

Cicik Udayana

Forest rehabilitation, biodiversity and ecosystem services in Java, Indonesia



PhD Thesis

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Abstract

Planting trees in deforested areas is regarded as important to increase the provision of ecosystem services, and enhancing biodiversity. Planting a desired tree species is termed rehabilitation. Biodiversity is the basis of ecosystem services, and as a rule, but not always, the two co-vary. The focus of forest restoration is changing from the provision of timber to a wider provisioning of different species of timber, various non-timber forest products and flood and erosion control. Biodiversity often increases with such wide-ranging service provision, although the resulting restored ecosystems do not include all species of primary forests. In Java, Indonesia, forests have been mainly rehabilitated by planting monocultures of exotic teak, *Tectona grandis* L.f., or mahogany, *Swietenia macrophylla* King. In this thesis, I investigate the effects of such rehabilitation on biodiversity components and ecosystem services and their changes over time since rehabilitation. Understory species richness, density, Shannon-Wiener diversity index, and the proportion of native plants, did not differ between the planted stand types or between them and the native forests. The proportion of native herbs and seedlings, species richness and Shannon-Wiener diversity index of saplings increased with time since rehabilitation. However, species composition differed between the two stand types, and between them and the native forest. Soil organic matter, concentration of total phosphorus, total nitrogen and total potassium, varied with soil order and altitude but largely not with stand type. Soil pH decreased with time since rehabilitation, and mahogany stands had a lower pH than teak stands. The number of useful herbs and useful exotic sapling species was highest in teak stands. The number of sapling species used as medicine, food and for construction increased with time since rehabilitation, while fodder and ornamental plants did not change over time. Useful exotic-annual, exotic-perennial, and native-perennial herbs decreased with increasing time since rehabilitation. I conclude that forest rehabilitation has had positive impacts with regard to species richness, Shannon-Wiener diversity index, plant density and proportion of native species of the understory plant community. Species composition, however, varied between the stand types and between planted stands and the native forest. To approach the species composition of natural ecosystems for their long-term functioning and the delivery of ecosystem services, forest rehabilitation should focus on plant community composition and biodiversity of native forests. This may require rehabilitation with a higher diversity of indigenous tree species, and perhaps zonation schemes, rather than only monocultures of teak or mahogany.

Key words: annual species, biodiversity, ecosystem services, exotic species, mahogany, native species, perennial species, forest rehabilitation, species diversity, species richness, teak, useful species.

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Sammendrag

Planting av trær i degraderte områder er en viktig restaureringsstrategi for å øke forsyningen av økosystemtjenester. Når vi planter spesifikke arter for enkelte formål, for eksempel tømmerproduksjon, kaller vi det rehabilitering. Biodiversitet er fundamentet for økosystemtjenester, og ofte, men ikke alltid, henger disse tett sammen. I mange tropiske områder, har fokuset for skogrestaurering endret seg i takt med økende avskoging, fra tømmerproduksjon til et bredere spektrum av økosystemtjenester som medisin, mat, dyrefôr, brensel, rent vann og regulering av flom og jordskred. Ved å ha et bredere fokus på økosystemtjenester ved restaurering, kan også biologisk mangfold bli bevart. På Java, i Indonesia, har eksotiske arter som mahogni *Swietenia macrophylla* King. og teak *Tectona grandis* L. f. blitt plantet for å rehabilitere degraderte skogområder. I denne avhandlingen undersøker jeg effekten av denne rehabiliteringen på biodiversitet og økosystemtjenester, og hvordan de endres over tid siden rehabilitering. Jeg fant at artsrikhet, Shannon-Wiener diversitetsindeks, og andel naturlig forekommende plantearter viste ingen forskjeller mellom bestand plantet med teak eller mahogni, eller mellom rehabilitert skog og naturskog. Andel naturlig forekommende urter og frøplanter og artsrikhet og diversitet av ungtrær økte med økende tid siden rehabilitering. Men artssammensetningen skilte seg mellom bestand av teak og mahogni, og mellom rehabilitert og naturlig skog. Innhold av organisk materiale i jordsmonnet og konsentrasjonen av totalt fosfor, nitrogen og kalium varierte ikke mellom bestand av teak og mahogni. Jordsmonnets egenskaper viste sammenheng med tetthet av urter, frøplanter og ungtrær. pH i jordsmonnet minket med økende tid siden rehabilitering, og var lavere i mahognibestand enn i teak. Antall nyttige urter og eksotiske ungtrær var høyest i bestand av teak. Antall arter brukt til medisin, mat og konstruksjon økte med økende tid siden rehabilitering, mens planter brukt som dyrefôr og pryddplanter endret seg ikke over tid. Nyttige eksotiske ettårige og flerårige urter, og naturlig forekommende flerårige urter minket med økende tid siden rehabilitering, mens andel naturlig forekommende ettårige urter økte med økende tid. Jeg konkluderer med at skogsrehabilitering har hatt positive effekter på artsrikhet, diversitet, tetthet og andel naturlig forekommende arter i felt- og busksjiktet, i tillegg til jordsmonnet og nytteplanter. Dette kan skyldes at de rehabiliterte områdene har ikke blitt hogd, og noen har fått lov å bli gamle (> 70 år). Artssammensetningen var derimot forskjellig mellom rehabilitert skog og naturlig skog, og mellom mahogni og teak. For å oppnå funksjonen og forsyningen av økosystemtjenester tilsvarende naturlige økosystemer, bør rehabilitering fokusere mer på naturlig plantesammensetning og diversitet.

List of papers

This thesis is based on the following original publications and submitted manuscripts, listed below.

Paper I:

Udayana, C., Andreassen, H.P., and Skarpe, C. Understory diversity and composition after planting of Teak and Mahogany, Yogyakarta, Indonesia. (Submitted to Journal of Sustainable Forestry).

Paper II:

Udayana, C., Skarpe, C., Solberg, S.Ø., Mathisen, K.M., and Andreassen, H.P. Soil properties after forest rehabilitation by planting teak and mahogany in Java, Indonesia. (2019). Forest Science and Technology. <https://doi.org/10.1080/21580103.2019.1673220>

Paper III:

Udayana, C., Andreassen, H.P., and Skarpe, C. (2019). Wood and non-wood forest products of Central Java, Indonesia. *Journal of Sustainable Forestry*, 38, 715-732.

Preface

To date, forest rehabilitation is a major concern of the Government of Indonesia to conserve biodiversity and ecosystem services. My study is the first to compare forest rehabilitation between teak and mahogany stands and native forest in Yogyakarta, Indonesia, and I have a unique data set with rehabilitated stands up to 74 years old. This PhD thesis is a scientific study, which revealed the benefit of rehabilitation on biodiversity and ecosystem services.

Many people contributed on this thesis. I am deeply thankful to all people and institutions that supported me during fieldwork, data analysis and writing phases of my PhD thesis. First of all, I would like to express my special appreciation and thanks to Associate professor Karen Marie Mathisen and Professor Harry P. Andreassen my main supervisors and Professor Christina Skarpe my co-supervisor. Karen Marie, your presence encouraged me to finish this thesis. You are always being available for help and discussions, and I appreciate that a lot. Christina Skarpe stayed several days in Wanagama, Yogyakarta to accompany me during field work. It was wonderful to observe vegetation with you. You have also taught me to use CANOCO, thank you very much. I was very sad when I lost Harry. He was a person who helped me with administrative stuff for PhD admission and provided me a nice reception when I arrived at Evenstad the first time. I deeply appreciated his support and kindness. I miss you forever, Harry. The three of you are great scientists who have helped me with patience, kindness and professionalism. Your guidance and persistent help make my goal possible. Thank you to have shared your knowledge with me and for helping me grow as a researcher.

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Evenstad, October 2019

Cicik Udayana

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1. Introduction

1.1 Ecosystem services, biodiversity, forest degradation and deforestation

Ecosystem services constitute the direct and indirect benefits to humans from ecosystems (Costanza et al. 1997; Millennium Ecosystem Assessment 2005; Chapin et al. 2006; Gamfeldt et al. 2013). We depend on these ecosystem services to a large extent. Ecosystem services have been divided into (1) *provisioning services*, such as timber, water, and non-timber forest products; (2) *cultural services*, providing recreational or spiritual benefits; (3) *regulating services* affecting climate, carbon sequestration, pollination, soil erosion, floods and water quality; and (4) *supporting services* such as soil formation, nutrient cycling and photosynthesis (Aerts and Honnay 2011). Some authors (Van Noordwijk et al. 2012) call all ecosystem services, except the provisional ones, for environmental services, which might to some extent facilitate the discussion. Here we stick, however, to the generally accepted ecosystem services. Many of the regulating and supporting ecosystem services are positively correlated with each other, while our exploitation of provisioning and cultural services seem largely to be a trade-off with regulating and supporting services (Lee and Lautenbach 2016). For example, clearing forests for increased agricultural production (provision of ecosystem services) in a recreational region may decrease the benefit of cultural ecosystem services, and may decrease the provision of regulating and supporting services.

Biodiversity is the variety and variability of life on all scales. It includes the variety between and within ecosystems, the variety of species within an ecosystem, and genetic variety within species and populations (Millennium Ecosystem Assessment 2005). Biodiversity is the basis for ecosystem services, and usually biodiversity and the provision of ecosystem services co-vary (Harrison et al. 2014), but this is not always the case (Bullock et al. 2011).

Forests are the most important terrestrial habitat with regard both to biodiversity and to the variety of ecosystem services delivered. Forests are sources of food, medicine and fuel for more than a billion people (FAO 2018), help mitigate climate change, and hold more than three-quarters of the world's terrestrial biodiversity (FAO 2018). However, ecosystem services are threatened by human degradation of biodiversity, and we now depend on the restoration of biodiversity to provide necessary structures for ecosystems to function well (Palmer et al. 1997; Lamb et al. 2005; Ruiz-Jaén and Aide 2005; Sabogal et al. 2015; Lamb 2018).

Deforestation is human efforts to convert forest lands to other purpose of land use (UNFCCC 2001) that implies the long-term or permanent loss of forest cover resulting in the transformation of forests into other land cover types (Sasaki and Putz 2009). Deforestation includes forests converted to agriculture, pasture, water reservoirs and urban areas, and, hence, with profoundly changed biodiversity (FAO 2001). Forest degradation arises from changes in the forest biodiversity which negatively affect the structure or function of ecosystems, and thus their capacity to supply ecosystem services (FAO 2001; ITTO 2002).

1.2 Indonesian forest cover and deforestation

Naturally, almost all Indonesia was covered by forest. Crop production became important around 3000 BC, and forest clearings increased over the millennia with an increasing human population and improved technology. Later, timber became valuable in itself, and from about 1700 the Dutch East India Company logged the Indonesian forests for the international market (Department of Forestry 1986). Deforestation mainly, but far from exclusively, occurs in tropical regions (ITTO 2002; Lamb et al. 2005; Norris 2016). Globally, the loss of Indonesia's primary rainforest ranks third after the Democratic Republic of Congo (DRC) and Brazil, with about 46% (339,888 ha) lost by 2018 (World Resources Institute 2019). In 1950, the total forest cover in Indonesia was about 193 million ha (Hannibal 1950). However, 59 million ha (31%) of forest has been lost from 1950 to 1997 (Tsujino et al. 2016), and a further 6.02 million ha of primary forests was lost from 2000 to 2012 (Margono et al. 2014). In 2016, Indonesia had lost about 38% of the forest cover present in 1950 (Grainger 2008; Ministry of Environment and Forestry 2017b). The last few years the deforestation rate has declined, because of more attention from the government (Ministry of Environment and Forestry 2018).

Java, with an area of 129,438.28 km², is Indonesia's most densely populated island. The island covers only 7% of the total area of Indonesia, but has 57% of the country's total population (more than 145 million people). The population density was 1,055 people per km² in 2015 (Statistics Indonesia 2016). Java's forest cover was around 2.2 million ha in 2000. It continued to diminish, with about 60% lost by 2009, leaving 800,000 ha (Forest Watch Indonesia 2011). High population pressure has been considered a cause of deforestation (Sunderlin and Resosudarmo 1999; Verburg and Bouma 1999). Forest clearing is directly driven by factors such as settlement, road construction, international trading demands, and forest fires (Sunderlin and Resosudarmo 1996; Geist and Lambin 2001).

Java's forests became a Dutch trading commodity when the Dutch East India Company gained access to Indonesia in the 1600s. Between the 1800s and Indonesia's independence in 1945, the Dutch and the Japanese monopolized the forestry sector, particularly regarding teak, for commercial trading activities (Department of Forestry 1986; Peluso 1992; Whitten et al. 1996). Java has experienced massive deforestation since the 1700s (Department of Forestry 1986) through exploitation for fuelwood and timber, forest conversion into coffee plantations, settlement areas, and illegal logging. After deforestation in Java during colonial times, some areas were left without vegetation. Various attempts to cultivate the land by the colonial powers, such as coffee plantations, failed. Degradation of the forests continued unabated due to major changes in the political situation. In 1998, the forests experienced pressures from illegal logging and forest encroachment when the incumbent President Soeharto resigned (Nawir et al. 2007).

1.3 Relationship between forest restoration, biodiversity and ecosystem services

The need to restore forests is almost universal, and the focus of restoration is changing. Where earlier a few ecosystem services were targeted, often timber, the need now is for a variety of timber and non-timber forest products, pollination, water, flood mitigation, carbon sequestration and mitigation of the changing climate (World Bank 2014). To meet these demands, restoration needs to go beyond the planting of one exotic timber tree, to a more complete restoration of biodiversity. Biodiversity is the provider of ecosystem services, but the relationship is not always direct (Bullock et al. 2011; Harrison et al. 2014). Mostly, a diverse production of ecosystem services corresponds to high biodiversity (Millennium Ecosystem Assessment 2005; Díaz et al. 2007). But a concentration on one or a few services can cause a decrease in biodiversity, and some have expressed a general fear that a focus on ecosystem services could jeopardize biodiversity (McCauley 2006). Bullock et al. (2011) did a meta-analysis of 89 restoration projects which indicated mainly positive correlation between biodiversity and ecosystem services, but they stress that there is not necessarily a causal relationship. Restoration projects focus often on production purposes, and are therefore designed specifically for ecosystem services not for biodiversity, but there is the hope for a positive correlation between ecosystem services provided and biodiversity. Also, time since the restoration started is important. Many species contribute both to biodiversity and the delivery of ecosystem services, in that, for example, trees provide timber and fuel, and at the same time are an essential part of a functioning ecosystem, providing food and habitat for

many other species. Similarly, other smaller plants provide fodder, ornament, material for construction and handicrafts and, together with many animals, food, and are also part of the functioning ecosystem.

Indonesia is home to one of the world's richest biological species diversity (USAID 2008). The tropical climate of the country supports a large number of species of animals and plants in natural tropical forests. This natural biodiversity is important to the Indonesian society (World Bank 2014). Around 40 million people directly or indirectly depend on forest, marine, coastal and agricultural ecosystems for income (UNCSD 1997). For people's daily lives, more than 6,000 species of plants and animals are used for food, handicrafts, medicines, fuel, and building materials (World Bank 1994). However, the loss of the forest cover has led to that some species are threatened with extinction, such as orangutan Sumatra *Pongo abelii*, orangutan Borneo *Pongo pygmaeus* (Ministry of Environment and Forestry 2017a). The Bali tiger *Panthera tigris balica* went extinct in the 1940s followed by Javan tiger *Panthera tigris javanica* in the 1980s (Panthera 2015). Many species of birds, amphibians and plants are also threatened (Sala et al. 2000; Sodhi et al. 2004).

The term "ecological restoration" is used to describe any process of assisting the recovery of biodiversity that has been degraded, damaged, or destroyed (SER 2004), with the aim of creating an ecosystem that is maintained by sustained ecosystem functions, including interactions among living organisms, soil building and maintenance, energy flow, and hydrological and chemical cycling (Ehrenfeld 2000). Stanturf et al. (2014) defined four strategies of forest restoration: (1) *rehabilitation* by restoring desired species composition, structure or processes; (2) *reconstruction* to restore original plant communities; (3) *reclamation* to restore land, which is devoid of vegetation; and (4) *replacement* of species with other species as a response to, for instance, climate change. I focus on rehabilitation in this thesis.

Teak plantations were developed by Hindus who migrated to Java around the 4th century. They planted teak using seeds brought from India (Ministry of Forestry 1986). The teak was a valuable tree species for the Hindus' belief that it would bring them prosperity (Nawir et al. 2007). Even though teak has allelopathic properties (Biswas and Das 2016), it is still planted. Up to now, Indonesian teak forests are mainly found in Java island (Pratiwi and Lust 1994).

More recently, forest rehabilitation has been carried out in Indonesia since colonial times. Since 1951, the Government of Indonesia has adopted a programme to rehabilitate degraded forests and lands (*Rehabilitasi hutan dan lahan-RHL*) (Santoso 2012). Following major floods in 1966 in Solo, Central Java, the government was forced to introduce more serious rehabilitation initiatives. In this period, conservation farming was implemented in sloping areas by applying soil and water conservation methods (Nawir et al. 2007) in order to reduce erosion and increase water holding capacity. Subsequently, in 2003, the Ministry of Forestry initiated a national movement for forest and land rehabilitation (*Gerakan nasional rehabilitasi hutan dan lahan-GNRHL /Gerhan*), in order to restore the degraded forests and lands. The rehabilitation program is divided into two types of reforestation (*reboisasi*) in the state forests and afforestation or greening (*penghijauan*) outside of the state forests. The objectives of the rehabilitation programs are to restore well-functioning forest ecosystems mainly for timber production and for conservation and protection of biodiversity by involving local communities (Ministry of Forestry 2013). The potential of rehabilitation by planting trees to maintain biodiversity and ecosystem services has yet to be fully assessed in the most densely populated island of Java, Indonesia.

2. Objectives

The main aim of this thesis is to investigate how rehabilitation by planting of non-native tree species 1) affects the provision of non-timber forest products, and 2) increases biodiversity over time. For this I studied biodiversity and ecosystem services related to understory plant communities, soil properties and useful plant species. In addition, the impact of time since rehabilitation was investigated. The study was carried out in Yogyakarta, Java Island, Indonesia. The rehabilitation consisted of planted stands of either one of the two non-native tree species teak, *Tectona grandis* L.f., or mahogany, *Swietenia macrophylla* King. I compared stands rehabilitated by teak with stands rehabilitated by mahogany, and compared these with native forests, which had never been logged or rehabilitated. More specifically I compared how:

1. Understory plant communities in teak stands differed from those in mahogany stands and how they both differed from those in the native forests. I also studied the effect of time since rehabilitation. I described the understory vegetation in terms of Shannon-Wiener diversity index (hereafter ‘diversity’), species richness, density of plants and proportion of native plants, and by analysis of the species composition (**Paper 1**).

2. Soil properties in rehabilitated stands differed with tree species planted (teak or mahogany) and from native forests. I also related soil properties to the time since rehabilitation. The soil properties I used were: soil pH, soil organic matter (SOM), total nitrogen (N), total phosphorus (P), and total potassium (K). I tested how soil properties and environmental variables (i.e. soil order, altitude) were associated with understory vegetation characters (i.e. species richness, density of plants, proportion of native plant species and diameter at breast height (**Paper 2**)).
3. Provisioning ecosystem services in the form of useful plants for humans (i.e. medicines, food, ornament and construction) and livestock (i.e. fodder) differed in abundance and occurrence between rehabilitated stands (teak or mahogany) and native forests (**Paper 3**).

3. Material and methods

3.1 Study area

I studied the government-owned state forests covering three regencies; Gunungkidul, Bantul, and Kulonprogo, of Yogyakarta Province, Java Island, Indonesia. The Yogyakarta Province is located between 110°24'19"- 110°28'53" E and 7° 15' 24"- 7° 49' 26" S (Figure 1).

Topographically, the province is situated at an altitude of 100-500 m above sea level. It has an area of about 3,186 km² with a population density of 1,168 people km⁻². The forest area of the province is 187 km² (6% land cover) (Statistics of Yogyakarta Province 2017). The study areas were surrounded by mixed plantations, farmland, agroforestry, teak plantations and mahogany plantations (Table 2). Yogyakarta has a tropical climate with mean monthly minimum and maximum temperatures of 23°C and 33°C, an average temperature of 27°C, and an average humidity of 86%. There are distinct rainy and dry seasons. The mean monthly rainfall is 255 mm which falls mainly from October to April, while the dry season is from May to September (BMKG 2016). In general, the soils are Mediteran, Lathosol, Rendzina in the Indonesian soil classification system (Wanagama I 1988; Balai KPH Yogyakarta 2014; Dinas Kehutanan & Perkebunan DIY 2015; BPDASHL Serayu Opak Progo 2018) and Inceptisols (Dinas Kehutanan & Perkebunan DIY 2015). These soil orders were transferred to the USDA soil taxonomy (Soil Survey Staff 2014), and correspond to Alfisols, Oxisols, Mollisols, and Inceptisols, respectively. Limestone and barren karst are dominant in Gunungkidul. Merapi is one of Indonesia's most active volcanoes located north of Yogyakarta which last erupted in 2010.

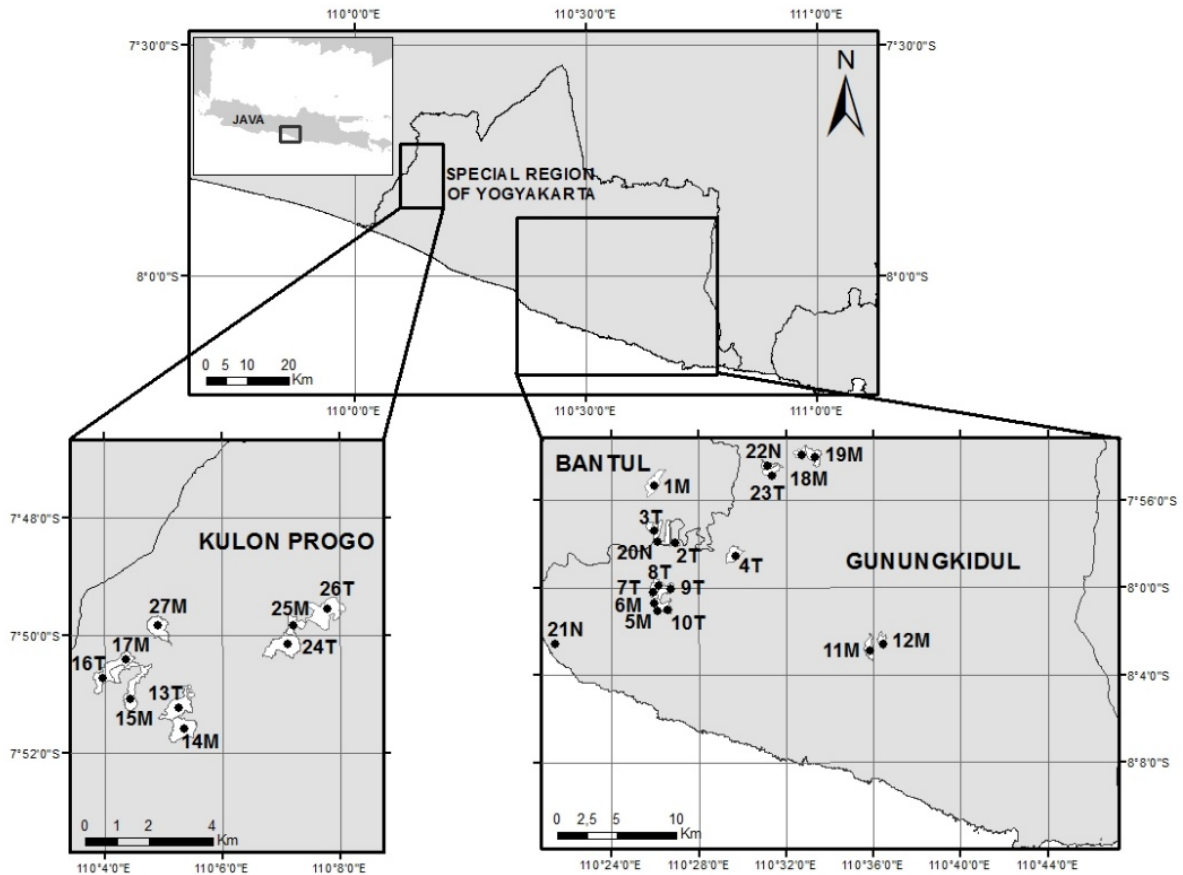


Figure 1. A map showing the stands where I surveyed vegetation and collected soil samples in Yogyakarta region in Java Island, Indonesia. The numbers refer to the areas in Table 2. M = mahogany stand, T = teak stand and N = native forest.

In rehabilitated stands, mahogany and teak were typically planted at a 2 m x 4 m spacing and thinned at the age of 10 and 15 years. The characteristics of each stand type are shown in Table 1. In production forests, the trees are usually logged at the age of 35 years, depending on the forestry ministry's decision. At the time of data collection, teak and mahogany in production forest had not yet been logged. At tree planting, intercropping systems were employed to enhance the income of local communities, but this system was limited by forest canopy closure. Food crops (i.e. corn, rice, peanut, cassava) were normally cultivated for 4 - 5 years after tree planting. Generally, chemical fertilizer was applied when cultivating food crops and at the time of planting of teak or mahogany. Cattle are not allowed to graze in these forests and are usually stall-fed (C. Udayana, pers. obs.). The previous land use of most of the study area was degraded forest or mixed plantation (Table 2).

I selected teak and mahogany stands planted between 1941 and 2003. These species are non-native tree species. Mahogany is native to Central and South America (Orwa et al. 2009).

However, it is now widely spread in most tropical forests across the globe, including in Java. Teak is native to India, Myanmar, Thailand and Laos (Verhaegen et al. 2010). It is now a naturalized species in Java (Soerianegara and Lemmens 1993; Pandey and Brown 2000). Native forests are virtually non-existent. The few remnants found in Yogyakarta Province are small and rare, mainly kept by local societies for cultural reasons.

3.2 Stand selection and characteristics

The stands were as suggested by the Governmental Forestry Service and by the Faculty of Forestry, University of Gadjah Mada, considering the year of planting and tree species planted. I surveyed 12 stands planted with teak and 12 with mahogany. The results of rehabilitation were compared with three remnants of more-or-less natural forest in Yogyakarta province, here called native forests. In total, 27 areas were surveyed (Table 1, Figure 1). The low number of native forests in the study was due to the difficulties of finding suitable sites because of the history of deforestation. The small sample size of native forests may affect my results. However, I believe they are representative of the few existing fragments of native forests.

Tabell 1. Stand type characteristics, values are stand type mean \pm SE. DBH is diameter at breast height (1.3 m). Species richness of trees include the planted species.

Stand	Sample size	Stand age (year)	DBH (cm)	Tree density (100 m ²)	Species richness of tree (100 m ²)
Mahogany	12	50 \pm 3	36.3 \pm 2.6	21 \pm 2.6	5 \pm 0.6
Teak	12	39 \pm 4	22.3 \pm 1.9	13.6 \pm 1	3 \pm 0.3
Native forest	3	Unavailable	15.2 \pm 3.2	27 \pm 5.9	9 \pm 0.8

The state forests are managed by the Governmental Forestry Service, the Faculty of Forestry, University of Gadjah Mada, and the Natural Resources Conservation Center (Yogyakarta). The Forest Law of 2004 considered the preservation of production forests, mainly for timber. However, some of the production forests in the study area have been changed from production to either protection or conservation forests (Table 2). This explains why some stands have been allowed to grow to an age of over 70 years. According to the Forestry Act of 1999 (UU No. 41/1999), the primary function of conservation forest is to conserve biological diversity

(i.e. flora, fauna) and its ecosystems. The function of protection forests is to regulate natural water systems, to prevent flooding, erosion, sea water intrusion, and to maintain soil fertility (Ministry of Environment and Forestry 2017b).

3.3 Data collection

Registration of vegetation in the field

Data were collected in May-June 2015. In each area, 3 plots of 10 x 10 m were established for vegetation sampling. I sampled four categories of plant species: (1) *herbs* including forbs, grasses and ferns; (2) *seedlings* defined as any woody species > 1 cm and ≤ 50 cm in height; (3) *saplings* encompassing woody vines and small trees > 50 cm and < 2.5 m in height, and (4) *trees* (woody plants > 2.5 m high). The three plots were selected by starting in the center of the area and walking in a random direction using a compass and a random distance selected from a list of random numbers. To minimize edge effects, I selected plots at least 10 m from the boundary of each area. Within each plot, the NW quarter constituted a plot of 5 m x 5 m that was used for sampling saplings, and in the NW corner of that plot, a 1 m x 1 m plot was used to sample herbs and seedlings.

Within each sampling plot, the plant species and the number of individuals per species were recorded. All plants were identified to local names in the field. Voucher specimens were collected, labelled, and sent to two laboratories, namely the Silviculture laboratory at the Faculty of Forestry, University of Gadjah Mada, Yogyakarta, and the plant conservation service of Purwodadi Botanic Garden, for identification.

The understory vegetation data was used in all 3 papers in the thesis, with a bit different focus. In Paper 1, I focused on the understory vegetation (i.e. herbs, seedlings, saplings), in Paper 2, I used all four plant categories (i.e. herbs, seedlings, saplings, trees) to relate vegetation characteristics to soil properties, and in Paper 3, I used herbs and saplings only to relate to different plant uses.

Soil sampling

In Paper 2, I investigated the soil properties: soil pH, soil organic matter (SOM), total nitrogen (N), total phosphorus (P), and total potassium (K). Soil samples for analysis of soil nutrients were taken from 0 – 15 cm depth, from each of the 81 plots, covering all 27 areas. Each sample was made up of four sub-samples taken from about a meter inside each corner of

the 10 m x 10 m tree plot. After sampling, the composite sample was air-dried, mixed, roughly sieved and put into labelled plastic bags before being sent to the laboratory of Indonesian Agency for Agricultural Research and Development (Yogyakarta) for analyses.

Soil laboratory analyses

Soil samples were rolled and passed through a 2 mm sieve before analyses. Soil pH was determined in water with a 1:2.5 soil:water mixture (Van Reeuwijk 2002). Soil organic carbon was measured by the Walkley and Black (1934) method and soil organic matter (SOM) was obtained by multiplying percentage soil organic carbon by the Van Bemmelen factor of 1.724 (USDA 2004). Total N was analysed by the Kjeldahl method (Van Reeuwijk 2002). Total phosphorus (P) and total potassium (K) were determined by HCl 25% extraction (USDA 2004). Phosphorus concentration was measured by GENESYS™ 20 spectrophotometer. The 240 FS AS atomic absorption spectrophotometer was used to determine potassium content.

Identification of useful plant species

For Paper 3, I searched for all uses of all recorded herbs and saplings from the 27 areas. I conducted a comprehensive search for each species' scientific name in using databases (i.e. Web of Science, Google Scholar). I used articles published in English only. I searched for uses such as medicine, food, fodder, construction and ornament. Use as firewood was not recorded, as all woody species could be used as such. Plant species were defined as useful if they had at least one use, with some plants having multiple uses.

In addition to the use, I compiled information for each plant species about growth habit (herb or woody species), status (native or exotic), and life cycle (annual or perennial). The databases I used were: Plant Resources of South-East Asia PROSEA 4 (Mannetje and Jones 1992), PROSEA 5 (Soerianegara and Lemmens 1993), PROSEA 8 (Siemonsma and Piluek 1993), PROSEA 12 (de Padua et al. 1999), and online databases such as the agroforestry database (Orwa et al. 2009), useful tropical plants database (Fern 2014), FAO Ecocrop (FAO 2007), PROTA4U (PROTA 2017), and the Germplasm Resources Information Network (USDA 2019).

3.4 Data analyses

I have generally used two types of statistical analyses throughout my thesis:

- 1) Generalized Linear Mixed Models with sampling site ($N = 27$) as a random effect (Hurlbert 1984). This analysis was used for relationships between stand type (teak, mahogany) or native forest and time since rehabilitation (explanatory variables) and vegetation characteristics (i.e. species richness, density, Shannon-Wiener diversity index, and proportion of native species), soil properties (i.e. pH, SOM, N, P, K), and number of useful plant species per plot as response variables. I used a poisson error distribution and log link function when analyzing count data (i.e. species richness and density). For the analysis of the proportion of native species I used a binomial error distribution and logit link function, and mixed linear models for the analysis of diversity and soil properties. I performed a backwards selection procedure by removing the least significant predictor until I had only statistically significant ($p < 0.050$) components in the model. More details are found in each paper. I also established species-accumulation curves by using individual-based rarefaction to examine the effect of stand types on species richness of understory vegetation. All mixed models and rarefaction curves were carried out using R (version 3.4.2; R Development Core Team 2015).
- 2) Ordinations using the CANOCO Software (CANOCO version 4.5 for Windows; Ter Braak and Šmilauer 1998) were used to visualize the distribution of species and plots in ordination space. For paper 1, Correspondence Analysis (CA) was first used to study gradients of species change, and, hence, plot positions in relation to their species composition. Environmental factors such as stand type (teak and mahogany), native forest and time since rehabilitation were included with best fit. Native forests were arbitrarily given the age of 300 years. Canonical Correspondence Analysis (CCA), including the environmental variables in the analysis, was used to test significance of the variables. Then the native forests were excluded and the species were ordinated for teak and mahogany stands only. The significance of environmental variables was tested with CCA. For paper 3, in the CA, I classified each plant species according to use, life cycle (annual/perennial) and plant status (native/exotic). In all ordinations I used the respective use category and stand type as environmental variables and added them to the graphs with best fit. Species with more than one utility were included in more than one ordination. I deleted seven sapling species and seven herb species as outliers because they did not fit in the graphs. I performed forward selection to test significance of the variables in Canonical Correspondence Analyses (CCA).

In the analysis using generalized linear mixed models, the effect of time since rehabilitation was investigated in a separate analysis, including only teak and mahogany stands. For Paper 2, I only had one site with Inceptisols (Table 2) and I therefore removed this site from further analyses of soil types.

4. Results and discussion

Rehabilitation was carried out to provide services for humans in Yogyakarta, to restore land and soil productivity, forest ecosystems and biodiversity (Nawir et al. 2007). The stands I studied were initially planted as production forests to provide timber, a provisional ecosystem service, but a number of them were later reassigned as protection forests or conservation forests (Table 2). These stands were allowed to grow old, > 70 years, allowing my studies of the long-term development of biodiversity in the form of understory vegetation, soil properties and provision of ecosystem services.

4.1 Mahogany stands vs teak stands

In general, I found no differences between mahogany and teak stands in terms of species richness, diversity, density or proportion of native species in the understory, when comparing stands with a broad range of time since rehabilitation. However, the species composition of herbs and saplings differed between these two stand types. The seedlings *Clerodendrum serratum* (L.) Moon. and *Leucaena leucocephala* (Lam.) de Wit. showed an affinity to mahogany, whilst other species, such as *Schoutenia ovata* Korth, occurred more in teak stands. For saplings, *Eupatorium odoratum* L. occurred in teak stands, whereas *Psychotria* sp. and *Arenga* sp. occurred in mahogany stands. The main tree species in the stands may affect the understory community. Teak leaf, root and bark have been reported to have allelopathic properties (John et al. 2007; Kole et al. 2011; Leela and Arumugam 2014). Allelopathy released through root exudates and biomass decomposition, might hamper the understory vegetation (Souto et al. 2001; Manimegalai 2012; Biswas and Das 2016). If some understory species are more tolerant than others to allelopathic substances from teak, this may explain the differences in species composition between teak and mahogany stands.

I also found differences in soil properties between mahogany and teak stands. Mahogany stands had a lower pH than teak stands (Figure 2). When forest is rehabilitated, the planted trees will influence the soil with their roots and litter from the start, thus, affecting soil properties (Broadbent et al. 2014). Amponsah and Meyer (2000) claim that under teak an

increase in leached Na, caused by high water infiltration, helps holding the pH up. In my study, mahogany stands were on average older than teak stands, but there was still a difference between stand types, even after correcting for the effect of age (Paper 2). Soil erosion has been found under teak stands, possibly as a result of the low density of understory vegetation, causing loss of topsoil and nutrients (Ribolzi et al. 2017) reducing the water holding capacity.

It has been found that soil properties such as soil pH, soil moisture, total soil carbon, and total nitrogen are associated with phenolic allelochemicals (Blum et al. 1993). Norouzi et al. (2015) reported that lowering of soil pH resulted in higher allelopathic activities of different plant species. Even though teak releases allelopathic substances, biodiversity in the soil may to some extent control allelopathic effects on the understory vegetation. Hence differences in pH may also be linked to differences in species composition of the understory between mahogany and teak.

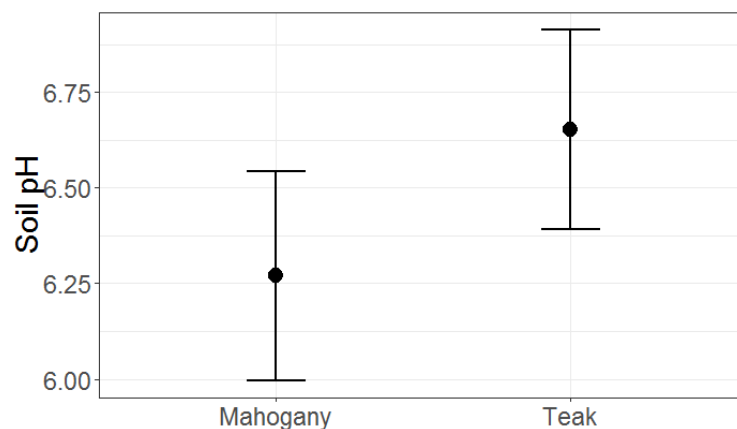


Figure 2. Analyses showing differences of mahogany stands and teak stands in soil pH at Yogyakarta, Indonesia. Bars in shows 95% confidence interval and dots show the estimated average after controlling for stand age.

Vegetation and soil properties in turn affect the delivery of provisioning ecosystem services, such as non-timber forest products. I found differences between stand types in this respect as well, as the species richness of useful herbs and useful exotic saplings were both higher in teak stands than in mahogany stands (Figure 3a and 3b respectively). Medicinal use of plants was the most common use among the species present in rehabilitated stands, and medicinal herbs were more associated with teak stands than mahogany (Figure 4a). Ornamental herbs on the other hand, were associated more with mahogany stands (Figure 4b). This indicates that

rehabilitated teak stands provide more non-timber forest products for local people than mahogany stands (Stepp and Moerman 2001).

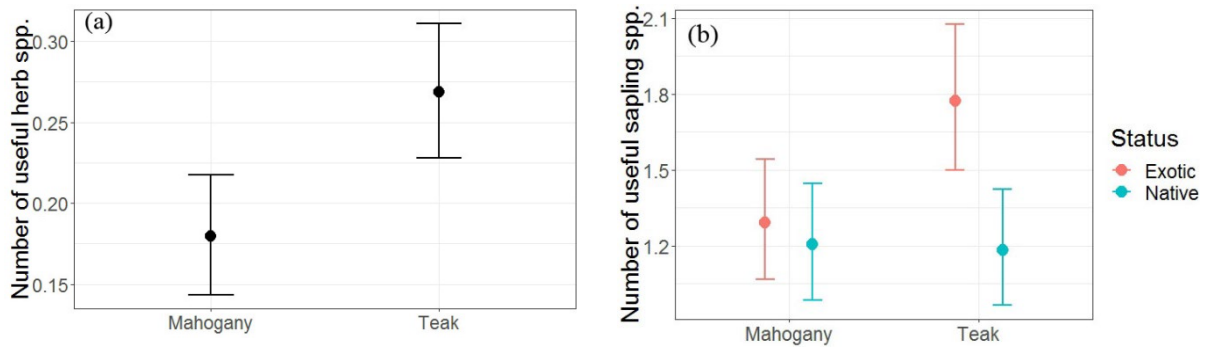


Figure 3. a) Number of useful herb species per m^2 (bars show 95% confidence interval) in teak and mahogany stands and b) the interaction between stand type (teak/mahogany) and plant status (exotic/native) on number of useful sapling species per $25 m^2$ in Yogyakarta, Indonesia.

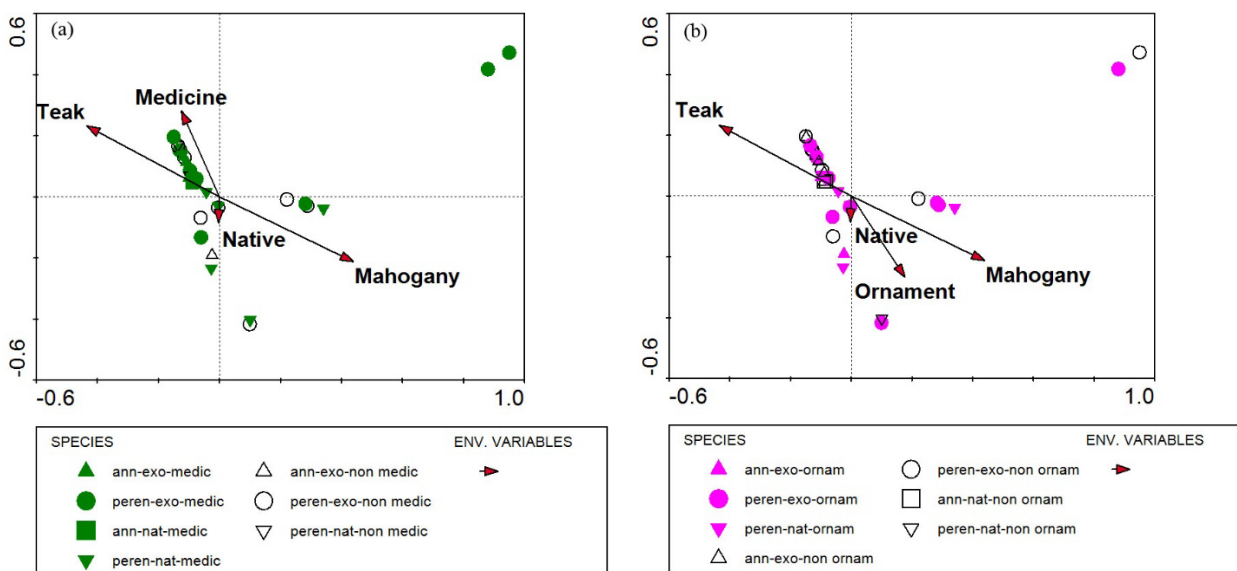


Figure 4. Ordinations with Correspondence Analyses showing herb species composition for a) medicine plants, b) ornamental plants. Significant environmental variables according to Canonical Correspondence Analysis are included with best fit.

4.2 Succession after forest rehabilitation

Overall, I found that many variables describing understory vegetation, soil properties and useful plants were related to time since rehabilitation. Rehabilitation of forests by planting trees accelerates the process of succession (Parrotta 1995; Wang et al. 2008). Tree planting, therefore, may contribute to biodiversity when implemented on degraded forests and lands (Bremer and Farley 2010). This was supported by my results, as species richness and

Shannon-Wiener index of saplings increased with stand age, while richness and Shannon-Wiener index of herbs decreased, although the proportion of native species increased. Trees promote understory plant colonization by improving the chemical and physical soil quality through root penetration and decomposition, soil biota activity, shading, increasing humidity and reducing temperatures (Lamb et al. 2005). Seed rain increases, as trees supply perching and nesting places for birds and bats spreading seeds, and habitat for small arboreal, ground-living and digging animals including invertebrates (Guevara et al. 1986; Ingle 2003; Muscarella and Fleming 2007). During the first decade, understory plants could germinate from the soil seed bank, basal shoots or root sprouts. Grasses, and, hence, fires, and exotic weeds are eventually suppressed by shading from the trees (Ludwig et al. 2004).

When investigating both time since rehabilitation and stand type, I found differences between teak and mahogany in how they responded over time. The density of seedlings and saplings increased through time in the mahogany stands and decreased or showed no change through time in the teak stands (Figure 5a, b). The species richness and diversity of saplings increased with time since rehabilitation in both teak and mahogany stands as a result of ongoing succession. My results were supported by a previous study from Indonesia that found understory species richness and diversity in teak plantations decreased with stand age (Nikmah et al. 2016). A study in South Sumatra, Indonesia, showed the highest species diversity of understory vegetation in mahogany stands compared to *Pinus merkusii* Jungh. & de Vriese, *Peronema canescens* Jack, and *Schima wallichii* (DC.) Korth. stands, 25 years after planting (Kunarso and Azwar 2013). A study from Costa Rica reported that a 10-year-old teak plantation had a lower density of woody stems than a 12-year-old abandoned pasture (Healey and Gara 2003). These studies were in line with my results showing that teak stands suppressed understory vegetation and limited the regeneration of other tree species, which again could be related to the allelopathic properties of teak. I found differences between teak and mahogany stands to become more apparent with increasing time since rehabilitation.

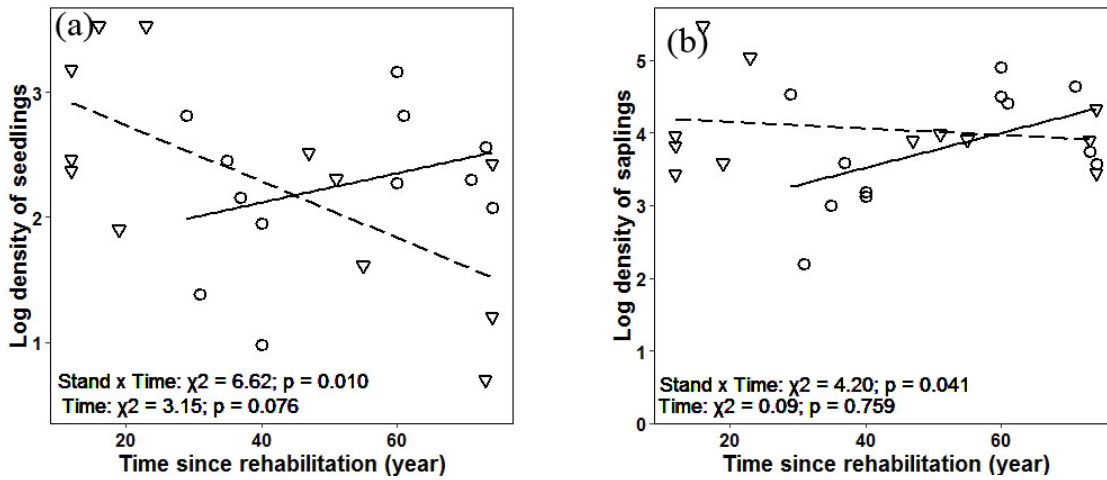


Figure 5. The effect of stand type and time since rehabilitation for a) seedlings and b) saplings in Yogyakarta, Indonesia. Dashed lines and triangles are the teak stands, solid lines and circles are the mahogany stands.

As stands mature, shade from the trees might hamper grasses, ferns, and light-demanding herbs and seedlings, and such modifications of site conditions contribute to the development of late successional species (Lugo 1997; Parrotta et al. 1997; Guariguata and Ostertag 2001). The proportion of native seedlings and species richness of saplings increased with time since rehabilitation (Figure 6a, b). The planted trees provide habitat for small climbing, digging, walking or flying animals pollinating flowers and spreading seeds from other areas with more plant species (Van der Pijl 1982). The older stands have more plant species and indigenous species in the sapling, seedling and annual herbaceous layers.

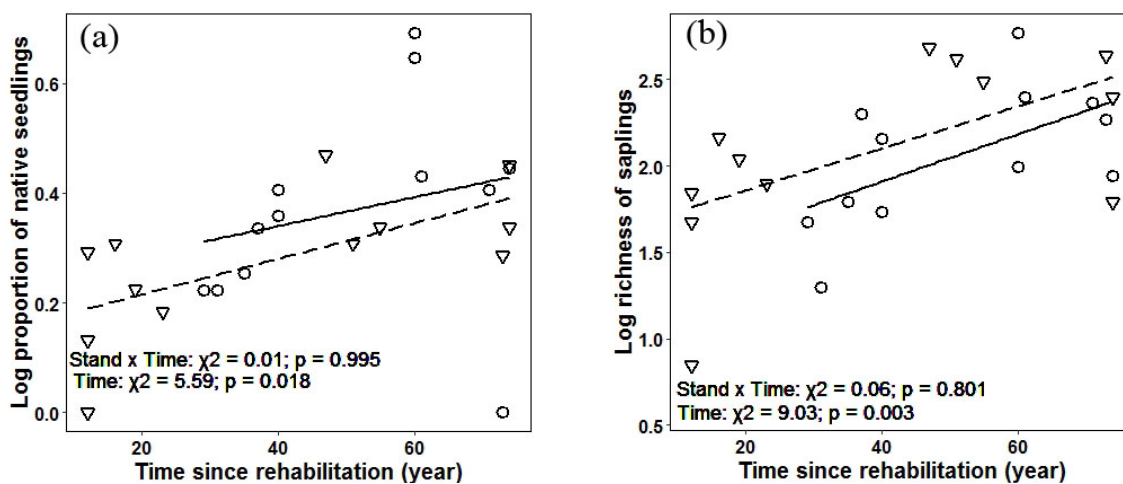


Figure 6. a) Proportion of native seedlings and b) species richness of saplings in relation to time since rehabilitation in teak (triangles and dashed lines) and mahogany (circles and solid lines) stands in Yogyakarta, Indonesia.

Species composition of herbs, seedlings and saplings also changed with time since rehabilitation. Time since rehabilitation influenced herb species composition in both teak and mahogany stands. Some herb species occurred in young stands, such as *Polytrias indica* (Houtt.) Veldkamp and *Spigelia anthelmia* L., whereas *Desmodium gangeticum* (L.) DC. and *Pteris ensiformis* (Burm.) occurred in old stands. For seedlings, time since rehabilitation also influenced species distribution, e.g. *Psychotria* sp. occurred in old stands. Exotic herb and seedling species decreased with the maturing of both stand types. Time since rehabilitation also influenced the distribution of sapling species e.g. *Psychotria* sp. and *Arenga* sp. occurred in old mahogany stands. Exotic saplings still occurred in old stands, e.g. *Eupatorium odoratum* L., *Lantana camara* L. and *Leucaena leucocephala* (Lam.) de Wit, which is in line with the results from linear models that I did not find an increase in the proportion of native saplings as stands matured.

In accordance with my expectation, soil pH decreased with time since rehabilitation, in both teak and mahogany stands (Figure 7). This was a result of succession (Aweto 1981; Perumal et al. 2017) and was in line with a previous study that found soil pH to decrease with time during primary succession in Sichuan, China (He and Tang 2008). In addition, a decrease of soil pH in second-growth forest 15, 45, 75 and ≥ 100 years after abandonment was reported by Bautista-Cruz and Del Castillo (2005) in Oaxaca, Mexico. Perumal et al. (2017), and Li et al. (2013) reported a decline of soil pH over 10, 18, and 30 years, respectively, as result of a succession. The soil acidity may be influenced by accumulation of litter on the soil surface.

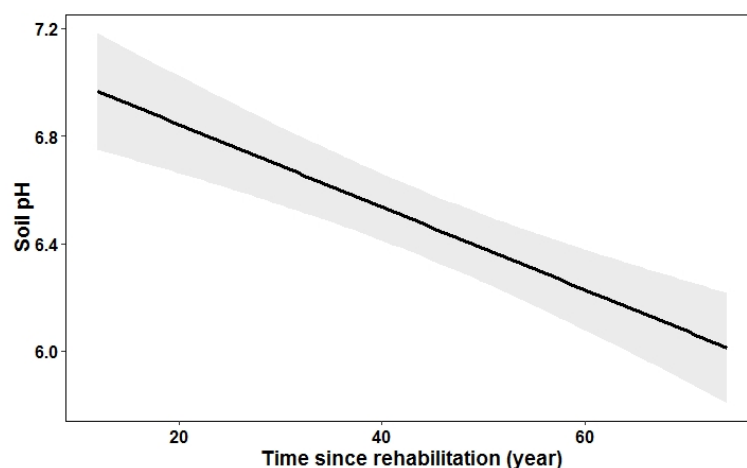


Figure 7. Analyses showing relations between soil pH and time since rehabilitation in Yogyakarta, Indonesia.

As expected, the time since rehabilitation affected the occurrence of useful species. I found the species richness of saplings used for medicine, construction and food increased with time since rehabilitation (Figure 8a). This showed a beneficial impact of maturing rehabilitated stands for provisioning ecosystem services. I found that useful exotic annuals and perennials, and native perennial herb species decreased with time since rehabilitation, while native annual herb species increased (Figure 8b). The stand age of both teak and mahogany changed the communities of herb species from more exotics in the young stands towards more natives in the old stands.

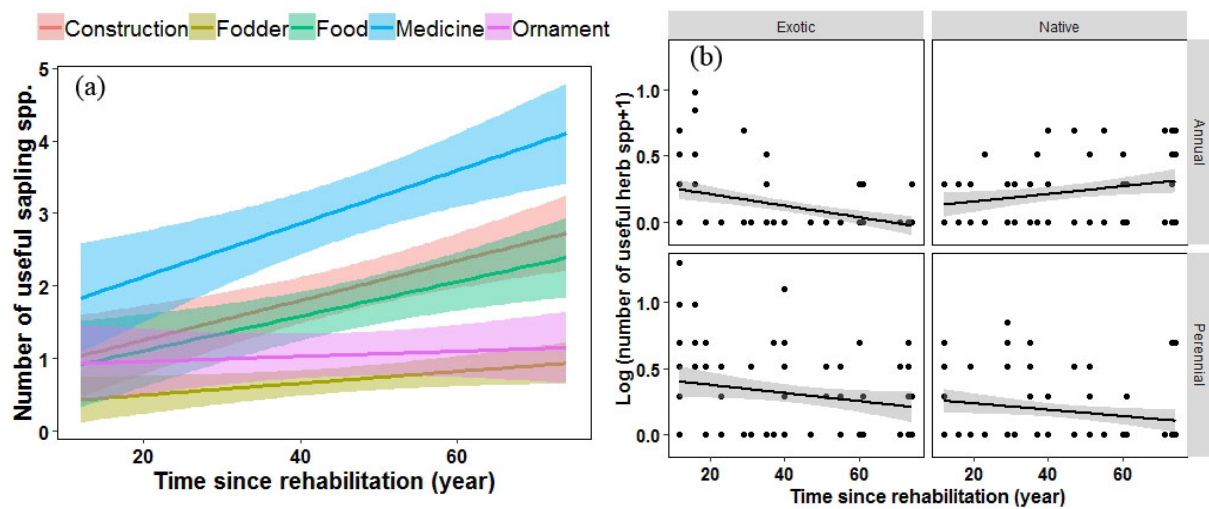


Figure 8. a) Species richness of useful saplings in relation to type of use and time since rehabilitation. b) Species richness of useful herbs, in relation to the interaction between plant status (exotic/native), life cycle (annual/perennial) and time since rehabilitation at Yogyakarta, Indonesia. Shaded area shows 95% confidence interval.

4.3 Native forest vs rehabilitated stands, differences and changes through time

Overall, my results did not support the expectation that higher species richness, density, diversity, and proportion of native plants are found in native forests than in rehabilitated stands. I found no differences between native forests and rehabilitated stands with regard to these vegetation characteristics, across all stands (Paper 1). However, I found that while old forests (41-74 years since rehabilitation) were approaching native forests in species richness, density, diversity and proportion of native plants, young stands were clearly more different in understory characteristics (Paper 1).

Furthermore, species composition differed between planted stands and native forest. Previous studies have found that although the number of species and general structure of a planted stand might approach that of a native forest after some 100 years, the species composition still differs, with native forests possibly containing more disturbance-sensitive species and species that require specific dispersal agents, mammals, birds, etc. (Denslow and Guzman G 2000; Guariguata and Ostertag 2001). To plant tree monocultures on degraded forest land can be a potential strategy to protect biodiversity and to enhance ecosystem services but the planted stands will not achieve the species composition of native forest (Bremer and Farley 2010; de Jong 2010; Chazdon 2013). Therefore, to the extent that the goal of rehabilitation is to restore previous species composition, which corresponds to the restoration type “reconstruction” as defined by Stanturf et al. (2014), planting stands with mixed native species would be advisable.

I did not find the expected effect that native forests would have higher nutrient concentrations than the rehabilitated stands. I found concentration of soil properties (i.e. pH, N, SOM, P, K) did not differ between the native forests and the planted stands (Paper 2). This may indicate that the concentration of soil properties in rehabilitated stands also approached those of native forests through time. However, these results could be limited by the low number of native forest sites sampled.

Contrary to my predictions, the native forests had a lower number of useful plant species than rehabilitated stands. I had expected more medicinal plants to be found in native forests, but my results did not support this. Many medicinal plants were found in the rehabilitated stands, especially teak stands, supporting the finding by Stepp and Moerman (2001) and Stepp (2004) that many medicinal plants are collected from disturbed land. This indicates that rehabilitated stands may provide ecosystem services, even though they differ in species composition from native forests, as also pointed out by (Leimona et al. 2015). It also shows that many exotic species are useful for local people.

The disappearance of many animals, such as mammals and birds from Java might be one reason for the difference in plant species between rehabilitated stands and the native forest. Many tropical trees with large fruits, depend on elephants, *Elephas maximus*, and large primates such as orangutang *Pongo* ssp. and the gibbons, *Hoolock* ssp. for seed dispersal (Babweteera and Brown 2010; Campos-Arceiz and Blake 2011), which might apply for

example to *Inocarpus fagifer* (Parkinson ex Zollinger) Fosberg 1941 and *Calophyllum inophyllum* L. Without these seed dispersers, seeds may just end up close the mother tree. Another possible reason for the difference in species between the native forests and the teak and mahogany stands is the presence or absence of mycorrhiza fungi (Peay et al. 2010; Essene et al. 2017). These fungi are often slow in establishing and sometimes quite particular about their habitat, but they may become very old, heavy and widespread. Some plant species can do without, or with various species of mycorrhiza, whereas others require specific mycorrhiza, and if the species is not present, they may not grow.

The native forests have been preserved for cultural reasons by local societies, but they are small fragments and they may be disturbed. The presence of native forest in the area was low, and the three sampled fragments were the only ones found to compare with the planted stands sampled. So, these three native forest fragments represent what is possible to compare rehabilitated stands with today, although they may not totally represent the continuous forests that once covered the study area. However, this comparison is still valuable, as I can see that their species composition differs much from the rehabilitated stands, but species richness, plant density, diversity and proportion of native species are similar. The surrounding deforested or rehabilitated areas may spread seeds into the native forests, as suggested by the occurrence of many non-native species. Still, the native forests had many species not occurring in the planted stands, as shown in paper 1, which showed large differences in species composition with rehabilitated stands. Some of these unique species may be disturbance sensitive, or require continuous old forest, although the >70 years of the oldest planted stands is a considerable age.

All the comparisons between rehabilitated stands and native forests in this study should be interpreted with caution, as the sample size of native forests was low. I surveyed 12 rehabilitated stands of teak and 12 with mahogany, but found only 3 native stands in the same area. In order to evaluate how sample size affected species richness estimates, I have made species-accumulation curves using individual-based rarefaction. The curves are approaching an asymptote for species richness (i.e. herbs, seedlings, saplings) in teak and mahogany stands (Figure 9a-c). However, the species-accumulation curves in native forests did not approach an asymptote, and number of species were lower than those in the teak and the mahogany stands. This difference is probably related to the number of areas sampled. Especially for herbs, the

sample size is rather low in native forest (Figure 9a), but this may also reflect the low abundance of herbs in this forest type.

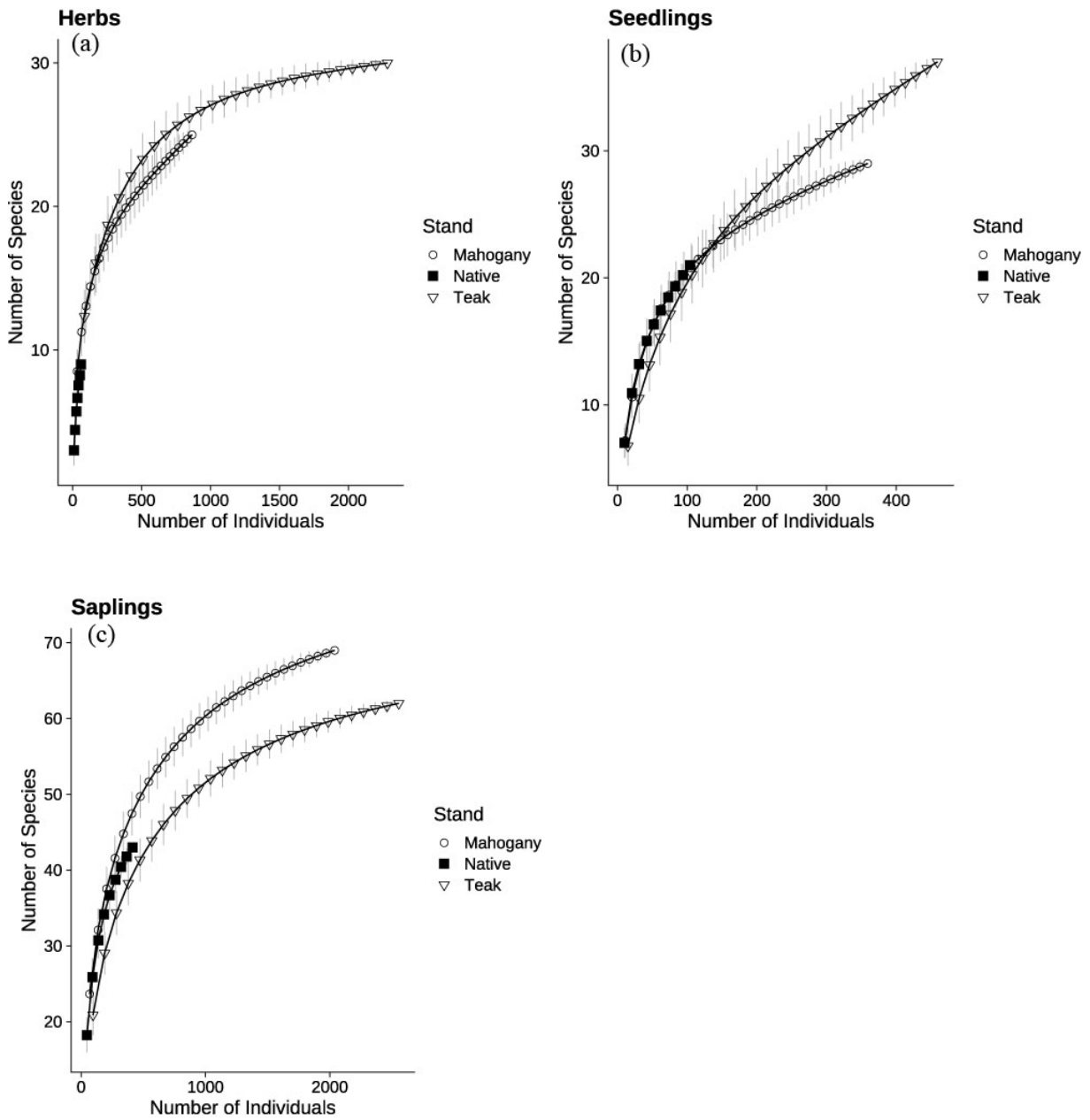


Figure 9. Rarefaction-based species accumulation curves, plotting species richness in relation to number of individuals for a) herbs, b) seedlings and c) saplings in three stand types in Yogyakarta forests, Indonesia. Bars represent the 95% confidence intervals.

4.4 Links between biodiversity and ecosystem services

I found several links between understory vegetation richness, diversity, and soil properties. Vegetation characteristics (e.g. density of plants) affect soil properties, and their decomposition rate affects nutrient-cycling efficiency (Singh et al. 2004; Tripathi and Singh 2005). As expected, there was a relationship between understory species richness, diversity, plant density and proportion of native plants on the one hand and soil properties on the other. My results showed that herb density was positively related to soil pH and P. The density of woody plants was positively related to total P, while density of seedlings and of woody plants were positively related to total N. Density of trees depended on soil order, and was negatively related to K. The analysis of understory vegetation showed that Leguminosae was the largest plant family found in the study area. Leguminous herbs, seedlings, and saplings are important components for biological nitrogen fixation, which may benefit the build-up of soil N (Barrios 2007). There is a positive relationship between plant species diversity or richness or, rather, the functional diversity, for example of plant functional traits, on the one hand and stability and resilience of ecosystem functions on the other (DeClerck et al. 2010; Aerts and Honnay 2011). Trees and soils interact for example through facilitation of soil biota and synergistic symbiosis (Barrios 2007; Barrios et al. 2012). The increase of tree species diversity improves soil fertility (Huston 1980; Long et al. 2012). This probably occurs also in these rehabilitated stands, but it is not yet studied.

When it comes to provisioning ecosystem services in terms of useful plants, I found that there was no clear positive relation to biodiversity in native forest. The number of useful plants was higher in rehabilitated stands than in native forest, and a higher number of useful plants were exotic rather than native. Species richness of herbs and saplings were higher for medicinal plants than for other uses. This result confirms previous findings (Hanum and Hamzah 1999; Ayantunde et al. 2009; Sahu et al. 2012; Fathurrahman et al. 2016). Although biodiversity and ecosystem services are not always positively correlated, my study showed that planting non-native tree species for rehabilitation contributed to both biodiversity and ecosystem services. Teak stands made a greater contribution to provisioning ecosystem services compared to mahogany stands.

4.5 Forest rehabilitation by planting exotic trees

Planting trees may enhance biodiversity when grown on degraded forests and lands (Bremer and Farley 2010). Monocultures of exotic species can even recruit understory vegetation

species valuable for the local human communities dependent on forests (Chazdon 2013; Wills et al. 2017) for commodities such as medicines, materials for construction, food, fodder and ornaments. My study supports the claim that exotic monocultures can be important for biodiversity and ecosystem services other than timber production, if they are allowed to mature to old age. These findings showed that rehabilitation is important for the livelihoods of human communities, as many useful plants were present in teak and mahogany stands. However, monocultures may be less attractive to wildlife than mixed plantations including indigenous species (Wunderle 1997). Many species of animals eat specific plants or are in various ways dependent on them, and the plants depend on the animals for pollination and dispersal of seeds. Consequently, biodiversity may develop slowly in monocultures. In my study, the native forests had different species composition compared to rehabilitated stands, and native forests were very rare in the area. In the future, maybe rehabilitation should focus more on native biodiversity, and therefore rehabilitation should use mixed tree species, including native species, to increase species diversity in a way that might approach that in natural forests.

5. Management implications

Over recent decades, deforestation has increased, particularly in tropical regions. Even though logging or timber harvesting in the future may be performed in ways that conserve more forest structure and biodiversity (e.g. selective logging), there will still be a need to rehabilitate tropical forests in the future. More research is therefore needed to ensure a knowledge-based rehabilitation of deforested areas.

Lamb et al. (2005) claim that planting one or a limited number of commercially important tree species at large spatial scales may be sufficient to restore many ecosystem services. The results in this thesis show that even single species stands of mahogany or teak restore many ecosystem services, especially if they are allowed to grow old. This is an economically attractive and logistically plausible solution, but may be risky on the long run as we may lose essential vegetation properties, such as species richness, Shannon-Wiener diversity index, and native plants and animals. Even so, my results indicate that old rehabilitated stands established as monocultures in early rehabilitation programs, also have conservation value in the future.

Any rehabilitation will probably improve the maintenance of ecosystem services we depend on. However, a large number of forest dwelling species, plants, animals and fungi, disappear with the disappearing of native forests (Sala et al. 2000; Sodhi et al. 2004). We may depend on these species to mitigate and for people, plants, animals and fungi to cope with the ongoing climate changes, as well as for many other uses. The forest biota interacts, in pollinating plants, dispersing seeds, burying seeds that may germinate and establish if the right mycorrhizal fungi is present. Trees provide habitat and nesting places for animals. In short, we need to preserve what can be preserved of this biodiversity.

It is necessary to protect the few remaining natural forests, and to surround them with forest that resembles the original one, as far as possible. In this context it is important to remember that these forest fragments were conserved by local communities using them for cultural events, and that such use must be allowed to continue. These native forests could be part of a zoning scheme. Zoning has not been much used in the tropics, but shows some success in temperate forests. For example the TRIAD is a kind of zoning where land is split in three parts, and is managed for 1) intense timber production, 2) ecosystem management and some timber production, and 3) conservation, with nothing harvested. The system has been tried in Canada with between 72 and 15% of the land used for intense timber production, 74 – 40% for ecosystem management and 12 – 20% for conservation (Côté et al. 2010). With clever location of timber production and ecosystem management the total volume of timber produced is often about the same as before the zoning scheme was introduced. The timber producing areas can be managed for efficient timber production, whereas in the ecosystem management areas planting should perhaps be with many tree species including many native ones, some trees should be allowed to grow old, and selective logging should be used. It would be interesting to see how such a zoning scheme could help protecting biodiversity, ecosystem services and native forests in the tropics, and Indonesia with its large areas of Government owned forests seem ideal for a test.

The alternative to zoning of the forested landscape is to treat the whole area more like ecosystem management, for example planting a mixture of native tree species, using selective logging, let tree age vary and leaving some trees to grow old. It is important to maintain a high plant functional diversity that may be the key to a sustainable and resilient ecosystem (Díaz et al. 2007). Native forests should be legally protected, and connected with corridors.

Payment for ecosystem services is a strategy often advocated primarily from the developed countries, meaning that the providers of an ecosystem service, such as clean water, get paid by those using the resource in order not to use other resources in a way that jeopardize it. The original monetary system has, however, been found not to work well in developing countries as it is socially unfair. Further, economic compensation is often rejected by the ecosystem providers, and a payment in kind has proven more desirable (Leimona et al. 2015). In my areas the land is owned by the government, and payment for ecosystem services from the government is hardly feasible.

6. Future perspectives

To improve our knowledge of rehabilitation of tropical forest ecosystems, further studies are needed. Below I point out some aspects that require further attention from researchers:

- We should study why the species differ between rehabilitated stands and native forest, and whether rehabilitated stands could achieve the same species composition as the native forest. The unique species for the native forest should be identified, and their dispersal strategies studied, first in existing data, then in the field. We should investigate if rehabilitated forest can approach native forest species composition by planting stands consisting of many different tree species, including native trees. We should record the understory vegetation to follow the development.
- The forests I worked in are owned by the government. I would suggest for the government to set up a landscape with zonation management of forest, following for example TRIAD. Preferably more than one scenario should be set up with different percent land used for timber production, ecosystem management and conservation. For each scenario timber harvest volume, soil erosion and water infiltration, understory vegetation properties and attributes of old forest should be recorded on the three land-use zones.
- I would set up a special study of medicinal plants. I would study which species are mainly used in my area. What plants are they, exotics or natives, annuals or perennials? Are they, or can they easily be cultivated? How conservative are the users, do they stick to one species for one purpose, or can they easily switch between species? I found many medicinal plants in teak stands. Teak is allelopathic, and I would study if this could influence the medicinal plants.

- Forest rehabilitation has been implemented by government for 74 years in Yogyakarta. This is still a short time in the life of a forest, but a long time for a planted timber stand. Time since rehabilitation was clearly an important factor for the development for rehabilitated forests. We need to continue to follow rehabilitated stands to gain longer time series in order to better understand the long-term succession of forest rehabilitation. Periodic monitoring in the future is therefore needed, for example assessments every five years.

7. Conclusions

Rehabilitation is restoring desired species composition, structure or processes. Planting of a desired tree species, often helps to speed up ecological processes (succession) to improve forest structure, ecological functions and biodiversity. Rehabilitation by planting exotic tree species, whether for timber production or to prevent flooding, landslides and effects of drought, can have positive effects on biodiversity and ecosystem services. Rehabilitated stands in this study approached the native forests in understory species richness, Shannon-Wiener diversity index, plant density and soil properties with time, as they were able to grow old without further disturbance. Rehabilitated stands can even recruit more species for provisioning of some ecosystem services than native forests, for example exotic useful plant species found in teak stands. However, rehabilitated stands of exotic tree species could only restore part of the original biodiversity, with species composition differing from that of native forests. Rehabilitation is used as a method to increase biodiversity and provide ecosystem services such as reducing soil erosion and flooding, increasing carbon sequestration and maintaining hydrological cycles for clean water. It is also used for provisioning of timber and non-timber forest products. To achieve these goals, as well as conservation of native forests, I suggest to try zonation, dividing the land into land use areas for effective timber production, for ecosystem management and for conservation. In addition, or in the environmental management zone, multiple tree species, including native ones, should be used for rehabilitation, and selective logging should be practiced.

Table 2. Stand type, area ID, region, forest function, previous land use, surrounding land use, stand age, altitude, and soil order. Stand age is only given for the rehabilitated sites (time since rehabilitation). MP = mixed plantation, AgroF = Agroforestry, M = mahogany, T = teak, N = native forest, m. a.s.l. meters above sea level.

Stand type	Area	Region	Forest function	Previous land use	Surrounding land use	Age (year)	Altitude (m.a.s.l.)	Soil order
Native forest	20 N	Bantul	protection	native forest	MP	none	400	Oxisols
Native forest	21 N	Gunungkidul	protection	native forest	MP, Farm	none	200	Alfisols
Native forest	22 N	Gunungkidul	conservation	native forest	MP	none	150	Mollisols
Mahogany	12 M	Gunungkidul	production	logged forest	MP, Farm	29	100	Alfisols
Mahogany	6 M	Gunungkidul	production	degraded forest	MP, Farm	31	300	Alfisols
Mahogany	1 M	Bantul	protection	degraded forest	Farm	35	450	Oxisols
Mahogany	15 M	Kulonprogo	production	mixed plantation	MP, M, T	37	220	Oxisols
Mahogany	5 M	Gunungkidul	production	degraded forest	MP, Farm	40	300	Alfisols
Mahogany	27 M	Kulonprogo	production	degraded forest	Farm, M, T	40	250	Oxisols
Mahogany	18 M	Gunungkidul	conservation	degraded forest	T, MP	60	200	Mollisols
Mahogany	19 M	Gunungkidul	conservation	degraded forest	MP, Farm	60	200	Inceptisols
Mahogany	11 M	Gunungkidul	production	logged forest	Farm	61	100	Alfisols
Mahogany	14 M	Kulonprogo	production	mixed plantation	MP	71	250	Oxisols

Mahogany	25 M	Kulonprogo	conservation	mixed plantation	MP	73	300	Oxisols
Mahogany	17 M	Kulonprogo	production	mixed plantation	MP	74	220	Oxisols
Teak	2 T	Bantul	protection	degraded forest	MP	12	380	Oxisols
Teak	4 T	Gunungkidul	production	degraded forest	M	12	100	Alfisols
Teak	7 T	Gunungkidul	production	degraded forest	M	12	300	Alfisols
Teak	3 T	Bantul	protection	mixed plantation	T, Farm	16	380	Oxisols
Teak	8 T	Gunungkidul	production	degraded forest	MP, Farm	19	300	Alfisols
Teak	10 T	Gunungkidul	production	degraded forest	MP, Farm	23	300	Alfisols
Teak	23 T	Gunungkidul	conservation	degraded forest	MP, T	47	100	Mollisols
Teak	9 T	Gunungkidul	production	degraded forest	MP, Farm	51	300	Alfisols
Teak	26 T	Kulonprogo	conservation	mixed plantation	AgroF, Farm	55	300	Oxisols
Teak	24 T	Kulonprogo	conservation	mixed plantation	MP	73	400	Oxisols
Teak	13 T	Kulonprogo	production	mixed plantation	MP, T	74	170	Oxisols
Teak	16 T	Kulonprogo	production	mixed plantation	MP, M, T	74	220	Oxisols

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Paper I

Understory diversity and composition after planting of Teak and Mahogany, Yogyakarta, Indonesia

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Abstract

Forest rehabilitation is when a desired tree species is planted in degraded forests or lands. Rehabilitation by planting a single tree species is a common way to restore exploited forests to maintain ecological processes. We compared woody and herbaceous understory vegetation between forests rehabilitated by planting mahogany (N = 12) or teak (N = 12) between 1941 and 2003, and with three native forests in Yogyakarta, Indonesia. Species richness, species diversity, density of plants and proportion of native plants did not differ between the rehabilitated areas and the native forest. Recently rehabilitated areas were different from the native forests while 41-70 years after rehabilitation, characteristics of understory vegetation approached those of native forest. We described species composition using ordination, and found it to differ between areas rehabilitated with teak and with mahogany and, particularly, between the rehabilitated areas and the native forests. Time since rehabilitation and tree species planted were important for the species composition of understory vegetation. We conclude that the selection of species for rehabilitation and letting rehabilitated areas mature are important for understory development and species diversity.

Keywords: Biodiversity, ecosystem function, ecosystem services, mahogany, native forest, rehabilitation, teak

Introduction

The restoration of degraded ecosystems has become a common task globally in order to restore biodiversity, ecosystem functions and to provide sustainable forestry and ecosystem services (Aerts and Honnay, 2011; Chapin, Oswood, Van Cleve, Viereck, & Verbyla, 2006; Guariguata and Ostertag, 2001; Lamb, 2018; Ruiz-Jaén and Aide, 2005). The focus of forest restoration programs has been to grow trees for timber production and to promote ecosystem functioning in terms of plant species richness, species diversity, density, functional diversity or species composition (Lugo, 1997).

Stanturf, Palik, & Dumroese (2014) defined four strategies of forest restoration: (1) *rehabilitation* by restoring a desired species composition, structure or process; (2) *reconstruction* to restore original plant communities; (3) *reclamation* to restore land, which is devoid of vegetation; and (4) *replacement* of species with other species as a response to, for instance, climate change. To reconstruct a tropical forest ecosystem might require the planting of more than 50 indigenous tree species (Hooper et al., 2005; Rodrigues, Lima, Gandolfi, & Nave, 2009). By contrast, Lamb, Erskine, & Parrotta (2005) show that rehabilitation, for example, by planting one or a limited number of commercially important tree species at large spatial scales, may be sufficient to restore many ecosystem services. Such rehabilitation is an economically attractive solution and planting one or a few species is the most common strategy for timber production following deforestation.

Succession may be accelerated by planting just one tree species, because trees promote various processes linked to species diversity (Parrotta, 1995; Wang, Wang, Yang, & Ji, 2008). Trees promote understory plant colonization by improving the chemical, physical and biotic soil quality through root penetration and decomposition, soil biota activity, shading, increasing humidity and reducing temperatures (Lamb, et al., 2005). Seed rain increases, as trees supply perching places for birds and bats dispersing seeds, and an environment for small

arboreal and ground-living and digging animals including invertebrates, pollinating, spreading and burying seeds (Guevara, Purata, & Van der Maarel, 1986; Ingle, 2003; Muscarella and Fleming, 2007). Grasses, and hence fires, and exotic weeds are suppressed by shading from the trees (Ludwig, de Kroon, Berendse, & Prins, 2004). However, although the species richness and general structure of a rehabilitated stand after about 100 years might approach that of a native forest, the species composition still differs (Denslow and Guzman G, 2000; Guariguata and Ostertag, 2001; Saldarriaga, West, Tharp, & Uhl, 1988). The dispersal of species depends on the species' ecology, on surrounding vegetation and on intensity, period and extent of previous land-use in the disturbed area. Such factors may influence the soil seed bank, basal shoots and root sprouts from possibly remaining stumps and roots. In addition, many species have specific requirements of environment, shade, humidity etc. (Guariguata and Ostertag, 2001) and perhaps on large mammals for spreading seeds (Babweteera and Brown, 2010; Campos-Arceiz and Blake, 2011).

Indonesia experienced massive deforestation during colonial times (Department of Forestry, 1986; Whitten, Soeriaatmadja, & Afiff, 1996). Some forest rehabilitation initiatives were implemented then and this has continued since independence in 1945 (Mursidin, 1997; Santoso, 2012). In the 1950s, Indonesia's total forest cover was around 193 million ha (Hannibal, 1950). Since then, both restoration and deforestation have been going on, and in 2016 the forest cover was estimated to be 120 million ha (Ministry of Environment and Forestry, 2017).

The rehabilitation of the forests has mainly been carried out by planting teak, *Tectona grandis* L.f., or mahogany, *Swietenia macrophylla* King, both exotics to Indonesia. Mahogany is naturalized in all forest types throughout the tropics, but is native to Central and South America (Soerianegara and Lemmens, 1993). Teak is native to Southeast Asia and occurs naturally in peninsular India, Myanmar, Thailand and Laos (Verhaegen, Fofana, Logossa, &

Ofori, 2010). Teak was introduced to Indonesia around the 4th century (Ministry of Forestry, 1986) and it is now more or less naturalized (Soerianegara and Lemmens, 1993). Both teak and mahogany are light-demanding successional species at least as young (Brown, Van Staden, Daws, Johnson, & Van Wyk, 2003; Kaosa-ard and Ngao, 1989) and both are prime timber species. Teak has been found to have allelopathic properties, which might hamper the development of understory (Biswas and Das, 2016; Manimegalai, 2012).

We investigated woody and herbaceous species in the understory of teak and mahogany stands planted from 1941 to 2003 in state forests in Java, Indonesia. These areas were established as production forest for timber, but some areas were later changed to protection forest and conservation forest (Table 1 suppl.). Protection forest and conservation forest were not cut, but the trees were allowed to grow old (> 70 years), thus providing suitable areas for long term studies. We compared the understory vegetation between teak stands and mahogany stands and studied its development over time since rehabilitation. We further compared these areas with native forest. We call the rehabilitated areas “stands” to distinguish them from the native forest.

Our aim was to follow teak stands and mahogany stands with different times since rehabilitation to see how the understory vegetation of herbs, woody seedlings and saplings developed with time, whether they differed between teak stands and mahogany stands, and how close they approached the native forest. We expected stands rehabilitated with teak to have a poorer development of understory vegetation than mahogany stands as a result of the allelopathy of teak litter (Brown, et al., 2003). With time since rehabilitation we expected an ongoing succession, with increasingly more species among saplings, fewer among herbs, and seedlings responding somewhere in between. Vegetation characteristics would, with time, approach those of the native forest. The species composition may, however, differ between the rehabilitated stands and the native forests, the latter containing disturbance-sensitive

species, species with particular environmental requirements and those with poor dispersal ability. We expected: (1) differences in species richness, species diversity, density and proportion of native species between teak stands and mahogany stands and between rehabilitated stands and the native forest; (2) that the species richness, diversity, density and proportion of native species in teak stands and mahogany stands would approach those of the native forests through time; and (3) that the species composition would differ between teak stands, mahogany stands and native forest.

Materials and methods

Study area

The study was conducted in the Gunungkidul, Bantul, and Kulonprogo regencies of Yogyakarta Province, Java Island, Indonesia, (between 110°24'19"- 110°28'53" E and 7° 15' 24"- 7° 49' 26" S; Figure 1). [Figure 1 here somewhere] Yogyakarta Province has a humid tropical climate with an average humidity of about 84 – 89%, and average temperature of 26.7°C. The mean monthly minimum and maximum temperatures are 22.6°C and 33.0°C. The average monthly rainfall is 254.7 mm. The rainy season is from October to April, and the dry season from May to September. Large parts of the area experience water shortage during the dry season. The topography is flat to undulating, with an altitude of 100-500 m above sea level. Volcanic landscapes include Sleman, Yogyakarta city, and parts of Bantul. Gunungkidul is dominated by limestone and barren karst (Statistics of Yogyakarta Province 2017). In Gunungkidul, the soil is mainly mediteran and lithosol (BAPPEDA (Provincial Development Planning Board), 2012). Regosol soils are dominant in most parts of Bantul (BAPPEDA (Provincial Development Planning Board), 2013), while in Kulonprogo, the soil type is dominated by lathosol (BPDASHL Serayu Opak Progo (Management Center of Watershed and Protection Forest), 2018).

Selection of stands

In our study areas, the state forests are managed by the Faculty of Forestry, University of Gadjah Mada, by the Governmental Forestry Service, and by the Natural Resources Conservation Center in Yogyakarta. They suggested 12 stands planted with teak and 12 stands with mahogany for this survey (Table 1 suppl.). In addition, we found three native forest fragments which were included, making a total of 27 stands. The stands rehabilitated with teak were planted between 1941 and 2003, those with mahogany were planted between 1941 and 1986. The number of native forest sites was limited due to the difficulties in finding suitable areas with, to our knowledge, no logging or rehabilitation. Even though the number was low and may limit the generality of our results, we believe they are representative for the few natural forests remaining in Yogyakarta province.

Teak and mahogany were planted at 2 m x 4 m spacing, and generally, thinned at the age of 10 - 15 years. Usually the trees in production forests are logged at the age of 35 years, but it depends on the decision of the forestry ministry. The sites differed depending on geology, altitude, species planted and size of the trees. The old teak stems of about 70 years were 30-40 cm in diameter at breast height (DBH; 1.3 m), the young were 8-15 cm. The DBH of 70-year old mahogany was 30-50 cm, and of young stems 15-25 cm. Tree density in mahogany stands was about 20 trees per 100 m², showing no trend with time since rehabilitation. Teak had 15 – 20 trees per 100 m² in the young stands, decreasing to 5 – 10 trees in old stands. Native forest had 27 trees per 100 m². Mahogany stands had on average \pm SE (5 ± 0.6) tree species per 100 m² (including the planted tree), whereas teak had an average of 3 ± 0.3 tree species. Native forest had on average 9 ± 0.8 tree species per 100 m².

Field procedures

Data were collected in May-June 2015. We sampled three categories of plant species: (1)

saplings, here encompassing woody vines, shrubs and trees > 50 cm and < 2.5 m in height; (2) seedlings defined as any woody species > 1 cm and ≤ 50 cm in height; and (3) herbs including forbs, grasses and ferns. Three sampling plots, 5 m x 5 m, about 100 – 300 m apart, were allocated randomly to each stand or native forest, making 81 plots in all. Saplings were recorded in each plot and herbs and seedlings were recorded within a 1 m x 1 m plot in the NW corner of each 25 m² plot. The number of individuals of each species was recorded in each sampling plot. All plants were identified by local names in the field. Voucher specimens were collected, labelled, and sent to two laboratories, namely the Silviculture laboratory at the Faculty of Forestry, University of Gadjah Mada, Yogyakarta, and Plant conservation service of Purwodadi Botanic Garden, for identification.

Data analyses

We analyzed 4 vegetation characteristics for saplings (per 25 m² plot), seedlings and herbs (per 1 m² plot) of the teak and mahogany stands as response variables:

1. Species richness, i.e., the number of species
2. Species diversity, estimated by the Shannon-Wiener index (Krebs, 1989)
3. Density, estimated as the number of individuals per plot
4. The proportion of native species of all species present per plot

We also analyzed the vegetation characteristics for native forests vs young stands (< 41 years) and native forests vs old stands ($\geq 41 - 74$ years). Forty-one years divided the teak stands and the mahogany stands in two equal parts.

To avoid pseudoreplication (Hurlbert, 1984) we used Generalized Linear Mixed Models in the analyses with the sampling areas ($N = 27$) as a random effect. We used a poisson error distribution (or quasipoisson if overdispersed) and log link function when analyzing count data (i.e. species richness and density). For the analysis of the proportion of

native species we used a binomial error distribution and logit link function, and finally linear mixed models for the analysis of diversity.

For all 4 responses, we first compared teak stands, mahogany stands and native forest. For the rehabilitated stands only, we then analyzed the effect of time since rehabilitation (i.e. number of years since the planting of teak or mahogany). The full model consisted of the fixed effects rehabilitation species (i.e. teak or mahogany), time since rehabilitation and the two-way interaction. We performed a backwards selection procedure by removing the least significant predictor until we had only statistically significant ($p < 0.050$) components in the model. All mixed models were carried out using R (version 3.5.3; R Development Core Team, 2015).

In order to study how patterns of plant species composition varied with stand/forest type and time since rehabilitation, a Correspondence Analysis (CA) was performed using CANOCO software (version 4.5 for Windows; Ter Braak and Smilauer, 1998). We first ran CA with the complete species data sets per plot and fitted stand type and time since rehabilitation (native forests were arbitrarily given an age (time) of 300 years) with best fit, showing plots and environmental variables in ordination space. As the large variation between the rehabilitated stands and the native forest caused the ordination to be compressed, we then excluded the native forest and showed the outcome for species using only the rehabilitated stands. Within CANOCO, a forward selection procedure in Canonical Correspondence Analysis (CCA) using a Monte Carlo permutation test ($p < 0.050$; 499 iterations; Ter Braak and Smilauer, 1998) was used to check for the significance of environmental variables (teak, mahogany, native forest and time since rehabilitation). When only the rehabilitated stands were included stands had to be either teak or mahogany, so if one stand type turned out significant the other one was as significant in the opposite direction. All species were

classified as native, exotic or of unknown origin. Herbs were also classified by whether they were annual or perennial.

Results

Plant species

Herbs

We recorded a total of 3208 individual herbs, comprising 47 species and 27 families. This included 10 species identified only to genus level (Table 2 suppl.). In teak stands, *Oplismenus burmannii* (Retz.) P. Beauv and *Clitoria ternatea* L. were the most common (occurred in most plots; numbers refer to Table 2 suppl.; note that numbering differs between herbs, seedlings and saplings). In mahogany stands, *Oplismenus burmannii* and *Cyperus* sp. dominated, and in native forests *Oplismenus burmannii* and *Alpinia nutans* (L.) Roscoe dominated. The native forest had few herbs (8 species) which were mostly exotics (63 %), while mahogany and teak had more (25 species, 40 % exotic and 30 species, 57 % exotic, respectively; Table 2). In native forest, the exotic species were all perennial, and of the native species 67 % were perennial, the rest annual. In mahogany sites 78 % of the exotics were perennial, and of the native species 77 %. In teak sites 67 % of the native species were perennial and 65 % of the exotic (Table 2 suppl.).

Seedlings

A total of 923 individual seedlings were recorded encompassing 59 species from 26 families. Of these, 15 species were identified only to genus level (Table 2 suppl.). Fabaceae was the largest family with eight species, followed by Rubiaceae comprising seven species.

Eupatorium odoratum L. and *Flacourtia jangomas* (Lour.) Raeusch were most common in teak stands, while *Swietenia macrophylla* King dominated in mahogany stands. In native

forests *Nauclea* sp., *Cissus* sp. 2 and *Eupatorium odoratum* L. were most common (Table 2 suppl.).

Saplings

We recorded a total of 5007 individual saplings, comprising 107 species and 36 families in the 5 m x 5 m plots. It included 22 species identified only to genus level (Table 2 suppl.). The family of Fabaceae was the most represented with 18 species, followed by 12 species of Rubiaceae, and 10 species of Euphorbiaceae. In teak stands, *Eupatorium odoratum* L. and *Lantana camara* L. dominated, and in mahogany stands *Dalbergia latifolia* Roxb. and *Leucaena leucocephala* (Lam.) de Wit dominated. The native forests were dominated by *Lantana camara* L. (64).

Species diversity, richness, density and proportion of native species in the understory

[Figure 2 here somewhere] The average measures of species diversity, richness, density and proportion of native species did not differ among teak stands, mahogany stands and native forests (all $\chi^2 = 3.68$, d.f. = 2, all $p > 0.159$). However, we found differences between young stands (< 41 years) and native forests. Species richness of herbs was higher in young stands than in native forests (Est. \pm SE: 0.82 ± 0.39 , Table 1), while species diversity of saplings, proportion of native seedlings and saplings were higher in native forests than in young stands (-0.65 ± 0.31), (-1.09 ± 0.52), and (-0.66 ± 0.31), respectively (Table 1). By >41 - 74 years since rehabilitation, species richness, species diversity, density and proportion of native species no longer differed between rehabilitated stands and native forest (Table 1).

We found many relationships with time since rehabilitation (Figure 2):

- Species diversity of saplings increased with time since rehabilitation in both teak and mahogany stands ($\chi^2 = 13.51$; d.f. = 1, $p < 0.001$);

- Species richness of herbs decreased ($\chi^2 = 8.25$, d.f. = 1, $p = 0.004$) while species richness of saplings increased ($\chi^2 = 9.03$, d.f. = 1, $p = 0.003$) with time since rehabilitation in both teak and mahogany stands. Species richness of seedlings tended to show an interaction between time and rehabilitation type ($\chi^2 = 3.13$, d.f. = 1, $p = 0.077$), with an increasing richness in the mahogany stands and a decreasing richness through time in the teak stands;
- There was an interaction between time since rehabilitation and type of stand with regard to the density of seedlings ($\chi^2 = 6.62$, d.f. = 1, $p = 0.010$) and saplings ($\chi^2 = 4.20$, d.f. = 1, $p = 0.041$) which increased in mahogany and decreased in teak stands.
- The proportion of native plants increased with time since rehabilitation in both teak and mahogany stands, most significantly for herbs ($\chi^2 = 8.15$, d.f. = 1, $p = 0.004$) and seedlings ($\chi^2 = 5.59$, d.f. = 1, $p = 0.018$).

Species composition

Herbs

Correspondence Analysis (CA) and forward selection with Canonical Correspondence Analysis (CCA) of herbs for teak stands, mahogany stands and the native forest showed that plot positions in the ordination space depended primarily on whether or not stands were teak ($F = 2.40$, $p < 0.002$) and tended to depend on time since rehabilitation ($F = 1.80$, $p = 0.068$). [Figure 3 here somewhere] Two plots with native forests were outliers (Figure 3). Excluding the native forests, ordination with CA and forward selection with CCA showed a strong influence of time since rehabilitation ($F = 3.90$, $p < 0.002$; Figure 3) for the herb species of the rehabilitated teak and mahogany stands. Many species such as *Polytrias indica* (Houtt.) Veldkamp (36) and *Spigelia anthelmia* L. (41) were common in the young stands, which also showed large variation along axis 2. For example, *Desmodium gangeticum* (L.) DC. (14) and

Pteris ensiformis (Burm.) (38) were typical for old stands (Figure 3).

Seedlings

Correspondence Analysis of the seedlings for rehabilitated stands and native forest showed four plots from native forests and one from teak as outliers (Figure 3). Forward selection in CCA showed influence of native forest and mahogany stand type and time since rehabilitation on distribution of plots, mahogany ($F = 2.20$, $p < 0.002$), time ($F = 2.10$, $p = 0.004$) and native forests ($F = 1.60$, $p = 0.016$). Correspondence Analysis of seedlings in the rehabilitated plots (teak and mahogany) only, and forward selection in CCA showed mahogany (and teak), ($F = 2.70$, $p = 0.002$) and time since rehabilitation ($F = 2.00$, $p = 0.002$) to influence species distribution. Many species showed an affinity to mahogany, such as *Clerodendrum serratum* (L.) Moon.(18) and *Leucaena leucocephala* (Lam.) de Wit (37), a few to teak, such as *Schoutenia ovata* Korth. (51), and some, such as *Psychotria* sp. (48) for a long time since rehabilitation.

Saplings

Correspondence Analysis of saplings using data from teak stands, mahogany stands and from native forest showed two plots from the native forests as outliers (Figure 3). Forward selection in CCA showed time since rehabilitation ($F = 2.80$, $p < 0.002$), native forests ($F = 3.17$, $p < 0.002$) and mahogany ($F = 1.50$, $p = 0.018$) to influence the distribution of plots (Figure 3). Running the CA analysis with forward selection in CCA without the native forests showed time since rehabilitation ($F = 4.30$, $p < 0.002$) and mahogany (and teak) ($F = 1.87$, $p < 0.002$) to influence the distribution of species. Mahogany and time since rehabilitation were highly correlated, and opposite in the graph to *Eupatorium odoratum* L. (45) which, thus, occurred in teak stands. Species with high scores for time since rehabilitation and mahogany along the first axis included *Psychotria* sp. (84) and along the second axis *Arenga* sp. (12; Figure 3).

Discussion

We did not find the expected effect of planted tree species on understory species richness, species diversity, density of plants or proportion of native species. Nor did we find differences in these understory measures in teak and mahogany stands compared with native forest.

Instead, we found multiple effects of time since rehabilitation, such that as rehabilitated stands matured, the understory characteristics became the same as those of the native forests.

However, species composition differed between teak and mahogany stands and between the rehabilitated stands and native forests. This difference was greatest between rehabilitated stands and native forests. To our knowledge, there is no scientific description of native forests in Yogyakarta and few studies of the understory vegetation in rehabilitated stands in Indonesia that could be used to support our results. We therefore use literature from other geographies, such as Latin America, in the discussion below to some extent.

Young stands, old stands and native forest

Species richness of herbs was higher in the young teak and mahogany stands than in the native forest. There was a tendency also for density ($p = 0.073$) of herbs to be higher.

Disturbance of the areas at logging and rehabilitation activities provide good sites for herbs to colonize, and the young planted stands have less shade than older stands. We never measured light, but the native forest is likely to have lowest light availability for understory vegetation as a consequence of dense canopy. When the stands matured the canopies leading to a decrease in herbs. In the old stands herb density and richness were no longer different from the native forest. The young stands had the same density of saplings as the native forests, but the species diversity was lower, possible as many species were adapted to grow in the shade, which developed gradually over time. The old stands did not show any difference in diversity of saplings to the native forest. The proportion of native species of seedlings and saplings

were lower in the young stands than in the native forest. The proportion was higher in the old stands as a natural consequence of more time for colonization and many species being adapted to growing in the shade.

Effects of time since rehabilitation, stand type and native forest

We found that the species diversity of saplings increased with time since rehabilitation in both teak and mahogany stands as a result of ongoing succession, while the diversity of herbs decreased. As stands mature, the shade from the tree canopy might hamper herb and seedling growth whereas saplings may increase (Guariguata and Ostertag, 2001). As a result we also found the species richness of herbs to decrease and the species richness of saplings to increase with time in both teak and mahogany stands.

In mahogany stands, time since rehabilitation had a positive effect on seedling and sapling plant density and a tendency for a positive correlation with the species richness of seedlings. By contrast, in teak stands, there was a negative relationship between seedling and sapling density and time since rehabilitation. A study in South Sumatra, Indonesia, showed a higher species diversity of understory in mahogany stands 25 years after planting than in *Pinus merkusii* Jungh. & de Vriese, *Peronema canescens* Jack, and *Schima wallichii* (DC.) Korth. Forest (Kunarso and Azwar, 2013). Teak stands in our study were, on average, younger than mahogany stands, 39 ± 4 years versus 50 ± 3 , so would not have reached the same point of maturity as the mahogany stands, but this does not explain the negative correlation between plant density and time since rehabilitation. Teak litter has allelopathic properties, which might reduce understory growth (Biswas and Das, 2016; Manimegalai, 2012). Even though Wolfe, Dent, Deago, & Wishnie (2015) found understory richness and diversity under planted teak to be comparable with an indigenous forest, a number of other studies in Indonesia and elsewhere have found understory species richness and diversity in

teak plantations to decrease with increasing time since rehabilitation (Healey and Gara, 2003; Nikmah, Jumari, & Wiryani, 2016). In contrast, a study in northern Thailand, where teak is indigenous, showed that a 37-year-old plantation of teak could facilitate the development of native woody species comparable to surrounding mixed deciduous forests (Koonkhunthod, Sakurai, & Tanaka, 2007). This indicates that where teak is indigenous, the local species might to some extent be adapted to its allelopathy. Our results suggest that in Indonesia, other tree species have more problems establishing in teak stands than in mahogany stands.

Generally, sapling diversity, species richness and density, in Indonesia and elsewhere, increase with time since rehabilitation, suggesting a sustainable forestry (Aide, Zimmerman, Herrera, Rosario, & Serrano, 1995; Baniya, Solhøy, & Vetaas, 2009; Mashudi, Susanto, & Baskorowati, 2016; Ruiz, Fandiño, & Chazdon, 2005). We confirmed these results both in teak and mahogany stands for diversity and richness of sapling species, while density of plants only increased in mahogany stands.

Martin, Moloney, & Wilsey (2005) used the proportion of native species as one attribute to measure restoration success. Disturbance of soil associated with deforestation and restoration activities can promote establishment of non-native species (Stoddard, McGlone, Fulé, Laughlin, & Daniels, 2011). In a grassland restoration study, the proportion of non-native species was higher in restored than in remnant sites (Martin, et al., 2005). It has also been pointed out that a rehabilitated ecosystem rarely arrives at the same species diversity and provision of ecosystem services as a native ecosystem (Bullock, Aronson, Newton, Pywell, & Rey-Benayas, 2011). At least the first part of that statement did not agree with our findings, which showed no difference in the species richness, species diversity, density and proportion of native species between native forests and the rehabilitated stands, although species composition did differ. Ecosystem function and, most likely, provision of ecosystem services, seem, to be mainly related to functional diversity, that is plants with different functional traits,

and also to spatial diversity (Aerts and Honnay, 2011; Díaz et al., 2007; Grime, 1998) which we did not study. It is, however, uncertain which functional traits are most important in relation to ecosystem function and provision of ecosystem services (Díaz, et al., 2007). A variety of functional traits, above and below the soil surface, means a better utilization of resources, more interactions and also more buffering against changing conditions, such as land use and climate.

Plant Communities

Species composition of the native forests was markedly different from the areas rehabilitated with teak or mahogany. This difference persisted with the aging of the planted stands, contrary to other understory characteristics. Many of the typical species for native forests, for example 10 of the 16 unique woody species, were native (and the origin of four was unknown). We do not know the ecology of the species specifically occurring in the native forests, but they may be sensitive to disturbance, have low dispersal rate or need the presence of certain other species such as special mycorrhizal fungi, or large mammals eating the fruits and spreading seeds (Babweteera and Brown, 2010; Campos-Arceiz and Blake, 2011). The communities of herbs and seedlings in teak and mahogany stands changed with time from more exotics in the newly rehabilitated stands to more natives in the older stands. Any plants originating from the soil seed bank, basal shoots or root sprouts should be among the species appearing within the first decade. The oldest rehabilitated stands were 74 years, and whether they would with time achieve a larger proportion of species also occurring in the native forests is uncertain (Guariguata and Ostertag, 2001).

Herbs

Correspondence Analysis of only teak and mahogany plots showed herb species to vary with time since rehabilitation, making up the first ordination axis. Species in the young stands also

showed variation along ordination axis two, reaching from *Borreria assurgens* (Ruiz & Pav.) Griseb (7) and *Mimosa pudica* L. (27) with negative values on axis two to *Polytrias indica* (Houtt.) Veldkamp (36) and *Themeda arguens* (Linné) Hack (45) with positive values. There seemed to be no significant relationship between axis 2 and the species planted. Most herbs with positive values on the axis were perennial and related to mahogany, and most with negative values were annual and related to teak. The two groups did not differ in exotic and native species, but the young stands generally had a dominance of exotic species. There was a dense cluster of species with an affinity to a longer time since rehabilitation, among them *Adiantum cuneatum* Langsd. & Fisch. (1), *Desmodium gangeticum* (L.) DC.(14) and *Pteris ensiformis* Burm. f. (38). In that group there was about the same species richness of exotics, natives and unknown species, and just around 18 % of the species were annual. There was a general decline in exotic species, in annuals and in herbs with the maturing of the stands and increasing shade and competition.

Seedlings

Correspondence Analysis of woody seedlings in the rehabilitated sites showed them to vary with species planted and with time since rehabilitation. Species characterizing older stands were mainly native or unknown, for example *Psychotria* sp. (48) and *Eugenia* sp. (44). Species in young teak stands were *Schoutenia ovata* Korth. (51) and *Sida acuta* Burm. f. (52), and in young mahogany stands *Clerodendron serratum* (L.) Moon (18). Species related to young stands contained many exotic and few unknown species. It is the same trend as for the herbs, with exotics to some extent disappearing as the stands mature.

Saplings

Correspondence Analysis of saplings in the rehabilitated sites showed a variation with species planted and with time since rehabilitation. Some species in old teak or mahogany stands or

mahogany stands with high scores on the second axis were *Psychotria* sp. (84) and *Eugenia* sp. (44), and with high scores on the first axis *Gluta renghas* L. (57), whereas *Sida rhombifolia* L. (91) grew in young sites. We did not find an increase in the proportion of native plants as stands matured. Exotics such as *Eupatorium odoratum* L. (45), *Lantana camara* L. (64) and *Leucaena leucocephala* (Lam.) de Wit (67) remained common in old stands – and also occurred in the native forests, which otherwise had a dominance of native species.

Conclusion

Our results show that forest rehabilitation in the Gunungkidul, Bantul, and Kolonprogo regencies by planting of exotic species for timber production, has also enhanced native species of the understory. Species richness, diversity, density and proportion of native species approached values for native forests through time. From a biodiversity perspective, it is therefore important to let rehabilitated stands mature. However, teak stands generally had a poorer development than mahogany stands concerning seedlings and saplings density. The species composition in teak and mahogany stands differed, and both were very different from the native forests. This, may have effects on ecosystem function and provision of ecosystem services.

Most, but not all, studies today show that ecosystem services are positively correlated to plant species or functional diversity, while we know much less about the effect of plant community composition. If the species composition of the plant community or its functional diversity are important for maintaining optimal ecosystem functioning and ecosystem services, there is a need to establish rehabilitation programs using a higher diversity of trees including indigenous species. In addition, a wide evaluation of forest restoration projects is

urgently needed to find what factors govern ecosystem functions, how these functions can be promoted, and how they result in ecosystem services for humans.

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Table 1. Results from linear mixed models showing richness (species richness), density, diversity (Shannon-Wiener diversity index), and proportion of native species (prop-native) comparing native forests (native) vs young stands (teak and mahogany; < 41 years) and old stands ($\geq 41 - 74$ years). * Significant values are at $p < 0.05$.

Characteristics	Vegetation	Native vs young stands			Native vs old stands	
		df	χ^2	p	χ^2	p
Richness	Herbs	1	4.18	0.041*	0.59	0.441
	Seedlings	1	0.96	0.327	0.17	0.680
	Saplings	1	2.36	0.125	1.17	0.280
Density	Herbs	1	3.22	0.073	0.98	0.322
	Seedlings	1	0.08	0.775	0.84	0.358
	Saplings	1	0.27	0.604	2.43	0.119
Diversity	Herbs	1	2.69	0.101	0.04	0.838
	Seedlings	1	2.39	0.122	0.43	0.514
	Saplings	1	4.41	0.036*	0.33	0.564
Prop-native	Herbs	1	1.01	0.315	0.22	0.641
	Seedlings	1	4.43	0.035*	0.15	0.703
	Saplings	1	4.49	0.034*	3.34	0.068

Table 2. Species richness of herbs, seedlings and saplings, by origin (with percentages in brackets), found in 25 m²

(saplings) or 1 m² (seedlings and herbs) plots within mahogany or teak stands and native forest.

Stands	herbs	Species richness			seedlings	Species richness			saplings	Species richness		
		Native	Exotic	Unknown		Native	Exotic	Unknown		Native	Exotic	Unknown
Mahogany	25	8 (32)	10 (40)	7 (28)	29	14 (48)	11 (38)	4 (14)	69	33 (48)	24 (35)	12 (17)
Teak	30	9 (30)	17 (57)	4 (13)	37	13 (35)	17 (46)	7 (19)	62	33 (53)	19 (31)	10 (16)
Native forest	8	5 (37)	5 (63)	0	22	10 (46)	8 (36)	4 (18)	43	24 (56)	11 (26)	8 (18)

Figure legends

Figure 1. The locations of the study areas and of stands sampled in the forests of Yogyakarta, Indonesia. T = teak (N=12), M = mahogany (N=12) and N = native forest (N=3). The numbers refer to the stands in Table 1 suppl.

Figure 2. The effect of time since rehabilitation for herbs, seedlings and saplings. Points show the mean of the 3 registered plots in each stand (N=27). Dashed line and triangles are the teak stands, the solid line and circles are the mahogany stands and the squares are native forests (native). As we have no age since rehabilitation for the native forests, except that we know the trees may be very old, they are located arbitrarily at the right end of the graph.

Figure 3. Ordinations with Correspondence Analyses for herbs, seedlings and saplings. Top three graphs show plots for teak stands (triangles, N=36), mahogany stands (circles, N=36) and native forest (squares, N=9). Bottom three graphs are only for rehabilitated stands and show species as points and the most common species as numbers relating to Table 2 suppl. Shown environmental variables are significant in Canonical Correspondence Analysis and are included with best fit.

Figure 1.

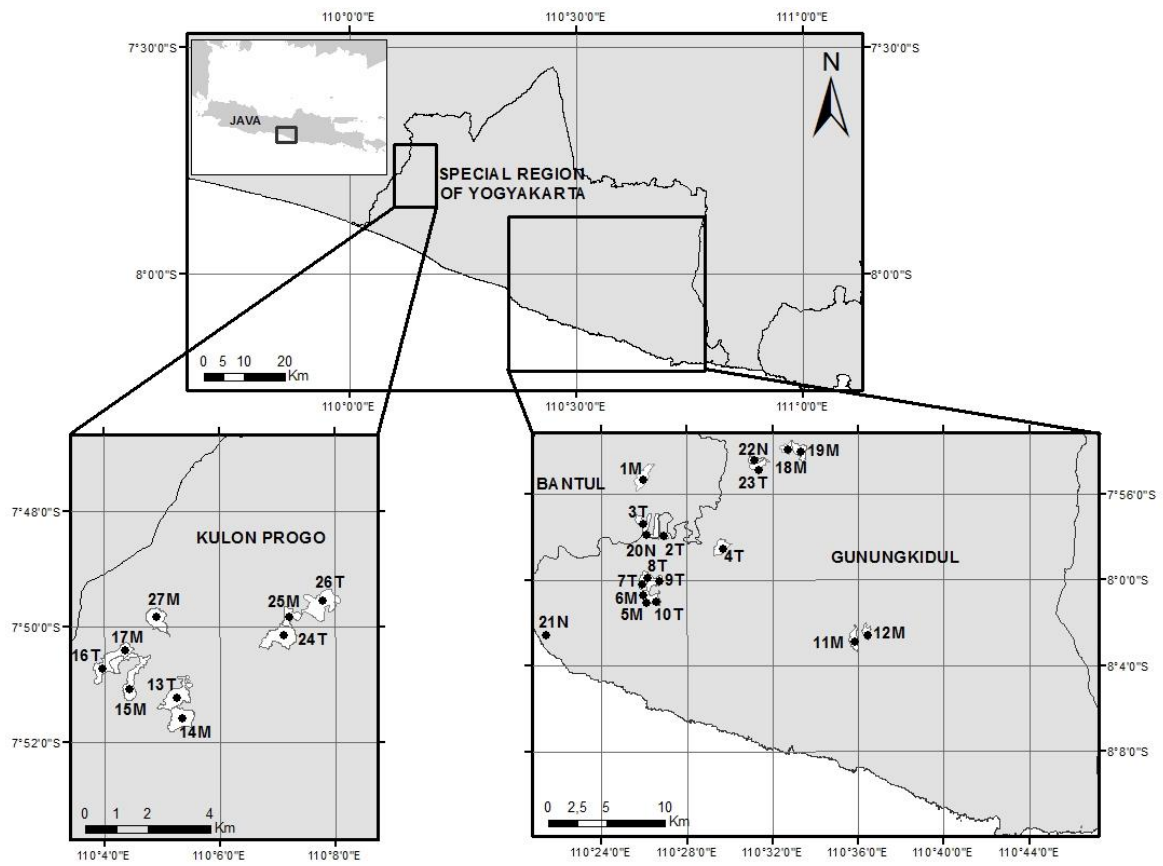


Figure 2.

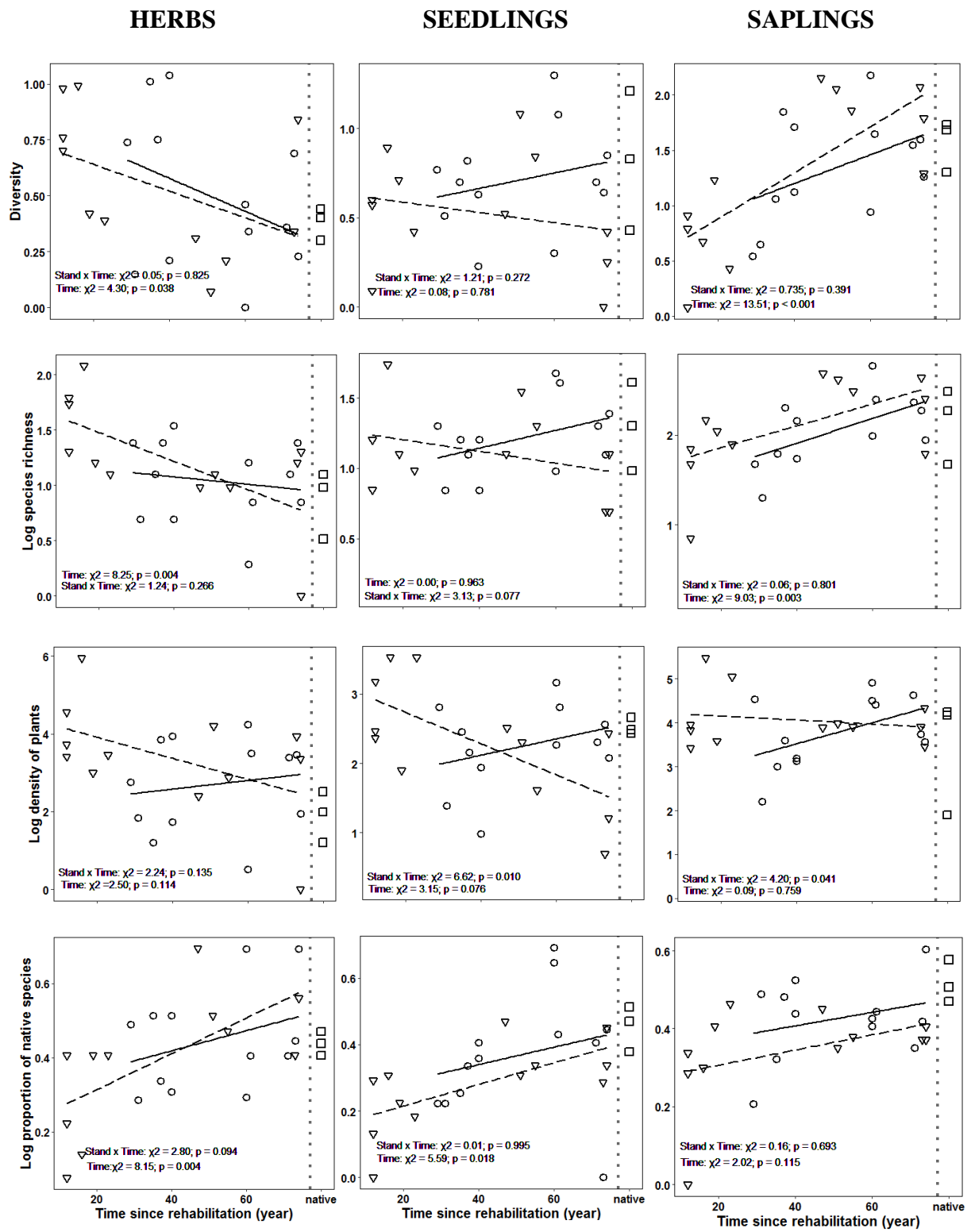
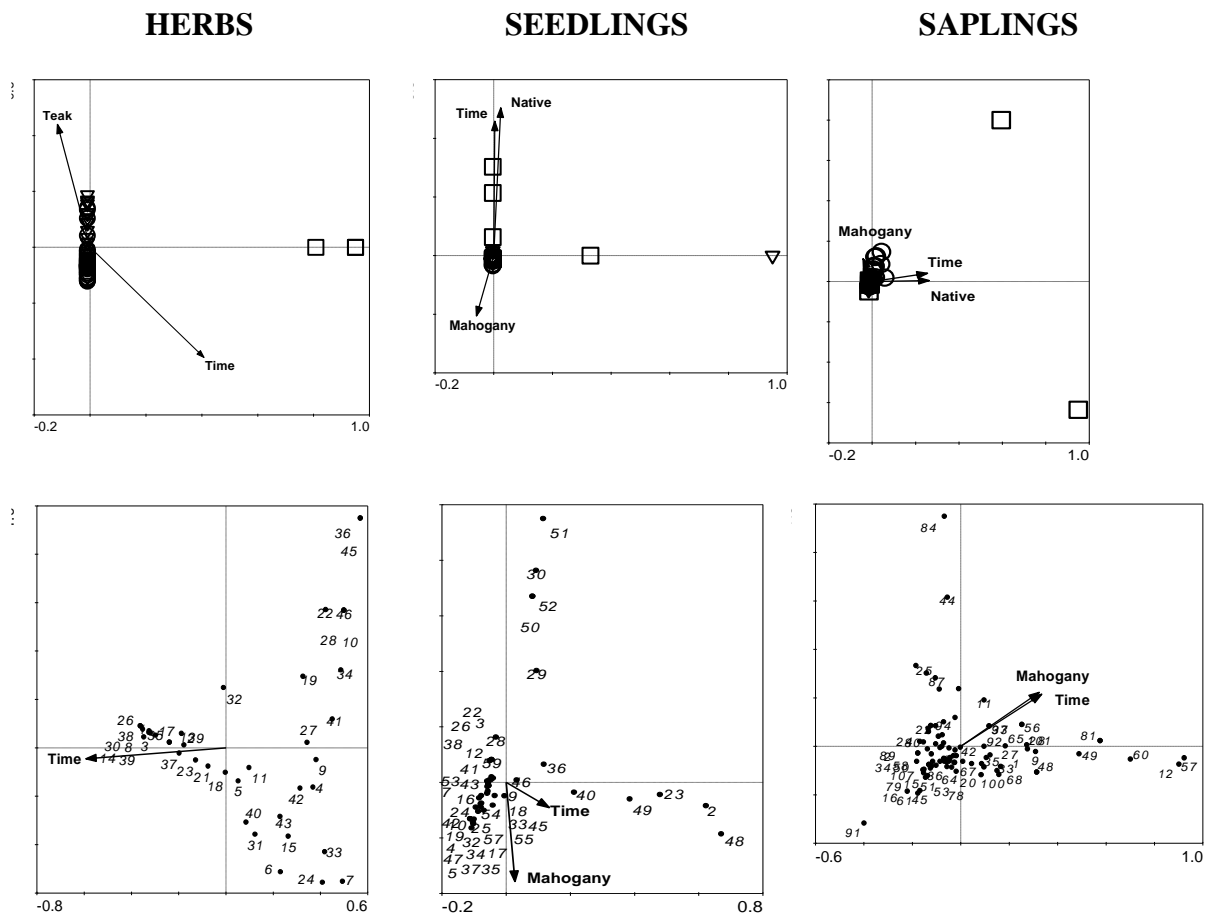


Figure 3.



SUPPLEMENTARY

Table 1. Stand type (Native = native forest), site, region, forest function, year of rehabilitation (planting with teak or mahogany), time since rehabilitation and altitude where the registration of the plant community was done for this study in 2015. For native forest, there is no time since rehabilitation, as they represent continuous forest cover. T = teak, M = mahogany and N = native forest.

Stand type	Site	Region	Forest function	Year of rehabilitation	Time since rehabilitation (year)	Altitude (m.a.s.l.)
Native	20 N	Bantul	protection	none	none	400
Native	21 N	Gunungkidul	protection	none	none	200
Native	22 N	Gunungkidul	conservation	none	none	150
Mahogany	12 M	Gunungkidul	production	1986	29	100
Mahogany	6 M	Gunungkidul	production	1984	31	300
Mahogany	1 M	Bantul	protection	1980	35	450
Mahogany	15 M	Kulonprogo	production	1978	37	220
Mahogany	5 M	Gunungkidul	production	1975	40	300
Mahogany	27 M	Kulonprogo	production	1975	40	250
Mahogany	18 M	Gunungkidul	conservation	1955	60	200
Mahogany	19 M	Gunungkidul	conservation	1955	60	200
Mahogany	11 M	Gunungkidul	production	1954	61	100
Mahogany	14 M	Kulonprogo	production	1944	71	250
Mahogany	25 M	Kulonprogo	conservation	1942	73	300
Mahogany	17 M	Kulonprogo	production	1941	74	220

Teak	2 T	Bantul	protection	2003	12	380
Teak	4 T	Gunungkidul	production	2003	12	100
Teak	7 T	Gunungkidul	production	2003	12	300
Teak	3 T	Bantul	protection	1999	16	380
Teak	8 T	Gunungkidul	production	1996	19	300
Teak	10 T	Gunungkidul	production	1992	23	300
Teak	23 T	Gunungkidul	conservation	1968	47	100
Teak	9 T	Gunungkidul	production	1964	51	300
Teak	26 T	Kulonprogo	conservation	1960	55	300
Teak	24 T	Kulonprogo	conservation	1942	73	400
Teak	13 T	Kulonprogo	production	1941	74	170
Teak	16 T	Kulonprogo	production	1941	74	220

Table 2. Plant species, family, status and life cycle, in brackets, (E = exotic, N = native, P = perennial A = annual) in native forest, mahogany and teak stands. Species with no life cycle given are perennial woody species. H = herbs; Sd = seedlings; Sp = saplings. The mean number of plants in 1 m² is presented. ‘Number in ordinations’ refer to numbers of plant species as used in the ordinations, i.e. different for herbs, seedlings and saplings. Plant species unique to the stand type are highlighted in bold italics.

Species	Family	Status & life cycle	Native forest			Mahogany			Teak			Number in ordinations			
			H	Sd	Sp	H	Sd	Sp	H	Sd	Sp	H	Sd	Sp	
<i>Abrus precatorius</i>	Fabaceae	E					0.003								1
<i>Acacia auriculiformis</i>	Fabaceae	N					0.167	0.027						1	2
<i>Acacia mangium</i>	Fabaceae	N					0.001								3
<i>Acacia villosa</i>	Fabaceae	E					0.010				0.012				4
<i>Adiantum cuneatum</i>	Pteridaceae	E (P)				2.278			0.417				1		
<i>Aeschynomene indica</i>	Fabaceae	U									0.004				5
<i>Albizia procera</i>	Fabaceae	N					0.001								6
<i>Allophylus cobbe</i>	Sapindaceae	E		0.111	0.053		0.028	0.009		0.028	0.032			2	7
<i>Alpinia nutans</i>	Zingiberaceae	N (P)	0.444										2		

<i>Alpinia sp.</i>	Zingiberaceae	U (P)			0.028				3	
<i>Amphilophium sp.</i>	Bignoniaceae	U			0.022					8
<i>Andrographis paniculata</i>	Acanthaceae	E (P)			0.028		0.611		4	
<i>Andropogon gerardii</i>	Poaceae	E (P)					0.028		5	
<i>Anomianthus dulcis</i>	Annonaceae	N	0.333	0.053	0.028	0.019		0.028	3	9
<i>Antidesma sp.</i>	Euphorbiaceae	U						0.001		10
<i>Ardisia humilis</i>	Primulaceae	E			0.278	0.048		0.028 0.048	4	11
<i>Arenga sp.</i>	Arecaceae	N			0.083	0.062			5	12
<i>Argyreia sp.</i>	Convolvulaceae	U						0.028 0.003	6	13
<i>Artocarpus elasticus</i>	Moraceae	N			0.004					14
<i>Barleria prionitis</i>	Acanthaceae	N						0.667 0.020		0.003 7 15
<i>Bauhinia scandens</i>	Fabaceae	N	1.000	0.036	0.472	0.009		1.111 0.042	8	16
<i>Bidens pilosa</i>	Asteraceae	E (A)						0.111		6
<i>Blighia sp.</i>	Sapindaceae	E						0.002		17
<i>Borreria assurgens</i>	Rubiaceae	E (P)						0.139		7
<i>Bridelia glauca</i>	Euphorbiaceae	N			0.013	0.028	0.003		0.009	9 18

Bridelia stipularis	Euphorbiaceae	N	0.009	0.028	0.003	0.083	0.004	10	19
Brucea javanica	Simaroubaceae	N			0.001		0.040		20
Buchanania arborescens	Anacardiaceae	N	0.222	0.009			0.002	11	21
Caesalpinia sappan	Fabaceae	E			0.011	0.028		12	22
<i>Calophyllum inophyllum</i>	Clusiaceae	E		0.018					23
Capparis acuminata	Capparaceae	N	0.111	0.040			0.002	13	24
<i>Capparis micracantha</i>	Capparaceae	N	0.111					14	
<i>Cassia obtusifolia</i>	Fabaceae	E			0.006				25
Cassia siamea	Fabaceae	E			0.002	0.028		15	26
<i>Christella dentata</i>	Thelypteridaceae	E (P)		0.194				8	
<i>Chrysopogon serrulatus</i>	Poaceae	N (P)				0.111		9	
Cissus sp. 1.	Vitaceae	U	0.009	0.722	0.154		0.016	16	27
Cissus sp. 2.	Vitaceae	U	0.556	0.027	0.013	0.667	0.011	17	28
<i>Citrus sp.</i>	Rutaceae	U			0.001				29
Clausena excavata	Rutaceae	N	0.022		0.003		0.006		30
<i>Cleistanthus sp. 1.</i>	Euphorbiaceae	U					0.001		31

<i>Cleistanthus sp. 2.</i>	Euphorbiaceae	U		0.004						32
<i>Cleome viscosa</i>	Capparaceae	E (A)				0.028			10	
<i>Clerodendrum serratum</i>	Verbenaceae	E			0.250	0.062			18	33
<i>Clerodendrum ugandense</i>	Verbenaceae	E						0.004		34
<i>Clitoria ternatea</i>	Fabaceae	E (P)	0.333	0.222		3.056			11	
<i>Costus speciosus</i>	Zingiberaceae	N (P)	0.333						12	
<i>Cyperus sp.</i>	Cyperaceae	E (P)	0.111	4.250		0.111			13	
<i>Dalbergia latifolia</i>	Fabaceae	N			0.472	0.194	0.111	0.060	19	35
<i>Decaspermum parviflorum</i>	Myrtaceae	N	0.111						20	
<i>Derris trifoliata</i>	Fabaceae	E	0.111					0.026	21	36
<i>Desmodium gangeticum</i>	Fabaceae	N (P)				0.167			14	
<i>Desmodium lineatum</i>	Fabaceae	E (P)				0.056			15	
<i>Dioscorea hispida</i>	Dioscoreaceae	N				0.002				37
<i>Diplazium lonchophyllum</i>	Athyriaceae	E (P)	0.111						16	
<i>Diplazium sp.</i>	Athyriaceae	U (P)		0.111					17	
<i>Discaria chacaye</i>	Rhamnaceae	E		0.004				0.001		38

<i>Dysoxylum macrocarpum</i>	Meliaceae	N			0.003					39
<i>Elephantopus scaber</i>	Asteraceae	N (P)			0.222			18		
<i>Erythrina microcarpa</i>	Fabaceae	N					0.001			40
<i>Eugenia aromatica</i>	Myrtaceae	N					0.001			41
<i>Eugenia cumini</i>	Myrtaceae	N			0.028	0.012	0.028	0.008	22	42
<i>Eugenia densiflora</i>	Myrtaceae	N		0.004						43
<i>Eugenia sp. 1.</i>	Myrtaceae	U			0.222	0.098	0.194	0.057	23	44
<i>Eupatorium odoratum</i>	Asteraceae	E	1.333	0.262	0.889	0.433	6.083	1.688	24	45
<i>Eupatorium sp.</i>	Asteraceae	E					0.028			25
<i>Euphorbia hirta</i>	Euphorbiaceae	E (A)					0.083		19	
<i>Ficus drupacea</i>	Moraceae	N					0.002			46
<i>Ficus grossularioides</i>	Moraceae	N					0.001			47
<i>Ficus palmeri</i>	Moraceae	E					0.028			26
<i>Ficus ribes</i>	Moraceae	N				0.004				48
<i>Ficus septica</i>	Moraceae	N				0.020		0.001		49
<i>Ficus sp.</i>	Moraceae	U		0.667						27

Flacourtia indica	Flacourtiaceae	E	0.067	0.194	0.042	0.083	0.022	28	50
Flacourtia jangomas	Flacourtiaceae	E	0.018	0.056	0.018	0.250	0.039	29	51
<i>Flemingia macrophylla</i>	Fabaceae	N	0.009						52
<i>Flemingia strobilifera</i>	Fabaceae	N				0.111	0.009	30	53
<i>Gardenia sp.</i>	Rubiaceae	E	0.444					31	
<i>Gliricidia sepium</i>	Fabaceae	E				0.004			54
<i>Globba sp.</i>	Zingiberaceae	N (P)		0.056				20	
Glochidion eriocarpum	Euphorbiaceae	E	0.009			0.002			55
<i>Glochidion zeylanicum</i>	Euphorbiaceae	E			0.006				56
Gluta renghas	Anacardiaceae	N	0.004		0.004				57
Glycosmis pentaphylla	Rutaceae	N	0.111	0.027	0.194	0.043	0.009	32	58
<i>Gmelina arborea</i>	Verbenaceae	E			0.001				59
Gnetum gnemon	Gnetaceae	E	0.004	0.028	0.012			33	60
Guettarda sp.	Rubiaceae	U	0.009		0.001		0.008		61
<i>Helminthostachys zeylanica</i>	Ophioglossaceae	N (A)		0.028				21	
Heteropogon sp.	Poaceae	U (P)	0.111		25.889			22	

<i>Impatiens sp.</i>	Balsaminaceae	E (A)						0.306		23				
Imperata cylindrica	Poaceae	N (P)			2.639			2.472		24				
<i>Inocarpus fagifer</i>	Fabaceae	N			0.013						62			
<i>Ipomoea rubra</i>	Convolvulaceae	E (P)	0.111							25				
<i>Ixora sp.</i>	Rubiaceae	U			0.013						63			
Lantana camara	Verbenaceae	E	0.667	0.262		0.194	0.046		0.056	0.144	34	64		
Leea aequata	Vitaceae	N			0.089		0.083	0.097		0.111	0.056	35	65	
<i>Leea sp.</i>	Vitaceae	U							0.139			36		
<i>Lepisanthes rubiginosa</i>	Sapindaceae	N			0.004							66		
Leucaena leucocephala	Fabaceae	E	0.333	0.116		0.139	0.134		0.028	0.092		37	67	
<i>Lindsaea trichomanoides</i>	Lindsaeaceae	E (P)									1.000		26	
Litsea glutinosa	Lauraceae	N						0.012		0.003			68	
Macaranga tanarius	Euphorbiaceae	N			0.013		0.028						38	69
<i>Mallotus paniculatus</i>	Euphorbiaceae	N	0.556	0.382									39	70
<i>Melaleuca leucadendra</i>	Myrtaceae	N						0.002		0.028			40	71
<i>Melochia umbellata</i>	Malvaceae	E								0.361			41	

<i>Mimosa pudica</i>	Fabaceae	E (P)			6.333				27	
<i>Mischocarpus sundaicus</i>	Sapindaceae	N		0.004						72
<i>Morinda citrifolia</i>	Rubiaceae	E			0.001					73
<i>Morus alba</i>	Moraceae	E				1.556			42	
<i>Mussaenda landia</i>	Rubiaceae	E			0.004					74
Mussaenda sp.	Rubiaceae	U			0.001	0.028			43	75
Nauclea sp.	Rubiaceae	U	2.222		0.001				44	76
<i>Neonauclea sp.</i>	Rubiaceae	N		0.040						77
Nephelium mutabile	Sapindaceae	E			0.002		0.009			78
<i>Ocimum tenuiflorum</i>	Lamiaceae	N (A)			3.250				28	
Oplismenus burmannii	Poaceae	N (A)	5.000	10.278	14.417				29	
<i>Orthiopteris sp.</i>	Dennstaedtiaceae	U (P)		0.167						30
<i>Oxalis barrelieri</i>	Oxalidaceae	E (A)		0.028						31
Paederia foetida	Rubiaceae	N		0.027	0.417	0.037	0.306	0.022	45	79
Paederia sp.	Rubiaceae	U	1.778	0.036	0.222	0.061	0.167	0.004	46	80
Passiflora sp.	Passifloraceae	U (P)		0.028		0.167				32

<i>Phyllanthus niruri</i>	Euphorbiaceae	E (A)			0.083			33		
Phyllanthus sp.	Euphorbiaceae	U (A)		0.028		0.500		34		
<i>Piper nigrum</i>	Piperaceae	E			0.028	0.006		47	81	
Platynerium sp.	Polypodiaceae	U (P)		0.306		0.083		35		
<i>Podocarpus neriifolius</i>	Podocarpaceae	N					0.003		82	
<i>Polyalthia sp.</i>	Annonaceae	U	0.013						83	
<i>Polytrias indica</i>	Poaceae	E (P)				0.333		36		
Porana volubilis	Convolvulaceae	N (P)		0.639		3.111		37		
<i>Psychotria sp.</i>	Rubiaceae	U			1.611	0.299		48	84	
<i>Pteris ensiformis</i>	Pteridaceae	N (P)		0.750				38		
Rubus rosifolius	Rosaceae	N				0.003	0.001		85	
<i>Santalum album</i>	Santalaceae	N					0.002		86	
Sauropus androgynus	Phyllanthaceae	N			0.056	0.007	0.056	0.010	49	87
Schleichera oleosa	Sapindaceae	E				0.004	0.028	0.008	50	88
Schoutenia ovata	Tiliaceae	N	0.022			0.034	0.167	0.070	51	89
<i>Selaginella pallescens</i>	Selaginellacheae	E (P)		0.417				39		

<i>Sida acuta</i>	Malvaceae	E				0.167	0.002	52	90	
<i>Sida rhombifolia</i>	Malvaceae	E				0.306	0.008	53	91	
Smilax zeylanica	Smilacaceae	N			0.004		0.003		92	
Spathoglottis plicata	Orchidaceae	N (P)		0.028		0.028		40		
<i>Spigelia anthelmia</i>	Loganiaceae	E (P)				0.194		41		
<i>Stachytarpheta indica</i>	Verbenaceae	E (A)				0.250		42		
<i>Sterculia foetida</i>	Sterculiaceae	N			0.001				93	
<i>Streblus asper</i>	Moraceae	N					0.008		94	
Streblus sp.	Moraceae	U			0.012	0.028	0.004	54	95	
<i>Suregada glomerulata</i>	Euphorbiaceae	N		0.040					96	
Swietenia macrophylla	Meliaceae	E	0.111		2.361	0.067	0.222	0.119	55	97
Synedrella nodiflora	Asteraceae	E (A)		0.306		0.500		43		
<i>Syzygium polyanthum</i>	Myrtaceae	N				0.002			98	
<i>Tacca palmata</i>	Taccaceae	N (P)		0.028				44		
Tectona grandis	Verbenaceae	E				0.003	0.019		99	
<i>Themeda arguens</i>	Poaceae	N (A)				0.333		45		

<i>Tinospora crispa</i>	Menispermaceae	N	0.111	0.013		0.028	0.019	56	100
<i>Tridax procumbens</i>	Asteraceae	E (P)			0.139			46	
<i>Uncaria sp.</i>	Rubiaceae	U			0.004				101
<i>Urena lobata</i>	Malvaceae	N			0.001	0.028	0.011	57	102
<i>Urophyllum arboreum</i>	Rubiaceae	N					0.002		103
<i>Vitex pinnata</i>	Verbenaceae	N					0.001		104
<i>Vitis sp. 1</i>	Vitaceae	E	0.111					58	
<i>Xanthosoma violaceum</i>	Araceae	E (P)	0.111					47	
<i>Ziziphus mauritiana</i>	Rhamnaceae	N	0.556	0.004	0.019	0.028	0.013	59	105
<i>Ziziphus rugosa</i>	Rhamnaceae	E		0.004					106
<i>Ziziphus sp.</i>	Rhamnaceae	U			0.006				107

Paper II

Soil properties after forest rehabilitation by planting teak and mahogany in Java, Indonesia

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ABSTRACT

We studied how rehabilitation of forests in Indonesia by planting teak, *Tectona grandis* (L.f.), and mahogany, *Swietenia macrophylla* (King), was associated with soil pH, organic matter, total nitrogen, total phosphorus, and total potassium. We also analyzed how soil properties and the environment (i.e. soil order, altitude, stand age) were associated with succession and compared rehabilitated stands with native forests. We found higher pH in teak compared to mahogany stands. The soil pH was lowest in the oldest stands (>70 years). Herb density was positively related to pH and to phosphorus, while density of seedlings and woody plants was positively related to nitrogen, potassium and phosphorus. Tree and herb species richness and tree density were positively associated with Oxisols, but negatively related to the proportion of native herbs. Species richness of herbs and density of seedlings decreased with time since rehabilitation, whereas species richness of woody plants increased. The proportion of native herbs and seedlings increased with stand age. We found few differences in soils between the planted stands and native forest. Our results demonstrated that successional vegetation of rehabilitated forests may play an important role in maintaining soil properties associated with soil order.

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Introduction



Supporting ecosystem services, such as nutrient cycling and soil formation, are essential for self-perpetuating ecosystems. We can describe these services by soil properties, such as the concentrations of nutrients, organic matter, minerals, physical properties and living organisms (Schoenholtz et al. 2000). Such properties can differ between soil types and ecosystems, and with species diversity (Huston 1980). Restoration of ecosystems by planting trees after deforestation may affect soil properties through various biological processes during succession (Jia et al. 2005).

Secondary vegetation succession is the development of vegetation after disturbance, including interactive changes in soil chemical, physical, and biological properties in plant communities, from pioneer species towards more mature “climax” species (Connell and Slatyer 1977). When planted trees grow, shading will increase and herbaceous vegetation might be shaded out, while non-pioneer woody species will increase, if they can compete with the planted species.

The interaction between plants and soil can affect both biotic and abiotic elements of soil, which influence the plant community (Wardle et al. 2004; van de Voorde et al. 2011). In natural ecosystems, trees and

soils interact through facilitation of soil biota (i.e. trees affect the environment for soil organisms, stimulate microbial activity, and contribute to nutrient inputs) and synergistic symbiosis (i.e. nitrogen fixing bacteria and leguminous trees) (Barrios 2007; Barrios et al. 2012). Soil fertility seems to improve with increasing tree species diversity (Huston 1980; Long et al. 2012). Soil organisms decompose organic materials, resulting in the release of CO₂ and synthesis of soil organic matter (Barrios 2007). Essential soil nutrients (i.e. nitrogen, phosphorus) are derived from the mineralization of soil organic matter through activity of soil microorganisms, which may increase plant growth (Dijkstra et al. 2006).

Massive deforestation in Java, Indonesia, took place during colonial times in the 1700s and onwards (Whitten et al. 1996). More recently, around 59 million ha of Indonesia’s forests were lost between 1950 and 1997 (Tsujino et al. 2016). Loss of forests continued by about 1.5 million ha per year during 2000–2009 (Forest Watch Indonesia 2011). The government of Indonesia has been rehabilitating degraded forestland since independence after the Second World War, mainly by planting teak *Tectona grandis* (L.f.) or mahogany *Swietenia macrophylla* (King) (Nawir et al. 2007). Here, we examined soil properties within stands

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of teak and mahogany plantations of various ages. The soil chemical properties we investigated were soil pH, soil organic matter (SOM), total nitrogen (N), total phosphorus (P), and total potassium (K). We tested how soil properties related to quantitative descriptors of plant communities, i.e. species richness, density of plants, proportion of native species (non-exotic), stand type (i.e. tree species planted) and stand age.

We hypothesized that the concentration of SOM, N, and K in the topsoil would increase as a result of succession, while pH and P concentration would decrease due to biological processes during succession (Aerts and Chapin 1999; Jia et al. 2005; Long et al. 2012). In addition, we compared soil properties in rehabilitated stands (mahogany and teak) with those in undisturbed native forests. We expected that soils under the native forests would have higher nutrient concentrations than the rehabilitated stands (Amponsah and Meyer 2000).

Materials and methods

Study area

The fieldwork was conducted in May-June 2015 in the Yogyakarta province, Java Island, Indonesia, (between $110^{\circ}24'19''$ – $110^{\circ}28'53''$ E and $7^{\circ}15'24''$ – $7^{\circ}49'26''$ S; Figure 1), in the state forests of Gunungkidul, Bantul, and Kulonprogo regency. The Yogyakarta area has a humid tropical climate with an average humidity of

86%, and average temperature of 27°C . The mean monthly minimum and maximum temperatures are 23°C and 33°C . Average monthly rainfall is 255 mm; the rainy season lasts from October to April, and the dry season from May to September. Large parts of the area experience water shortages during the dry season. The Yogyakarta province is 3186 km^2 , the population is 3.6 million, and the forest area is 187 km^2 (6% land cover). The topography is flat to undulating, with an altitude of 100–500 m above sea level. Limestone and barren karst dominate in the Gunungkidul area (Statistics of Yogyakarta Province 2017). Modern volcanic and alluvial deposits scattered in middle miocene reworked volcanic deposits (Smyth et al. 2008) characterize the Yogyakarta region. Merapi is the nearest modern volcanic center with the last large eruption in 2010.

After deforestation in Java during colonial times, some areas were left barren. Various cultivation attempts by the colonial powers, such as coffee plantations, failed. Since Indonesia's independence in 1945, the government has gradually rehabilitated the land by planting primarily teak or mahogany (Santoso 2012; Balai KPH Yogyakarta 2014). Grazing in these area is not allowed, with livestock usually being stall-fed. Intercropping systems were employed to enhance income of the local communities, but this system was limited by forest canopy closure. Food crops were normally cultivated for about 4–5 years after tree planting,

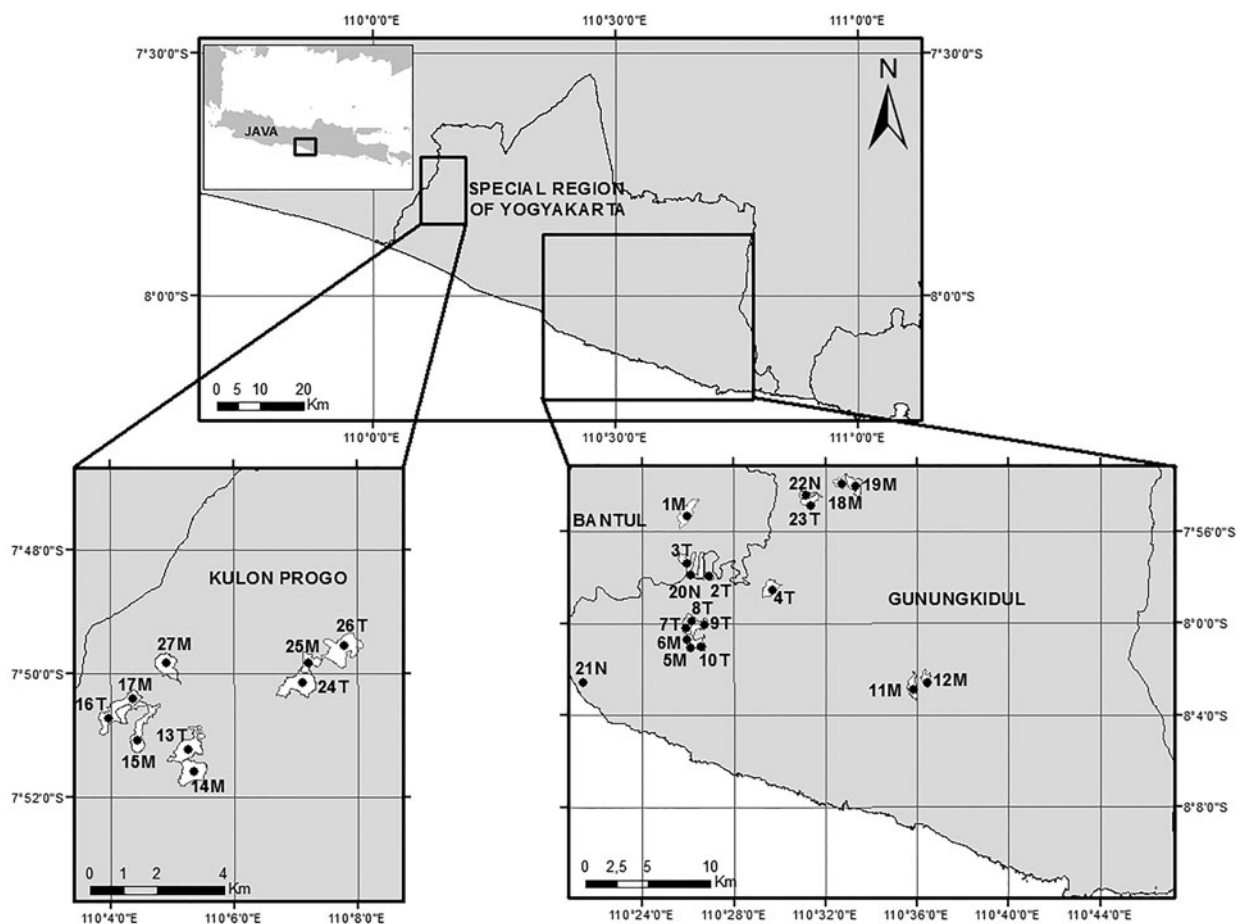


Figure 1. A map showing the stands where we took vegetation and soil samples in the forests in Yogyakarta region in Java Island, Indonesia. The numbers refer to the stands in Supplementary Table 1. M: mahogany; T: teak and N: native forest.

after which the shade from the trees impeded further cultivation. Generally, chemical fertilizer was applied when cultivating food crops and at the time of planting of teak or mahogany (C. Udayana, pers. obs.).

Stands sampled in the present study were planted between 1941 and 2003, here referred to as teak stands and mahogany stands. Mahogany is native to Central and South America (Orwa et al. 2009) but is now widespread in tropical forests globally, including in Java, Indonesia. Teak occurs naturally in peninsular India, Myanmar, Thailand and Laos (Verhaegen et al. 2010). It is now more or less naturalized in Java (Pandey and Brown 2000).

Stand selection and characteristics

Stands were selected based on forest rehabilitation history (e.g. year of planting, tree species planted) as suggested by the Governmental Forestry Service and by the Faculty of Forestry, University of Gadjah Mada. We surveyed 24 stands in total planted with teak and mahogany. In addition, we found and surveyed three areas of remaining natural forest fragments, which had never been rehabilitated, here referred to as native forests (Supplementary Table 1; Figure 1), for comparison with planted forest stands. The small sample size of native forest stands was because there is very little native forest remaining in the area, due to the history of deforestation.

The planted stands are managed by the Governmental Forestry Service, the Faculty of Forestry, University of Gadjah Mada, and the Natural Resources Conservation Center (Yogyakarta). Mahogany and teak were typically planted at a 2×4 m spacing and thinned at the age of 10 and 15 years. The trees are usually logged at the age of 35 years, depending on the forestry ministry's decision. The diameter at breast height (DBH; 1.3 m) of old mahogany stands of around 70 years was in the 30–50 cm range, and old teak stands were 30–40 cm DBH. Tree density in mahogany sites was on average about 20 trees per 100 m^2 , with an average \pm SE (5 ± 0.6) tree species per 100 m^2 (including the planted species), in both in old and young stands. Teak stands had 15–20 trees per 100 m^2 in the young stands, decreasing to 5–10 in old stands, and an average of 3 ± 0.3 tree species. This can be compared to native forests that had, on average, 9 ± 0.8 tree species and a tree density of 27 ± 5.9 trees per 100 m^2 .

In the study area, soil orders were typically mediteran, latosol, rendzina, and inceptisol (Wanagama 1988; Yogyakarta 2014; Dinas and Perkebunan 2015; BPDASHL Serayu Opak Progo 2018). These soil orders were transferred to the USDA soil taxonomy (Soil Survey Staff 2014), and correspond to Alfisols, Oxisols, Mollisols, and Inceptisols, respectively. The different stand types were fairly uniform with respect to soil order, but with regional differences. In Gunungkidul, the soil is mainly Alfisols or Mollisols, while Oxisols are dominant in Bantul and Kulonprogo (Supplementary Table 1). Alfisols are moderately

weathered with clear horizons, typically found under forest vegetation. Oxisols are old soils with a low natural fertility, dominated by iron oxides, quarts and weathered clay minerals, and they are common on sloping lands in the tropics/subtropics. Mollisols are fertile soils with a thick surface layer rich in organic matter and with a high base saturation, typically found under long-term grasslands. Inceptisols are young deposits that are slightly developed (Eswaran and Reich 2005).

Field procedures

We surveyed vegetation and took soil samples in three plot replicates randomly selected in each stand, approximately 100–300 m from each other, giving a total of 81 plots within 27 stands (Supplementary Table 1). We surveyed vegetation in the following categories; herbs (i.e. forbs, grasses, and ferns), seedlings (seedlings of woody species >1 cm and ≤ 50 cm high), woody plants (>0.5 m ≤ 2.5 m high), and trees (>2.5 m high). Each plot was 10×10 m and this area was used for recording tree species. In the NW quarter of each plot, a 5×5 m plot was used for sampling woody plants, and in the NW corner of that plot, a 1×1 m plot was used for sampling seedlings and herbs. In each sampling plot we counted the number of plants of each species in the respective plant category. The plant species were identified with help of plant taxonomists of the Silviculture laboratory at the Faculty of Forestry, University of Gadjah Mada, Yogyakarta, and plant conservation service of Purwodadi Botanic Garden.

Soil samples were taken for chemical analysis from 0 to 15 cm depth, from each of the 81 plots, across all 27 forest stands. Each sample was made up of four sub-samples taken from about a meter inside each corner of the 10×10 m tree plot. Before sampling, surface litter was removed. After sampling, the composite sample was air-dried, mixed, roughly sieved, and put into labeled plastic bags before being sent to the laboratory of Indonesian Agency for Agricultural Research and Development (Yogyakarta) for analyses.

Soil laboratory analyses

Soil samples were rolled and passed through a 2-mm sieve for analyses. Soil pH was determined in water with a 1:2.5 soil:water mixture (Van Reeuwijk 2002). Soil organic carbon was measured by the Walkley and Black (1934) method and soil organic matter (SOM) was obtained by multiplying percentage soil organic carbon by the Van Bemmelen factor of 1.724 (USDA 2004). Total N was analysed by the Kjeldahl method (Van Reeuwijk 2002). Total phosphorus (P) and total potassium (K) were determined by HCl 25% extraction (USDA 2004). Phosphorus concentration was measured by GENESYSTM 20 spectrophotometer. The 240 FS AS atomic absorption spectrophotometer was used to determine potassium concentration.

Table 1. Results from backwards selection of variables (stand type, soil type, age, altitude) explaining soil chemical properties in rehabilitated stands.

Predictors	Soil properties										
	pH			Nitrogen		SOM		Phosphorus		Potassium	
	df	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
Stand type	1	4.03	0.045*	0.20	0.654	3.28	0.070	0.62	0.431	3.60	0.058
Soil type	2	4.37	0.113	1.54	0.462	1.83	0.401	6.99	0.030*	0.28	0.869
Age	1	8.58	0.003*	0.63	0.427	0.20	0.655	0.28	0.598	0.30	0.583
Altitude	1	8×10^{-4}	0.978	0.04	0.839	1×10^{-4}	0.993	4.95	0.026*	6.23	0.013*

Only significant variables were included in the final model.

*Significant values are at $p < 0.05$.

Data analyses

Our data were balanced with respect to the number of teak and mahogany stands and with respect to soil order found in the respective stand categories (Supplementary Table 1). We only had one site with Inceptisols and we therefore removed this site from further analyses. As region was highly confounded with soil order, we chose to use soil order in the statistical models instead of region, as this could give more biological information.

We used the five soil chemical properties (i.e. pH, SOM, N, P, and K), as response variables in linear mixed models. Log-transformation was applied for P and K to achieve a normal distribution. We first compared soil properties between rehabilitated and native forests. Then we compared soil properties between mahogany ($n = 11$) and teak ($n = 12$) stands among the rehabilitated sites. We used age as a predictor in the model, as age was only defined for rehabilitated stands. Predictor variables added to the model were stand type (mahogany/teak), age since planting, altitude, and soil order. We added site as a random intercept to the model. We performed a backwards selection procedure using the “drop1 command” (Zuur et al. 2009), by removing the least significant predictor until we had only significant ($p < 0.050$) components in the model.

To study the effect of soil properties, soil order, and stand age on the vegetation we used the following response variables: species richness, defined as the total number of species present; vegetation density, as the number of individual plants present; proportion of native species of all species; and DBH of trees. We used a Poisson error distribution and log link function when analyzing species richness and vegetation density. For the analysis of the proportion of native species, we used a binomial error distribution and logit link function. For analyzing the DBH, we used normal error distribution and identity link function (Crawley 2011). All the data analysis were carried out using R (version 3.4.2; R Development Core Team 2015).

Results

Comparing the rehabilitated stands (teak and mahogany) showed that mahogany stands had a lower average soil pH than teak stands (relative difference between teak and mahogany (for the following values, estimate \pm SE is reported) 0.38 ± 0.19 , Table 1;

Figure 2(a)). In rehabilitated stands, pH decreased with age since rehabilitation (-0.01 ± 0.004 , Table 1; Figure 2(b)). Soil pH showed no relationship with soil order or altitude (Table 1). Nitrogen and SOM showed no relationship with any of the explanatory variables (Table 1). Total P varied with soil order, being highest in Oxisols (relative difference in Oxisols versus Alfisols: 0.19 ± 0.19) and lowest in Mollisols (relative difference in Mollisols versus Alfisols: -0.72 ± 0.34 , Table 1; Figure 2(c)). P also decreased with increasing altitude (-0.002 ± 0.001) but showed no relationship with stand type or age (Table 1). Total K responded in the opposite way, increasing with altitude ($0.002 \pm 9 \times 10^{-4}$, Table 1) but showed no relationship with age or soil order. The effect of stand type on total K was near significant ($p = 0.058$; Table 1).

We found no clear differences in any of the soil properties between the native forests and the rehabilitated forests (Table 2), although the model showed a tendency towards a difference in soil pH and N due to soil orders ($\chi^2 = 5.52$, $df = 2$, $p = 0.063$) and ($\chi^2 = 4.89$, $df = 2$, $p = 0.087$), respectively. The effects of altitude and soil order on other soil properties were similar to those of rehabilitated stands and are therefore not repeated here.

Species richness of herbs was negatively related to stand age (-0.02 ± 0.004), whereas species richness of woody plants ($0.01 \pm 4 \times 10^{-3}$) and trees ($0.02 \pm 5 \times 10^{-3}$) were positively related to age (Table 3). Species richness of herbs and trees were also related to soil order, with the highest richness of herbs in Oxisols (relative difference in Oxisols vs Alfisols: 0.58 ± 0.19) and lowest in Mollisols (relative difference in Mollisols vs Alfisols: -0.34 ± 0.45 , Table 3). For tree species, the highest richness was in Mollisols (relative difference in Mollisols versus Alfisols: 0.91 ± 0.33) and lowest in Alfisols (relative difference in Oxisols versus Alfisols: 0.58 ± 0.19 , Table 3). There was no relationship between species richness of any plant groups and soil properties (Table 3). Species richness of seedlings did not show any relationship with any of the explanatory variables (Table 3).

Density of herbs was positively related to soil pH (1.36 ± 0.12) and to total P ($0.02 \pm 4 \times 10^{-3}$) and negatively to SOM (-1.21 ± 0.04) and total K ($-0.01 \pm 5 \times 10^{-3}$), but showed no relationship with N, stand age or soil order (Table 3). Density of seedlings was negatively related to the age of the stand ($-0.02 \pm 9 \times 10^{-3}$) and soil pH (-0.58 ± 0.16) and positively to N (4.10 ± 0.82) and K ($0.02 \pm 8 \times 10^{-3}$), but showed no

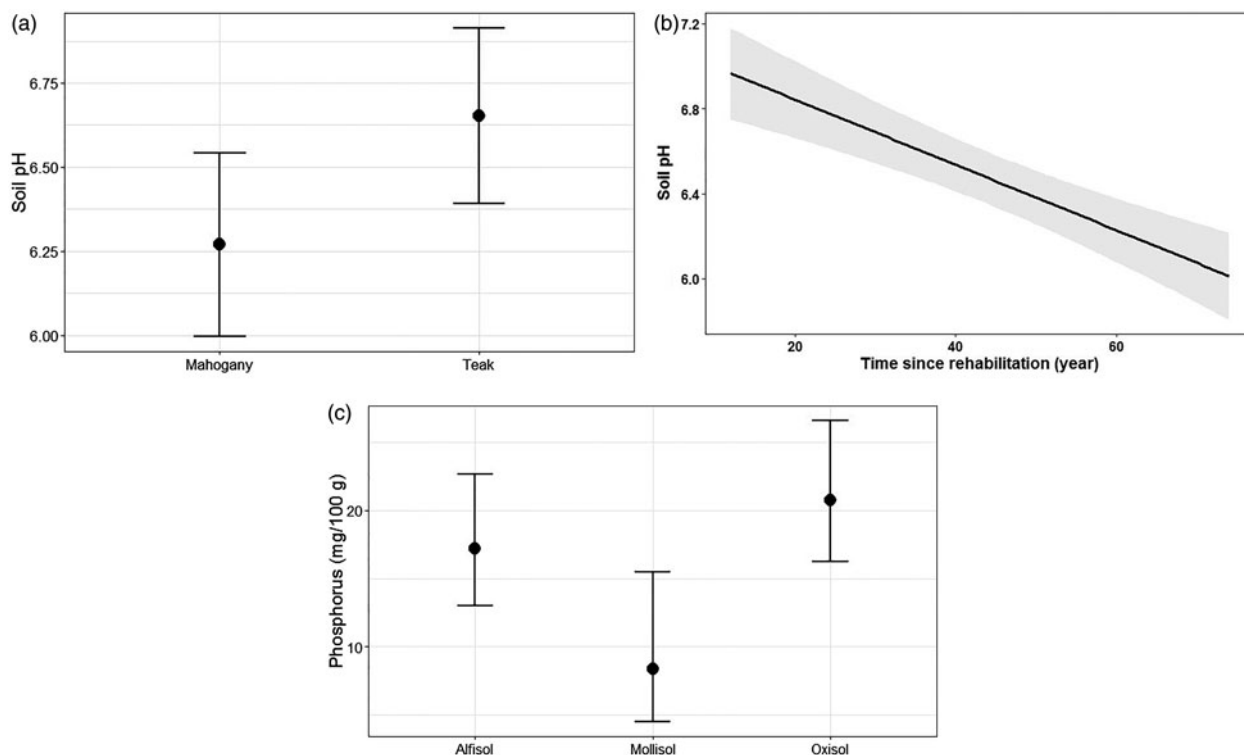


Figure 2. Soil properties in rehabilitated stands estimated from linear mixed models showing (a) differences in pH between stand types, (b) relationship between soil pH and age since rehabilitation, (c) total P in relation to soil order. Shaded area in (b) and bars in (a) and (c) shows 95% confidence intervals.

Table 2. Results from linear mixed models showing soil chemical properties comparing rehabilitated stands versus native forests (forest type).

Soil properties	χ^2	df	p
pH	0.21	1	0.649
Nitrogen	1.30	1	0.254
SOM	0.86	1	0.353
Phosphorus	1.65	1	0.199
Potassium	3.55	1	0.060

*Significant values are at $p < 0.05$.

relationship with SOM, P or soil order (Table 3). Density of woody plants was negatively related to soil pH (-0.29 ± 0.07) and positively to N (1.17 ± 0.30) and P ($0.02 \pm 2 \times 10^{-3}$), but there was no relationship with SOM, K, age, or soil order (Table 3). Density of trees depended on soil order, with the highest density in Mollisols (relative difference in Mollisols versus Alfisols: 1.03 ± 0.30) and lowest in Alfisols (relative difference in Oxisols versus Alfisols: 0.28 ± 0.18). Density of trees was also negatively related to K (-0.01 ± 0.01), but showed no relationship with pH, N, SOM, P, or stand age (Table 3). The proportion of native herbs increased with increasing stand age ($0.03 \pm 8.6 \times 10^{-3}$), and varied with soil order, being highest in Mollisols (relative difference in Mollisols versus Alfisols: $34.62 \pm 17.73 \times 10^6$) and lowest in Oxisols (relative difference in Oxisols versus Alfisols: -0.96 ± 0.40 , Table 3). The proportion of native seedlings was positively related to stand age (0.02 ± 0.008), as was the DBH of the planted trees (0.55 ± 0.08 , Table 3). The proportion of native plants and DBH showed no relationship with any soil properties, while the proportion of native woody plants and trees showed no relationship with any of the explanatory variables (Table 3).

Discussion

As expected, we found soil pH decreased with age in both rehabilitated stand types. Mahogany stands, which were somewhat older than teak stands, had a lower soil pH than teak stands. However, we did not find the expected effect of stand type or age on other soil properties, which is surprising in relation to earlier studies (Huston 1980; Long et al. 2012). Li et al. (2013) examined available nutrients and showed an effect of succession, but we examined the total concentration of nutrients and we could not see any effect of succession over a timespan of >70 years.

We found no clear differences in any of the soil properties between native forests and the planted stands. This could indicate that soil parameters of rehabilitated stands approached those of native forests with time. We should however keep in mind the low number of native forest sites sampled.

We saw that soil pH decreased with increasing age of the planted stands, supporting Aweto (1981), Perumal et al. (2017), and Li et al. (2013) who observed a decline in soil pH over 10, 18, and 30 years, respectively, as result of a succession. We showed that this decline continued with age. Accumulation of litter on the soil surface may indirectly contribute to the soil acidity due to a high carbon concentration. Comparing the two tree species used for rehabilitation, mahogany stands had a lower pH than teak stands, after controlling for age (on average mahogany stands were older than teak stands, 50 ± 3 years versus 39 ± 4 , respectively). In humid tropical climates, high temperatures and precipitation can decrease soil pH due to leaching

Table 3. Results from backwards selection for vegetation as response variables in rehabilitated stands (teak and mahogany) showing richness (species richness), density, proportion of native plants (Prop-native) and tree diameter at breast height (DBH).

Vegetation	Predictor variables													
	pH		N		SOM		P		K		Age		Soil type	
	χ^2_1	<i>p</i>	χ^2_1	<i>p</i>	χ^2_1	<i>p</i>	χ^2_1	<i>p</i>	χ^2_1	<i>p</i>	χ^2_1	<i>p</i>	χ^2_2	<i>p</i>
Richness														
Herbs	0.04	0.845	0.57	0.451	3.63	0.057	1.30	0.255	0.58	0.444	14.72	<0.001*	10.24	0.006*
Seedlings	0.69	0.404	0.10	0.749	0.49	0.485	0.02	0.895	0.04	0.849	0.11	0.744	1.29	0.525
Woody plants	0.53	0.468	0.08	0.771	2.50	0.114	1.57	0.210	0.53	0.467	8.24	0.004*	0.98	0.613
Trees	2.56	0.110	0.41	0.521	0.83	0.362	0.14	0.690	0.16	0.691	8.04	0.005*	6.04	0.049*
Density														
Herbs	119.62	<0.001*	3.41	0.065	1117.37	<0.001*	23.37	<0.001*	6.65	0.009*	0.07	0.795	1.23	0.541
Seedlings	14.21	<0.001*	27.23	<0.001*	2.25	0.133	1.06	0.302	6.72	0.009*	4.31	0.038*	4.10	0.129
Woody plants	17.06	<0.001*	15.53	<0.001*	1.19	0.275	58.51	<0.001*	2.57	0.109	0.27	0.601	2.56	0.279
Trees	0.31	0.581	0.003	0.953	0.82	0.364	0.28	0.594	4.01	0.045*	0.76	0.382	9.30	0.009*
Prop-native														
Herbs	0.02	0.875	2.89	0.089	2.39	0.122	0.35	0.552	3.53	0.060	14.74	<0.001*	13.53	0.001*
Seedlings	0.82	0.366	0.31	0.579	0.69	0.407	1.37	0.242	0.01	0.912	4.09	0.043*	1.42	0.491
Woody plants	0.07	0.786	0.03	0.864	0.07	0.788	0.53	0.466	0.31	0.578	1.90	0.168	0.52	0.772
Trees	0.43	0.514	0.13	0.715	0.34	0.561	0.42	0.519	0.19	0.665	0.49	0.483	4.62	0.099
Tree DBH	0.82	0.366	0.37	0.543	2.08	0.149	0.10	0.748	1.00	0.316	27.32	<0.001*	0.28	0.870

SOM is soil organic matter.

*Significant values are at $p < 0.05$.

(Shamshuddin and Daud 2011). Acidity of soil is also caused by mineralization of organic matter and N fixation by legumes (Fageria and Nascente 2014). Further, pH tended to be related to soil order, being highest in the fertile Mollisols and lowest in Oxisols. This could be because Oxisols, which is poor in K, Ca, and Mg, is highly weathered (Von Uexkull 1986).

The results showed that total P and total K responded differently to altitude, with P decreasing with increasing altitude and K increasing with increasing altitude, in both the analyses including native forest and only rehabilitated stands. The soil orders were to some extent sorted according to altitude, with Oxisols somewhat more common in the higher areas and Alfisols in the lower, possibly explaining part of this difference. Given that the land was sloping, P could also have been washed away in soil particles by surface runoff, thus being lower in the topsoil at higher altitude. Regarding total K, old and weathered soils often have lower K concentration than young soils, and especially young volcanic soils (Graham and Fox 1971). Presence of young or medium young volcanic rocks in higher areas in the region may explain our increase of K with altitude.

Species richness of herbs and tree seedlings decreased with increasing age of the stand, while the density of herbs was unaffected. Species richness of woody plants and trees increased, but density decreased with increasing age. From succession theory, we know that after disturbance of the soil surface by deforestation and restoration activities, herbs colonize the bare ground, and the establishment of non-native species can be promoted (Stoddard et al. 2011). In our study, the proportion of exotic herbs decreased with increasing stand age, while the proportion of native species increased. Martin et al. (2005) used the proportion of native species as an attribute to measure restoration success. Species richness of woody plants and trees increased as the stands matured, as many of these

species are adapted to growing in a dense forest. As their size and the size of the planted trees increased, their density decreased due to competition for space, light, water and nutrients.

Our study showed that herb density was positively related to soil pH, whereas seedling density and woody species density were negatively correlated to pH, which agrees with their responses to the age of the stands. Herbs responded in the opposite way to seedlings and woody plants as a result of succession. We also saw that the density of herbs and of woody plants were positively related to total P but negatively to total K, while density of seedlings and of woody plants were positively related to total N. Our previous analyses showed that Leguminosae was the largest plant family found in the study area (Udayana et al. 2019). It shows that leguminous herbs, seedlings, and woody plants, are important components for biological nitrogen fixation, which may benefit the build-up of soil N (Barrios 2007).

We know that a high total concentration of nutrients does not necessarily mean that these are available for plants, but there is an equilibrium between the total and the plant available pools. Nutrients stimulate plant growth, but plants also maintain nutrients within the soil/plant system. As an example: a poor plant density would make the soil more prone to erosion, thus would lead to loss of topsoil and nutrient loss. Dense vegetation, with deep roots, would help nutrient circulation as fine roots decompose and new roots take up the nutrients (Schoenholtz et al. 2000; Healey and Gara 2003).

The negative association between plant density and K is surprising. There might be additional elements in the K rich soils masking the result of K. Volcanic deposits may contain high K, but also too high levels of certain trace elements. The negative effect of K could be caused by imbalances in the uptake of other elements (Mengel and Kirkby 1980), such as trace elements on which we have no data.

Conclusion

Ecosystem services, related to vegetation and soil may increase with age since rehabilitation, when trees, woody plants, and native herbs increase. We would have expected to see soil organic matter and nutrient reservoirs increase with the growing vegetation, but we got few such responses. Although the oldest stands were >70 years, this is still a short time for the reservoirs to change. On the other hand, changes in soil pH were detected, which decreased through time. The soil pH under mahogany stands was lower than teak stands. Soil nutrient elements were positively associated with density of herbs, seedlings, and woody plants showing that litter abundance of the understory may supply the topsoil with a number of nutrients, such as nitrogen and phosphorus through decomposition. The results also showed that species richness of trees and density of trees were positively associated with Oxisols which had the highest phosphorus concentration. It seems that trees are a key factor for improving nutrient-poor Oxisols.

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Disclosure statement

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Paper III

Wood and non-wood forest products of Central Java, Indonesia

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ABSTRACT

We investigated herb and woody species at rehabilitated forests planted by mahogany and teak, and original, not rehabilitated forests in Yogyakarta, Indonesia. Plant species were classified into five use categories: medicine, food, fodder, ornament, and construction. We registered 142 species belonging to 54 families known as useful species with at least one, often more, use categories. The number of useful species was highest for medicine use (107 species). There was a dominance of exotic herb species used for food and annual herbs used for fodder. The number of useful herbs and exotic woody species was highest in teak stands. The number of woody species used for medicine, food, and construction was higher than those for ornament and fodder. All herb species decreased with time, except annual native, that increased. Around 50% of the useful species occurred only once in one site, and some species showed a distribution restricted to one type of stands. Overall, our results seem to show that rehabilitated stands are doing well with regard to useful herb and woody species. We suggest strategies for plant and ecosystem conservation, especially for rare native plant species and species with restricted distribution.

KEYWORDS

Useful plants; mahogany; teak; non timber forest product; rehabilitation; Indonesia


Introduction

The reason for people to select certain plants for different uses is a key question in ethnobotany (Alencar, Araújo, Amorim, & Albuquerque, 2010; Gaoue et al., 2017; Soldati, de Medeiros, Duque-Brasil, Coelho, & Albuquerque, 2017). First, the plant species must have the qualities for which it is used. If few species have the quality required, they are worth searching for also in situations that are difficult to reach, collect, or handle. Hence, collection is a trade-off between value and availability. If many species have the quality, species easy to collect will be collected first (Gaoue et al., 2017; Soldati et al., 2017).

The ongoing global changes in forest use with extensive clear-cuts, often followed by planting of monospecific stands of exotic timber trees (Carnus et al., 2006; Lamb, 2018; Lamb, Erskine, & Parrotta, 2005), have also affected the undergrowth and what plant species that are available (Voeks, 1996). Plants with known qualities, for instance for medicinal use, might be confined to the original vegetation in non-cut forests, and be rare or absent in disturbed forests (Voeks, 1996). However, also weedy plants found in disturbed areas have been shown to play a major

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role in traditional plant collection (Stepp & Moerman, 2001). For plants with more general uses as food, fodder or construction, people often show flexibility and learn to use new species, or start using species that became common as a result of forestry (Medeiros, 2013). These species, often exotic, may therefore be more common in the rehabilitated stands.

Many of the species increasing after cutting the forest are invasive exotic species (Alencar et al., 2010; Alencar, Santoro, & Albuquerque, 2014; Bennett & Prance, 2000; Gama, de Paula, Da Silva, Junior, & de Medeiros, 2018), while native species might be rare (Kala, 2005). The exotic species are strong competitors with fast growth, and some use allelopathic chemicals to dominate the vegetation and anti-herbivorous substances to avoid herbivory. The fast growth might make plants interesting as food or fodder, and allelopathic and anti-herbivorous chemicals might be interesting for medicine use (Voeks, 1996).

South-east Asia has a wide-spread use of wild plants. It is also an area with intense cutting of forests, followed by rehabilitation by single-species plantations (Lamb, 2018; Lamb et al., 2005). The species composition of herbaceous and spontaneous woody vegetation in these stands is different from that in the rapidly shrinking original forests. Thus, people depending on collecting wild plants might be under pressure.

We studied the sustainability of wild forest species used by people in Java Island, Indonesia, after logging and rehabilitation by planting a single tree species. Plant uses were classified as medicine, food for humans, fodder for livestock, ornament, and construction. We compared uses in plantations of teak, *Tectona grandis* (L.f.), and of mahogany, *Swietenia macrophylla* (King), and in fragments of original forest. We hypothesized that: 1) the original forest would have more species used for medicine and more native plant species than the rehabilitated forests, while the rehabilitated forests would have more rare species than the original forest; 2) plants with general uses as food or fodder would include many annual and/or exotic species and mainly be found in the planted stands; 3) the number of useful species would increase with increasing time since rehabilitation; and 4) there would be differences in useful species found in stands with teak and with mahogany. Hypotheses 3 and 4 arise from previous analyses where we show that rehabilitated forests approach the original forests in vegetation quantitative measures, but not in species composition (Udayana, Andreassen, & Skarpe, 2019).

Materials and methods

Study area

We worked in the Gunungkidul, Bantul, and Kulonprogo regency (between 110°24'19"–110°28'53" E and 7° 15' 24"– 7° 49' 26" S) in the province of Yogyakarta, Java Island, Indonesia (Figure 1). Much of the forest in this area was cut in colonial time or later. After independence in 1945 rehabilitation of the forests increased (Santoso, 2012), mainly by planting teak or mahogany (C. Udayana, pers. comm), neither of which is indigenous to Indonesia.

The Yogyakarta Province has a tropical humid climate with average humidity of 84–89% and average temperature of about 26.7°C. The mean monthly minimum and maximum temperatures are 22.6°C and 33.0°C. Annual precipitation is about 3 000 mm. There is a distinct alternation between a rainy season lasting from October to April and a dry season from May to September. Large parts of the area experience water shortage



Figure 1. Map of study area, Indonesia, and Yogyakarta Province highlighted.

during the dry season. The topography is flat to undulating mainly between 100 and 500 m above sea level (Statistics of Yogyakarta Province, 2017).

People live mainly as cultivators with perennial fields. Livestock is largely stall-fed, and fodder is cut for them in the forests.

Field survey

Twenty-seven sites with three sampling plots in each were established for data collection, making a total of 81 sampling plots. Twelve sites had been rehabilitated by planting teak between 1941 and 2003, 12 sites by planting mahogany between 1941 and 1986 and three sites were fragments of original forest never rehabilitated. The low number of original forests sampled was due to the lack of potential sites. The non-rehabilitated forests found and used here were saved for cultural reasons and the trees were protected. The non-rehabilitated forests were small.

At each site, we selected three plots 5 m x 5 m randomly. One plot of 1 m x 1 m was located in the NW corner of each of these 5 m x 5 m plots. We sampled two categories of plant species: (1) herbs including forbs, grasses, and ferns in the 1 m² plot; (2) woody species encompassing woody vines, shrubs, and trees >50 cm and <2.5 m in height in the 25 m² plot. Voucher specimens were collected, labeled, and sent to two laboratories, namely the Silviculture laboratory at the Faculty of Forestry, University of Gadjah Mada, Yogyakarta, and Plant conservation service of Purwodadi Botanic Garden, for identification.

Classification of species distribution

We classified the distribution of useful plant species into four categories: (1) widespread species occurring in all stand types (mahogany, non-rehabilitation, teak); (2) intermediate species occurring in two stand types; (3) restricted species occurring at least twice in one stand type; and (4) rare species occurring just once in any of the stand types.

Literature review

We conducted a comprehensive search using databases available through the system of Inland Norway University of Applied Sciences. We used species names to search for used plants, then found information on use, growth habit, status (native, exotic), and life cycle (annual, perennial). The search was compiled from book databases as primary sources (Plant Resources of South-East Asia PROSEA 4 (Mannetje & Jones, 1992), PROSEA 5 (Soerianegara & Lemmens, 1993), PROSEA 8 (Siemonsma & Piluek, 1993), PROSEA 12 (de Padua, Bunyaphatsara, & Lemmens, 1999), and online databases (the agroforestry database, <http://www.worldagroforestry.org/output/agroforestry-database>), (useful tropical plants database, <http://tropical.theferns.info/>), (FAO Ecocrop, <http://ecocrop.fao.org/>), (PROTA4U, <http://www.prota4u.info/>), the Germplasm Resources Information Network (GRIN, <http://www.ars-grin.gov/>)).

All the recorded plants were classified according to their use as medicine (e.g. poultice, essential oils, herbal drugs), human food (e.g. fruits, leafy green vegetables, other vegetables, condiments), fodder for livestock and ornament (e.g. pot plants, element of garden, houseplant) (Priyadi et al., 2010). For woody species, we also included construction (e.g. house construction, boat building, furniture, interior finish, household implements, music instruments, wood sculptures, and carvings). Use as firewood was not recorded, as all woody species could be used as such (C. Udayana, pers. comm.). Useful plant species have at least one use category, with some having multiple uses. We classified each plant species to the number of uses, 1–4 for herb species and 1–5 for woody species.

Data analyses

For each site, we estimated the mean number of useful plant species per plot and used it as a response in linear models. There was a total of 27 sites in the analyses with all stand types included, and 24 sites in the analyses with rehabilitated forests only (i.e. analysis including time since rehabilitation). For each site, we split the plant species into uses (medicine, food, fodder, ornament, construction [woody species]), plant status (indigenous, exotic) and, for herbs, life cycle (annual, perennial). For herbs, there was a total of 16 potential combinations per site and for woody species 10 (the difference is due to no herbs being used for construction and all woody species being perennials). Total sample size in the linear models was, respectively, 432 and 384 for herbs in models with all stand types and with rehabilitated stands only, and 270 and 240 for woody species in models with all stand types and with rehabilitated stands only.

Due to positive skewness of response variables, we applied a logarithmic transformation, $\log(Y + 1)$ to approach the assumptions of homoscedasticity and normal distribution (McDonald, 2014). The full model consisted of stand (teak, mahogany, non-rehabilitated), use of plant, life cycle, plant status, and the four-way interaction. For the rehabilitated forests, where we had a time since rehabilitation, we used number of useful species as

response in models testing the effect of time since rehabilitation (as a continuous variable), stand (mahogany, teak), use of plant, life cycle of plant, plant status and the five-way interaction between predictor variables. We selected the most parsimonious model by applying a backward selection from the full model until we had only statistically significant ($p < .050$) components left in the model. All models were carried out using R (version 3.4.2; R Development Core Team, 2015).

We made nine ordinations with Correspondence Analysis (CA) of the plant species, i.e. one for each plant use separated for herbaceous and woody plants. In the CA each plant species was classified according to use, life cycle and plant status. In all ordinations, we used the respective use category and stand type as environmental variables and added to the graphs with the best fit. Species with more than one utility were included in more than one ordination. Seven woody species and seven herb species had to be deleted as outliers because they did not fit in the graphs. Forward selection and Monte Carlo simulations ($p < .050$, 499 iterations; Ter Braak & Šmilauer, 1998) in Canonical Correspondence Analyses (CCA) were used to get an idea about the significance of environmental variables. All CA and CCA were performed in the Canoco software (version 4.5 for Windows; Ter Braak & Šmilauer, 1998).

Results

Plant species characteristics

Thirty percent of the herbs were annual and the proportion of annual versus perennial herbs did not differ between stand types ($\chi^2 = 0.01$, d.f. = 2, $p = .993$; Table 1). Among herbs there were more exotic useful species (34) than native (21), while it was the opposite in woody species with more native (89) than exotic (54) species ($\chi^2 = 9.31$, d.f. = 1, $p = .002$). All stand types showed the same tendency with a higher proportion of exotic herb and of native woody species.

Plant species distribution

We recorded a total of 154 plant species encompassing 47 herb species and 107 woody species, where 28 species were identified only to genus level. Out of these, 142 species (45 herbs and 97 woody species) belonging to 54 families are known as useful species. Almost half of the useful species, 49%, was found once in one site and was therefore defined as rare (Table 1). There was a tendency for more woody species than herbs to be widespread in all three stand types (Table 2; Supplementary Table). There was, however, no significant difference in the distribution frequency between herbs and woody species presented in Table 1 ($\chi^2 = 4.21$, d.f. = 3, $p = .230$).

Thirty-three percent of the species could be used as medicine irrespective of whether it was a herb or a woody species (Table 3). Also, 32% of the herbs could be used as ornaments, while the number of species for other uses was <23%. There was no difference in the frequency of various uses between herbs and woody species presented in Table 3 ($\chi^2 = 0.97$, d.f. = 3, $p = .808$). There was little difference in the number of used plant species (rare or not) between teak and mahogany stands, both in herbs and woody species. However, non-rehabilitated stands had fewer useful species than the rehabilitated stands (Table 1).

Table 1. The number of species in the different stands, status (native or exotic) and life cycle (annual and perennial), depending on whether they were defined as rare (occur only once) versus restricted (R – occur in only one stand type), intermediate (I – occur in two stand types) or widespread (W – occur in all three stand types) (R + I + W) in the upper rows of the table, and according to use in the lower rows of the table. Note that some species exist in different stand types and have multiple uses.

Plant category Distribution	Teak				Mahogany				Non-rehabilitated			
	Native		Exotic		Native		Exotic		Native		Exotic	
	Ann.	Peren.	Ann.	Peren.	Ann.	Peren.	Ann.	Peren.	Ann.	Peren.	Ann.	Peren.
Herb species												
Rare	1	2	1	4	1	3	2	4	1	1	1	2
R + I + W	1	5	3	7	1	4	3	5	1	0	0	2
Total	2	7	4	11	2	7	5	9	2	1	1	4
Woody species												
Rare		7		4		7		7		9		2
R + I + W		26		15		25		17		15		9
Total		33		19		32		24		24		11
Use category												
Medicine	2	37	4	21	1	11	2	11	1	7	1	3
Food	1	23	3	11	0	9	2	9	0	4	0	2
Fodder	1	6	1	9	0	4	1	4	0	2	0	1
Ornament	0	13	1	14	1	7	1	6	1	2	0	2
Construction		14		11		8		7		10		1

Table 2. The number (percentage) of species in different distribution categories.

Plant category	Rare (occur only once)	Restricted (occur in 1 stand type)	Intermediate (occur in 2 stand types)	Widespread (occur in all 3 stand types)
Herb species	25 (56%)	7 (15%)	10 (22%)	3 (7%)
Woody species	44 (45%)	12 (12%)	22 (23%)	19 (20%)

Table 3. The number (percentage) of species in different use categories, depending on whether they were defined as rare (occur only once) versus restricted (R – occur in only one stand type), intermediate (I – occur in two stand types) or widespread (W – occur in all three stand types) (R + I + W). Note that some species have multiple uses and are therefore counted in several of the use categories.

Plant category Distribution	Medicine	Food	Fodder	Construction	Ornament
Herb species					
Rare	14 (50%)	10 (67%)	5 (50%)		12 (48%)
R + I + W	14 (50%)	5 (33%)	5 (50%)		13 (52%)
Total	28 (36%)	15 (19%)	10 (13%)		25 (32%)
Woody species					
Rare	32 (41%)	12 (39%)	10 (43%)	24 (43%)	27 (50%)
R + I + W	47 (59%)	19 (61%)	13 (57%)	32 (57%)	27 (50%)
Total	79 (33%)	31 (13%)	23 (9%)	56 (23%)	54 (22%)

Number of uses per plant species

The number of uses per plant species ranged from 1 to 3 for herbs, where 41% of the herb species had only one use, 36% had two uses and 23% had three uses (Table 4). The number of uses for woody plants ranged from 1 to 5. Most of the woody plants had 2 (35%) or 3 uses (33%), followed by 1 (21%), 4 (6%) or 5 (4%) uses. There were no woody species with five uses, and only two herb species with three uses in non-rehabilitated stands (Table 4).

Table 4. The number of useful plant species grouped by the number of potential uses and stand type. Note that the same plants may be present in different stand types.

Stand types	Number of potential uses									
	Herb species				Woody species					
	1	2	3	4	1	2	3	4	5	
Teak	13	10	5	0	11	21	19	4	2	
Mahogany	9	9	7	0	13	22	17	5	5	
Non-rehabilitated	3	3	2	0	9	12	16	1	0	
Total	25	22	14	0	33	55	52	10	7	

The herbs with highest number of uses (three different uses) were *Bidens pilosa* (medicine, fodder, and food), *Pteris ensiformis*, and *Tacca palmata* (medicine, ornament and food) in mahogany stands, and *Stachytarpheta indica* (medicine, ornament, food) and *Tridax procumbens* (medicine, fodder, food) in teak stands. *Synedrella nodiflora* (medicine, fodder, food) and *Imperata cylindrica* (medicine, ornament, fodder) in teak and mahogany stands, and *Clitoria ternatea* (medicine, ornament, food) in all types of stands (Supplementary Table). The woody species with five uses were *Acacia mangium*, *Albizzia procera*, *Cassia siamea*, and *Sterculia foetida* in mahogany stands, *Gliricidia sepium* in teak stands, and *Schleichera oleosa* in mahogany and teak stands.

Number of useful plant species

There was no interaction effect between stand type and uses on the total number of useful herb species per 1 m² plot ($F_{6,408} = 1.13, p = .344$) or woody plant species per 25 m² plot ($F_{8,248} = 0.91, p = .512$). However, the number of useful herb species per plot was higher in teak than in mahogany and non-rehabilitated stands ($F_{2,418} = 5.04, p < .001$; Figure 2).

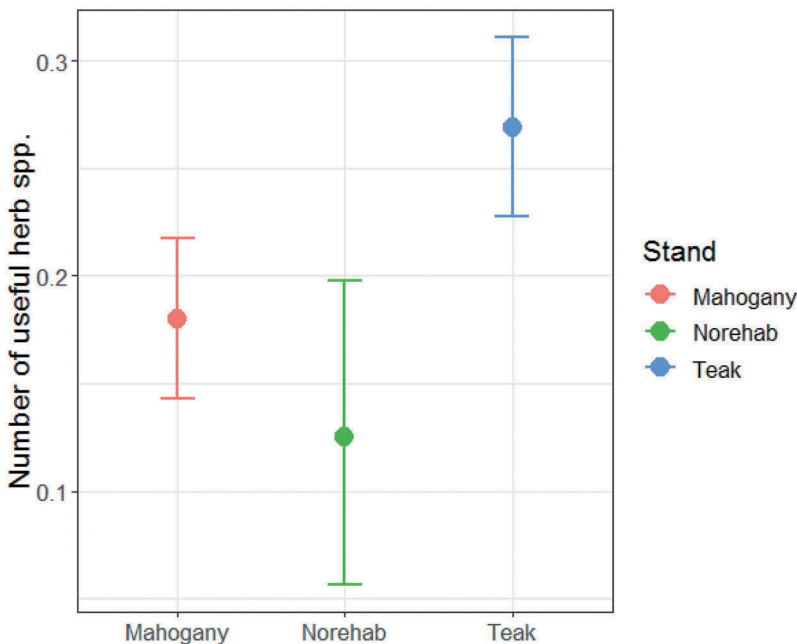


Figure 2. The total number of useful herb species per plot (m²) in different stand types.

We found an interaction effect between use and plant status ($F_{3,401} = 10.05$, $p < .001$; [Figure 3a](#)) and between use and life cycle ($F_{3,418} = 18.37$, $p < .001$; [Figure 3b](#)), with regard to the number of useful herb species per plot. The number of native herb species used for fodder was higher than that of exotic species, and the number of exotic herb species used for food was higher than that of native species ([Figure 3a](#)). The number of annual herb species used as fodder was higher than that of perennial species, and the number of perennial herb species used as ornament was higher than that of annual herb species ([Figure 3b](#)).

Regarding the number of useful woody species per plot (25m²), there was an interaction effect between stand type and plant status ($F_{2,256} = 4.55$, $p = .011$; [Figure 4a](#)), and between plant use and status ($F_{4,256} = 3.30$, $p = .01$; [Figure 4b](#)). In teak stands the number of useful exotic species was higher than the number of native species ([Figure 4a](#)). The number of native and exotic woody species was similar for different uses, except for ornament use, where exotic species were more common than native species ([Figure 4b](#)).

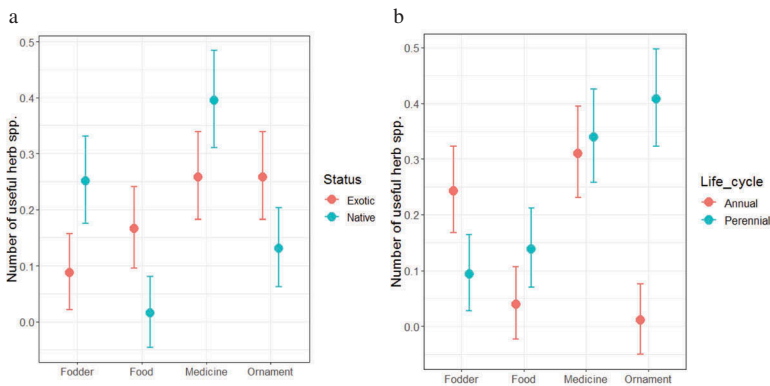


Figure 3. Interaction effects between (a) plant uses and plant status; and (b) plant uses and plant life cycle, on the number of useful herb species per plot (m²).

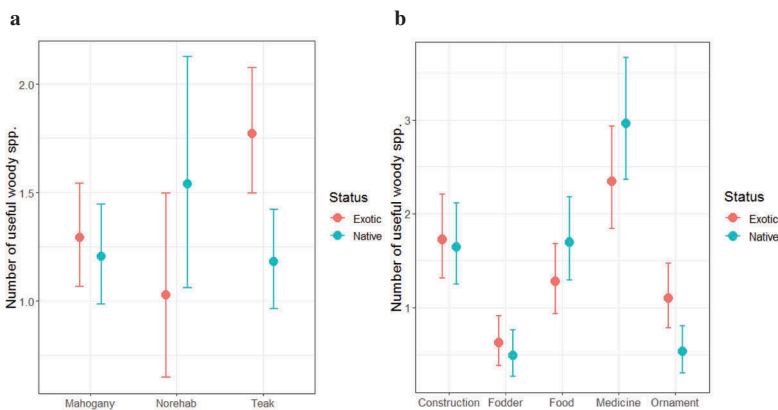


Figure 4. Interaction effects between (a) stand type and plant status; and (b) plant uses and plant status, on the number of woody species per 25 m².

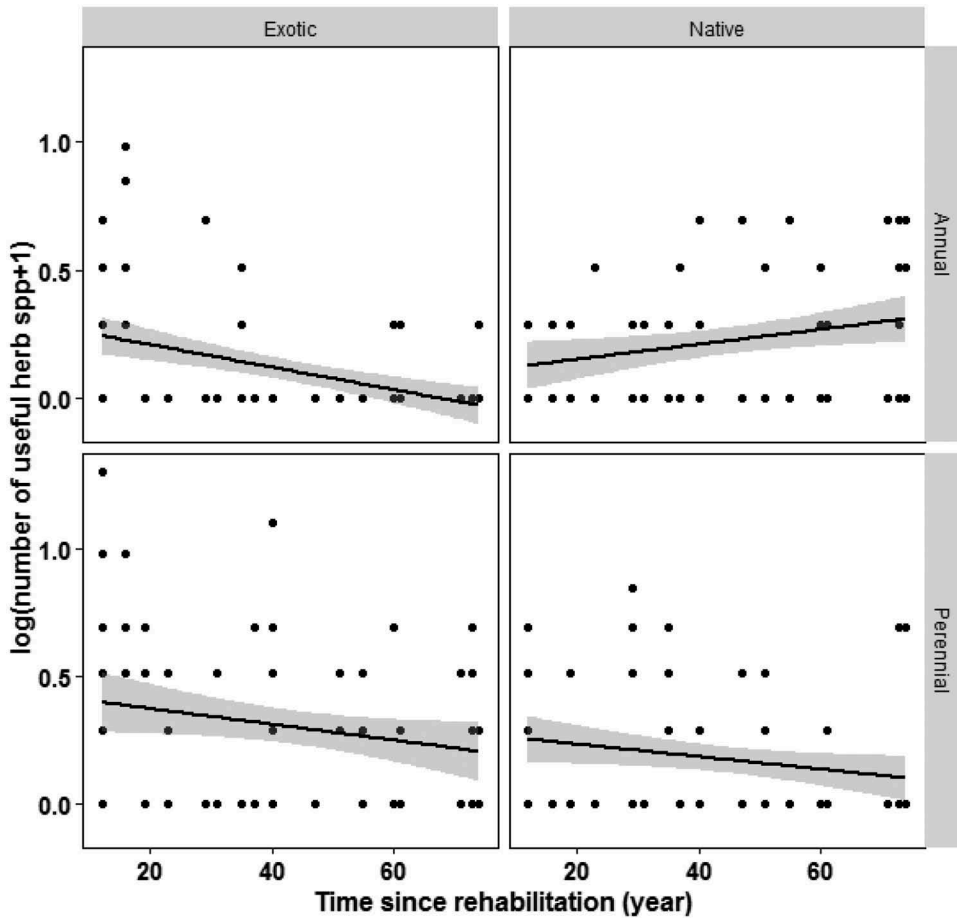


Figure 5. Interaction effects between plant status, plant life cycle and time since rehabilitation (year) on the number of useful herb species per plot (m^2).

In rehabilitated stands (teak and mahogany), we found a three-way interaction effect in the number of herb species per plot with regard to time since rehabilitation: exotic species and native perennial species decreased, while native annual species increased with time since rehabilitation ($F_{1,350} = 9.16$, $p = .003$; Figure 5).

For the number of woody plant species per plot, we found an interaction effect of plant use and time since rehabilitation ($F_{4,223} = 2.85$, $p = .025$). The number of woody species per plot for medicine, construction, and food tended to increase with time since rehabilitation, while the number of species for fodder and ornament did not change with time (Figure 6).

Ordinations of herb species

CA and forward selection and Monte Carlo simulations in CCA showed influence of stand type on species composition (teak: $F = 3.54$, $p < .002$; mahogany: $F = 3.48$, $p < .002$; non-

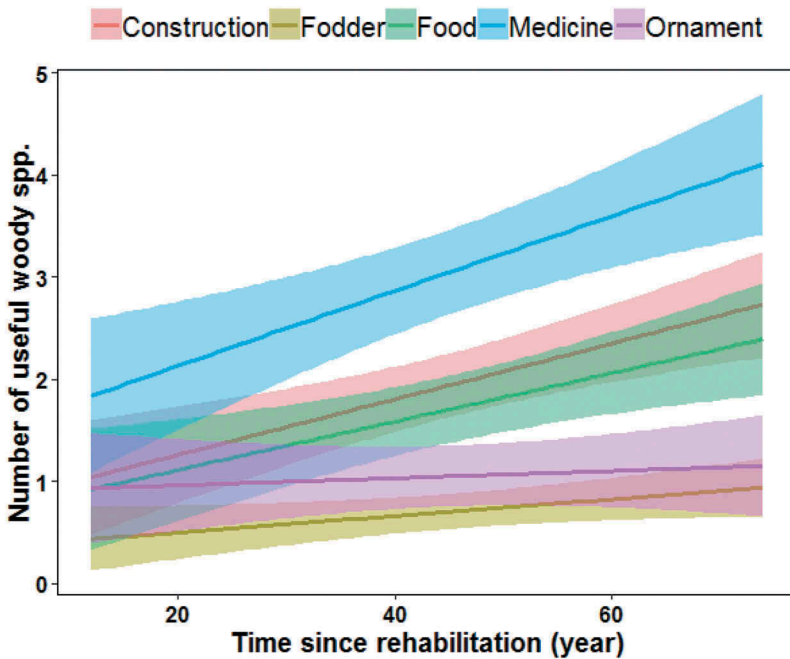


Figure 6. Interaction effects between plant uses and time since rehabilitation (year) on the number of woody species per plot (25 m²).

rehabilitated: $F = 4.20$, $p < .002$; **Figure 7**). Most medicine species showed affinity to teak, while some, mainly perennial-exotic species, were drawn to mahogany and some perennial native species to non-rehabilitated natural forest. Food species were with few exceptions related to teak, and fodder plants to teak, mahogany and non-rehabilitated stands. Of ornament plants, about half showed affinities to teak and the rest to mahogany and non-rehabilitated.

Ordinations of woody species

CA and forward selection in CCA of woody plant species showed an influence of stand types on species distribution (teak: $F = 3.51$, $p < .002$; mahogany: $F = 3.62$, $p < .002$; non-rehabilitated: $F = 5.33$, $p < .002$; **Figure 8**). Woody plant species for fodder did not show a clear affinity, although teak dominated, whereas food species seemed mainly to occur in non-rehabilitated and teak stands. Medicine woody plants also showed an affinity to non-rehabilitated stands. Ornament plants were negatively, and construction plants positively, related to non-rehabilitated stands.

Discussion

Summary of results

We can summarize our results according to our hypothesis as follows:

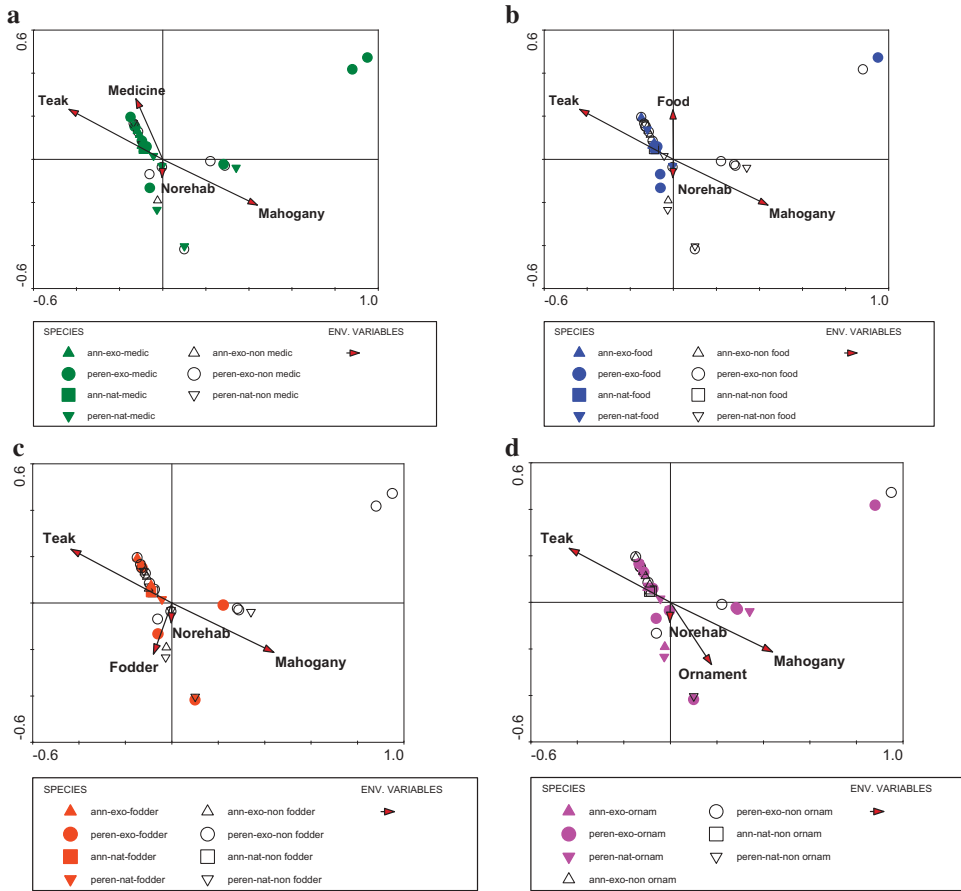


Figure 7. Ordinations with Correspondence Analyses for herb species. Graphs show useful species composition for (a) medicine, (b) food, (c) fodder, and (d) ornament. Significant environmental variables are included with best fit.

- (1) Hypothesis 1 that the original forest would have more species used for medicine and more native plant species than the rehabilitated forests, while the rehabilitated forests would have more rare species than the original forest, was not confirmed by our results. Actually, single species stands of the exotic trees, teak, and mahogany, had a relatively large number of useful herbs and woody species compared to the few stands of non-rehabilitated natural forests.
- (2) Hypothesis 2 that many plants used as food or forage would be annual and/or exotic and be found in the rehabilitated stands was partly confirmed. Food plants were mainly exotic, and plants used as fodder were annual and exotic, and were mainly found in the rehabilitated stands.
- (3) Hypothesis 3 that the number of useful plant species would increase with time since rehabilitation was also confirmed for woody species that could be used for medicine, construction, and food, whereas ornament and fodder species did not change. For herbaceous species, there was a decrease in number of useful species except for native annual plants that increased.

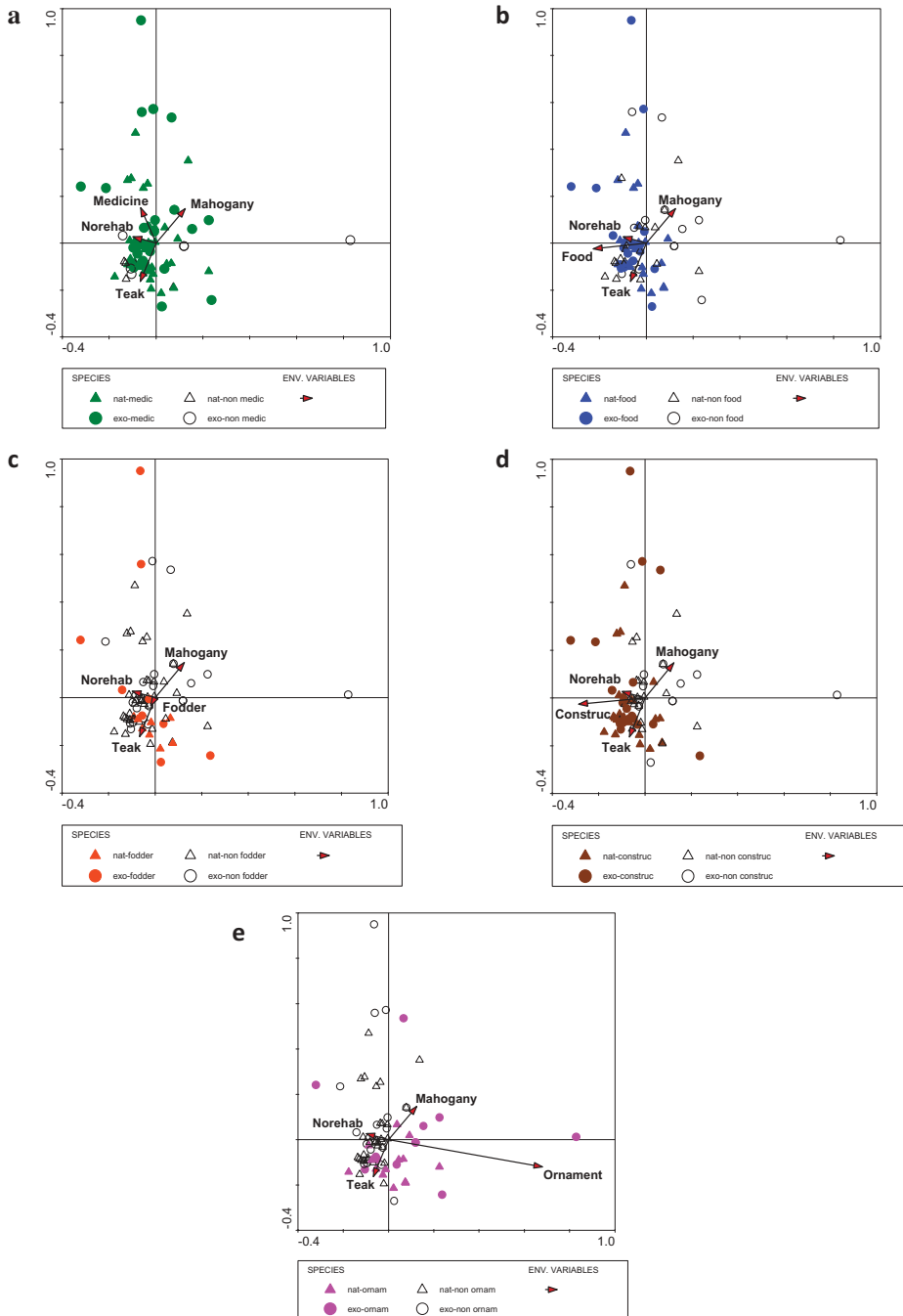


Figure 8. Ordinations with Correspondence Analyses for woody species. Graphs show useful species composition for (a) medicine, (b) food, (c) fodder, (d) construction, and (e) ornament. Significant environmental variables are included with best fit.

- (4) Hypothesis 4 that there would be differences in plant occurrences between the stand types was partly confirmed by the ordinations, as for instance teak stands had more useful species than the other stand types.

Plant species distribution

About half of the plant species registered were classified as rare as they occurred only once in one site. There were many more widespread species in woody plants than in herbaceous species, which might reflect the more stable nature of woody plants, establishing and growing with the stand, competing for light and other resources. Species with restricted distribution were more common among herbaceous than woody plants, possibly as many herbaceous pioneer species establish and stay for one or a few years before being out-competed by other herbs or by the growing tree stand.

Species distribution depends on the availability of suitable habitat, the capacity to disperse to these habitats, and the capacity of populations to persist after establishment (Ehrlén & Eriksson, 2000). Long distance seed dispersal can be critical (Cain, Milligan, & Strand, 2000), and more so the more the forest is fragmented. Long distance dispersal often needs the assistance of insects, birds or mammals, who's occurrence in turn can depend on vegetation composition and structure (Carnus et al., 2006).

Plant species that had an intermediate or widespread distribution usually had few occurrences in non-rehabilitated stands (Table 1). It should be remembered that there were 12 stands each of teak and mahogany, but only 3 stands of non-rehabilitated natural forest. This may have been too few to show a representative species distribution. This might explain why there is only one useful woody species with restricted distribution in the non-rehabilitated forest, *Macaranga tanarius*.

Number of uses per useful species

Multiple use of plants is quite common. More than 50 000 plant species have been used as medicine in many countries around the world (Schippmann, Leaman, & Cunningham, 2002). Out of these, about 1 000 species can be found in Indonesia (Schippmann et al., 2002). However, many of the same species can also contribute as food species, often collected to provide side dishes and diversity and serving as a source of vitamins and minerals (Pardo-De-Santayana, Tardío, & Morales, 2005). Furthermore, legumes are commonly used as fodder for ruminants in much of the dry tropics, probably due to their high nitrogen content as they are nitrogen fixing (Simbaya, 2002; Topps, 2009), and some of these species do also serve as human food, e.g. *Leucaena leucocephala* (Garcia, Ferguson, Neckles, & Archibald, 1996).

More complex plants, such as trees and shrubs, are more likely to be useful plants (with potential uses from bark and wood) than herb species (Tardío & Pardo-de-Santayana, 2008). We found similar results as 41% of the herbs had only one use, while 33% of the woody plants had three uses. As medicine use is the most common, most combinations contain medicine, often together with food (57 cases) or fodder (21 cases).

Multiple use was most common in the rehabilitated stands. There were no woody species with five uses, and only two herb species with three uses in the non-rehabilitated stands.

Similar results were mentioned by Lykke, Kristensen, and Ganaba (2004) and Ayantunde, Hiernaux, Briejer, Udo, and Tabo (2009), who recorded multipurpose uses of woody plants. We do not know the reasons for this pattern, but useful and sought for plants in the non-rehabilitated forests might have been collected to rareness or extinction (Kala, 2005).

Number of useful plant species

We found a higher number of useful herb species per plot in teak than in mahogany or non-rehabilitated stands. For woody species, there was no difference between stands, but exotic species dominated in teak, suggesting a more disturbed environment in teak plantations than in mahogany (Biswas & Das, 2016; Bruijnzeel, Bonell, Gilmour, & Lamb, 2005; Manimegalai, 2012). Hence, the higher number of useful herb species in teak plantations than in non-rehabilitated stands might partly be explained by the few stands of original forest sampled, but could also depend on collectors' preference for weedy species on disturbed land (Stepp, 2004).

The number of useful native woody plants did not differ between stand types, but the number of exotic species was highest in teak stands. Also, the number of useful herbaceous species was higher in teak than in mahogany and non-rehabilitated stands. Tropical primary forest is usually considered most important for traditional plant collectors, but as pointed out by Stepp and Moerman (2001), the use of plants growing in disturbed sites have often been overlooked as well as the use of new exotic plants (Medeiros, 2013). We found that exotic species was mainly used for food and annual species for fodder. This might indicate the use of short-lived species exploring disturbed sites, such as some weedy species.

Annual and perennial, native and exotic, herbs and woody species were all used for medicine. This multiple source of medicine plants might be the reason that they were frequently used also as food and fodder. The more specific medicine plants may contain poisonous substances and might be found in the natural forests (de Padua et al., 1999).

Ordination of herb species

We used CA to identify species patterns and the environmental influence on useful plant species. Environmental variables (stand type and use) influenced the position of many of the useful species in the ordinations. Seven herb species did not fit in the graphs and were excluded. These were mainly rare and native species, although not many occurred in the non-rehabilitated stands.

There was a general aggregation of useful herbs towards teak stands, supporting Stepp (2004) on the great importance of weedy species in plant collection. In addition, for medicinal plants, some native perennial species had affinity to non-rehabilitated stands and to mahogany. That suggests the dual distribution of many species in disturbed sites and a few specific ones in non-rehabilitated stands. As expected, food and fodder species were mainly fast-growing exotic species mainly in the teak stands, but also a few in non-rehabilitated and mahogany stands. Ornament plants showed the largest spread around the non-rehabilitated and mahogany stands.

Ordination of woody species

CA of woody species showed a variation in useful plant species composition with stand type. Seven species did not fit in the graph and were excluded. These were mainly ordinary species with uncommon allocation in the ordination graphs. There were more woody species than herbaceous, and the spread of species was greater. All use categories showed more or less concentration around teak stands, strongest for food and fodder species. Medicine had a spread of species with affinity to mahogany along axis 2, but not specifically native or exotic species. Ornament woody species, showed a strong negative relationship to non-rehabilitated stands, illustrating the group's exotic character. Woody species for construction, on the other hand, had many species occurring in teak stands and many in non-rehabilitated stands, with a widespread of species along axis 2 and mahogany.

Conclusion

This study is unique as we have used a large data sample at the plant species level to analyze how plant uses correlate with forest rehabilitation. Generally, our results are quite positive for the sustainability of rehabilitated stands showing that they are doing well with regard to the number of useful species. Still, we know what species are collected today, but not what was collected from natural forests before forest clearance and rehabilitation. In addition, rehabilitated forests have a different species composition compared to non-rehabilitated forests with unknown long-term consequences for sustainability. Forest plantations are relatively young anthropogenic ecosystems compared to natural forests, and with just one tree species they offer fewer habitats than a natural forest with a mixture of species, life forms, ages of trees and of dead wood. Plantations of exotic trees are known to suppress native vegetation (Braun & Vogt, 2014; Tulod, Casas, Marin, & Ejoc, 2017; Wijesinghe & de Silva, 2012).

Our results are of course affected by the number and location of the non-rehabilitated forests. The small fragments of natural forest are difficult to find. They are still the least disturbed stands we observed and have served as a reference for an original natural forest. While teak stands have the highest number of useful herb species, they are the most disturbed stands (Biswas & Das, 2016; Bruijnzeel et al., 2005; Manimegalai, 2012). We do not know whether the limited occurrence of rare species and species with restricted distribution is natural or caused by deforestation and rehabilitation. It shows, however, the need for protection of species and ecosystems for plant collectors and to promote the functioning of ecosystems and general ecosystem services. This requires a forestry with planting of stands with more species and more indigenous species (Carnus et al., 2006; Lamb, 2018; Lamb et al., 2005). By mixing stands with different species compositions and ages, intermingled with what remains of natural forest stands and stands with rehabilitation of the original tree species composition, landscape biodiversity is promoted (Carnus et al., 2006). Connectivity between stands facilitates the distribution of animals, that help with pollination and long-distance seed dispersal.

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