological and economic analysis. Ecol Appl 4:581–592. https://doi.org/10.2307/1941959

Singleton VL, Rossi JA (1965) Colorimetry of total phenolics with phosphomolybdic-phosphotungstic acid reagents. Am J Enol Vitic 16:144–158. https://doi.org/10.5344/ajev.1965.16.3.144

Sist P, Fimbel R, Sheil D, Nasi R, Chevallier M-H (2003) Towards sustainable management of mixed dipterocarp forests of South-east Asia: moving beyond minimum diameter cutting limits. Environ Conserv 30:364–374. https://doi.org/10.1017/S0376892903000389

Slik JF, Arroyo-Rodríguez V, Aiba SI et al (2015) An estimate of the number of tropical tree species. Proc Natl Acad Sci 112:7472–7477. https://doi.org/10.1073/pnas.1423147112

Soepadmo E, Wong KM (1995) Tree Flora of Sabah and Sarawak, vol 1. Sabah Forestry Department, Forest Research Institute Malaysia, Sarawak Forestry Department, Kuala Lumpur

Soepadmo E, Saw LG (2000) Tree Flora of Sabah and Sarawak, vol 3. Sabah Forestry Department, Forest Research Institute Malaysia, Sarawak Forestry Department, Kuala Lumpur

Soepadmo E, Wong KM, Saw LG (1996) Tree Flora of Sabah and Sarawak, vol 2. Sabah Forestry Department, Forest Research Institute Malaysia, Sarawak Forestry Department, Kuala Lumpur

Soepadmo E, Guan SL, Chung RCK (2002) Tree Flora of Sabah and Sarawak, vol 4. Sabah Forestry Department, Forest Research Institute Malaysia, Sarawak Forestry Department, Kuala Lumpur

Soepadmo E, Saw LG, Chung RCK (2004) Tree Flora of Sabah and Sarawak, vol 5. Sabah Forestry Department, Forest Research Institute Malaysia, Sarawak Forestry Department, Kuala Lumpur

Soepadmo E, Saw LG, Chung RCK, Kiew R (2007) Tree Flora of Sabah and Sarawak, vol 6. Sabah Forestry Department, Forest Research Institute Malaysia, Sarawak Forestry Department, Kuala Lumpur

Sterck FJ, Bongers F, Newbery DM (2001) Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. Plant Ecol 153:279–292. https://doi.org/10.1023/A:1017507723365

Sterck FJ, Poorter L, Schieving F (2006) Leaf traits determine the growth-survival trade-off across rain forest tree species. Am Nat 167:758–765. https://doi.org/10.1086/503056

Straka TJ, Bullard SH (1996) The land expectation value calculated in timberland valuation. Apprais J 64:399–405

Subiakto A, Rachmat HH, Sakai C (2016) Choosing native tree species for establishing man-made forest: a new perspective for sustainable forest management in changing world. Biodiversitas J Biol Divers. https://doi.org/10.13057/biodiv/d170233

Sullivan MJ, Lewis SL, Affum-Baffoe K et al (2020) Long-term thermal sensitivity of Earth's tropical forests. Science 368:869–874. https://doi.org/10.1126/science.aaw7578

Svatoňová T, Herák D, Kabutey A (2015) Financial profitability and sensitivity analysis of palm oil plantation in Indonesia. Acta Univ Agric Silvic Mendel Brun 63:1365–1373. https://doi.org/10.11118/actaun201563041365

Symington CF, Ashton PS, Appanah S (2004) Foresters' manual of Dipterocarps. Forest Research Institute Malaysia, Kuala Lumpur

Thomas E, Jalonen R, Loo J, Boshier D, Gallo L, Cavers S, Bordács S, Smith P, Bozzano M (2014) Genetic considerations in ecosystem restoration using native tree species. For Ecol Manag 333:66–75. https://doi.org/10.1016/j.foreco.2014.07.015

Venn TJ (2005) Financial and economic performance of long-rotation hardwood plantation investments in Queensland, Australia. For Policy Econ 7:437–454. https://doi.org/10.1016/j.forpol.2003.08.003

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116:882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Walsh RPD, Newbery DM (1999) The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. Philos Trans R Soc Lond Ser B: Biol Sci 354:1869–1883. https://doi.org/10.1098/rstb.1999.0528

Wildayana E (2016) Formulating oil palm investment decision in tidal wetlands of South Sumatra, Indonesia. J Wetlands Environ Manag. https://doi.org/10.20527/jwem.v2i2.48

Wills J, Herbohn J, Hu J, Sohel S, Baynes J, Firn J (2018) Tree leaf trade-offs are stronger for sub-canopy trees: leaf traits reveal little about growth rates in canopy trees. Ecol Appl 28:1116–1125. https://doi.org/10.1002/eap.1715

Winarni B, Lahjie A, Simarangkir B, Yusuf S, Ruslim Y (2018) Forest gardens management under traditional ecological knowledge in West Kalimantan, Indonesia. Biodiversitas 19:77–84. https://doi.org/10.13057/biodiv/d190113

Wong TM (1982) A dictionary of Malaysian timbers. Forest Research Institute Malaysia, Kuala Lumpur

Wright JS (2010) The future of tropical forests. Ann N Y Acad Sci 1195:1–27. https://doi.org/10.1111/j.1749-6632.2010.05455.x

WWF (2012a) Living forests report: Forest products. WWF, Gland

WWF (2012b) Living forests report: forests and energy. WWF, Gland

Yamada T, Moriwaki Y, Okuda T, Kassim AR (2016) Long-term effects of selective logging on dipterocarp populations in the Pasoh Forest Reserve, Malaysia. Plant Ecol Divers 9:615–626. https://doi.org/10.1080/17550874.2016.1185653

Zanne AE, Lopez-Gonzalez G, Coomes DA, Ilic J, Jansen S, Lewis SL, Miller RB, Swenson NG, Wiemann MC, Chave J (2009) Data from: towards a worldwide wood economics spectrum, Dryad, Dataset