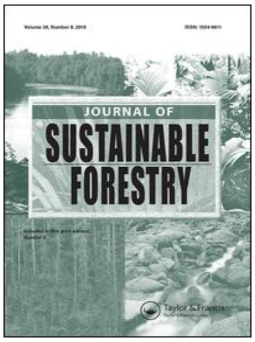

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Understory diversity and composition after planting of teak and mahogany in Yogyakarta, Indonesia

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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 mahogany (N = 12) or teak (N = 12) planted from 1941 until 2003 in Yogyakarta, Indonesia. Understory vegetation of these areas was compared with that of three native forests. 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 41–74 yr 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 & Honnay, 2011; Chapin, Oswood, Van Cleve, Viereck, & Verbyla, 2006; Guariguata & Ostertag, 2001; Lamb, 2018; Ruiz-Jaén & 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, and 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).

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Supplemental data for this article can be accessed here.

By contrast, Lamb, Erskine, and 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 & 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 yr might approach that of a native forest, the species composition still differs (Denslow & Guzman G, 2000; Guariguata & 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 & Ostertag, 2001) and perhaps on large mammals for spreading seeds (Babweteera & Brown, 2010; Campos-Arceiz & 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 & 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 fourth century (Ministry of Forestry, 1986) and it is now more or less naturalized (Soerianegara & 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 & Ngao, 1989) and both are prime timber species. Teak has been found to have allelopathic properties, which might hamper the development of understory (Biswas & 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

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 yr) and old stands (≥41–74 yr). * Significant values are at p < .05.

		Native vs. young stands			Native vs. old stands	
Characteristics	Vegetation	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

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 yr), 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 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

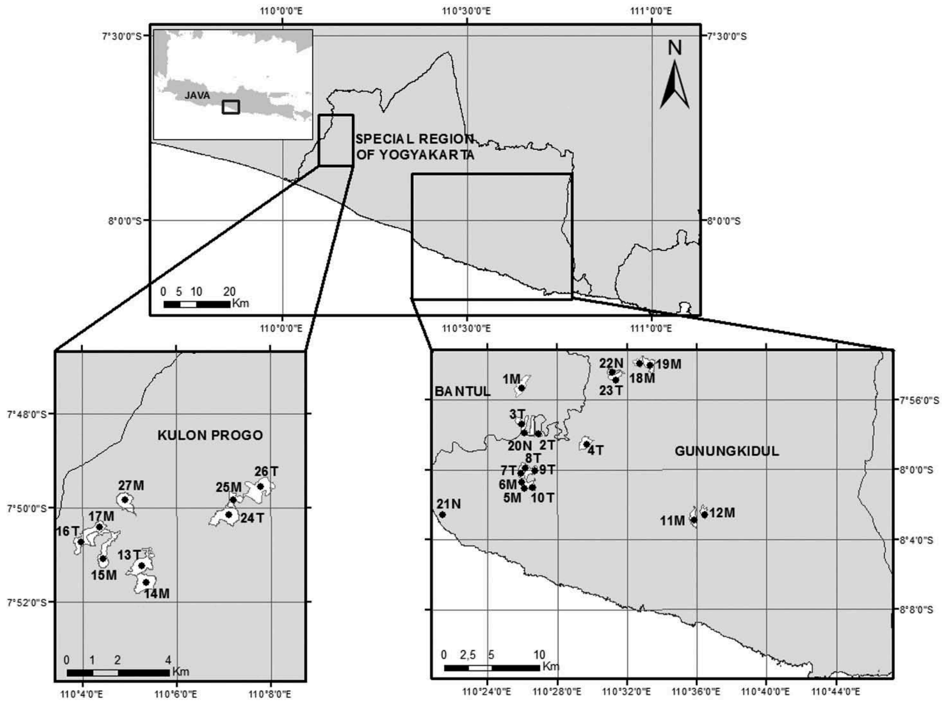

Figure 1. The locations of the study areas and of stands sampled in the forests of Yogyakarta, Indonesia. T = teak (N = 12), M = mahogany (N = 12) and N = native forest (N = 3). The numbers refer to the stands in Table 1 suppl.

a humid tropical climate with an average humidity of about 84–89%, and an 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 Centre 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 × 4 m spacing, and generally, thinned at the age of 10–15 yr. Usually the trees in production forests are logged at the age of 35 yr, 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 yr were 30–40 cm in diameter at breast height (DBH; 1.3 m), the young were 8–15 cm. The DBH of 70-yr-old mahogany was 30–50 cm, and of young stems 15–25 cm. Tree density in mahogany stands was about 20 trees per 100 m^2, showing no trend with time since rehabilitation. Teak had 15–20 trees per 100 m^2 in the young stands, decreasing to 5–10 trees in old stands. Native forest had 27 trees per 100 m^2. Mahogany stands had on average ± SE (5 ± 0.6) tree species per 100 m^2 (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 m^2.

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 × 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 × 1 m plot in the NW corner of each 25 m^2 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, 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.

Data analyses

We analyzed four vegetation characteristics for saplings (per 25 m^2 plot), seedlings and herbs (per 1 m^2 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 yr) and native forests vs old stands (≥41–74 yr). 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 four 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 backward selection procedure by removing the least significant predictor until we had only statistically significant ($p < .050$) 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 & 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 yr) 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 < .050; 499 iterations; Ter Braak & 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 the 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.).

Table 2. Species richness of herbs, seedlings, and saplings, by origin (with percentages in brackets), found in 25 m^2 (saplings) or 1 m^2 (seedlings and herbs) plots within mahogany or teak stands and native forest.

	Species richness											
Stands	Herbs	Native	Exotic	Unknown	Seedlings	Native	Exotic	Unknown	Saplings	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**	3 (37)	5 (63)	0	**22**	10 (46)	8 (36)	4 (18)	**43**	24 (56)	11 (26)	8 (18)

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 × 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

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 $p > .159$). However, we found differences between young stands (<41 yr) and native forests. Species richness of herbs was higher in young stands than in native forests (Est. ± 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 yr 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, $p < .001$);

Species richness of herbs decreased ($\chi^2 = 8.25$, d.f. = 1, $p = .004$) while species richness of saplings increased ($\chi^2 = 9.03$, d.f. = 1, $p = .003$) 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, $p = .077$), 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, $p = .010$) and saplings ($\chi^2 = 4.20$, d.f. = 1, $p = .041$) 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, $p = .004$) and seedlings ($\chi^2 = 5.59$, d.f. = 1, $p = .018$).

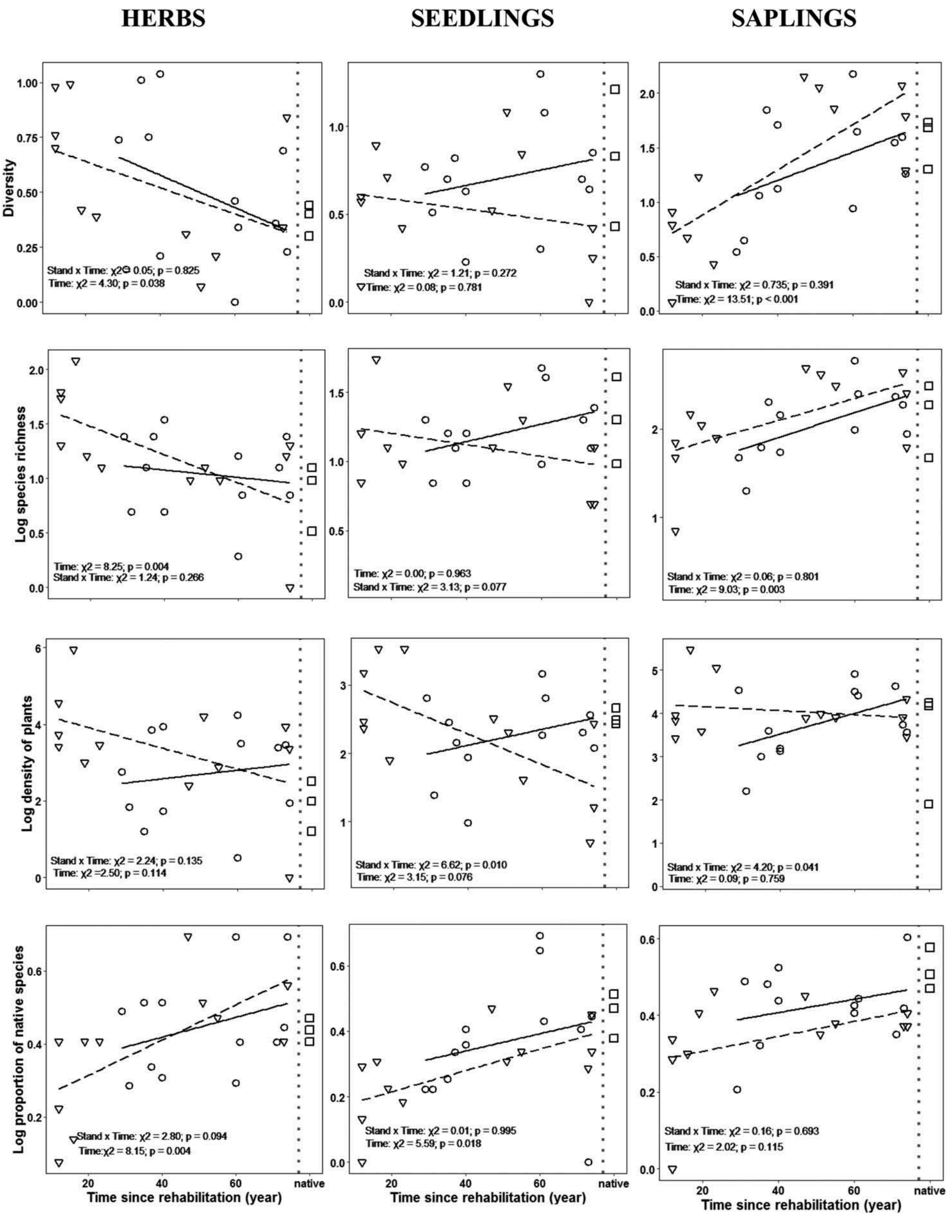

Figure 2. The effect of time since rehabilitation for herbs, seedlings, and saplings. Points show the mean of the three registered plots in each stand (N = 27). Dashed line and triangles are the teak stands, the solid line and circles are the mahogany stands and the squares are native forests (native). 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. Note varied Y-axes ranges.

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, $p < .002$) and tended to depend on time since rehabilitation (F = 1.80, $p = .068$). [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, $p < .002$; Figure 3) for the herb species of the rehabilitated teak and mahogany stands. Many species such as *Polytrias indica* (Houtt.) Veldkamp (36) and *Spigelia anthelmi*a 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 the influence of native forest and mahogany stand type and time since rehabilitation on the distribution of plots, mahogany (F = 2.20, $p < .002$), time (F = 2.10, $p = .004$) and native forests (F = 1.60, $p = .016$). Correspondence Analysis of seedlings in the rehabilitated plots (teak and mahogany) only, and forward selection in CCA showed mahogany (and teak) (F = 2.70, $p = .002$) and time since rehabilitation (F = 2.00, $p = .002$)

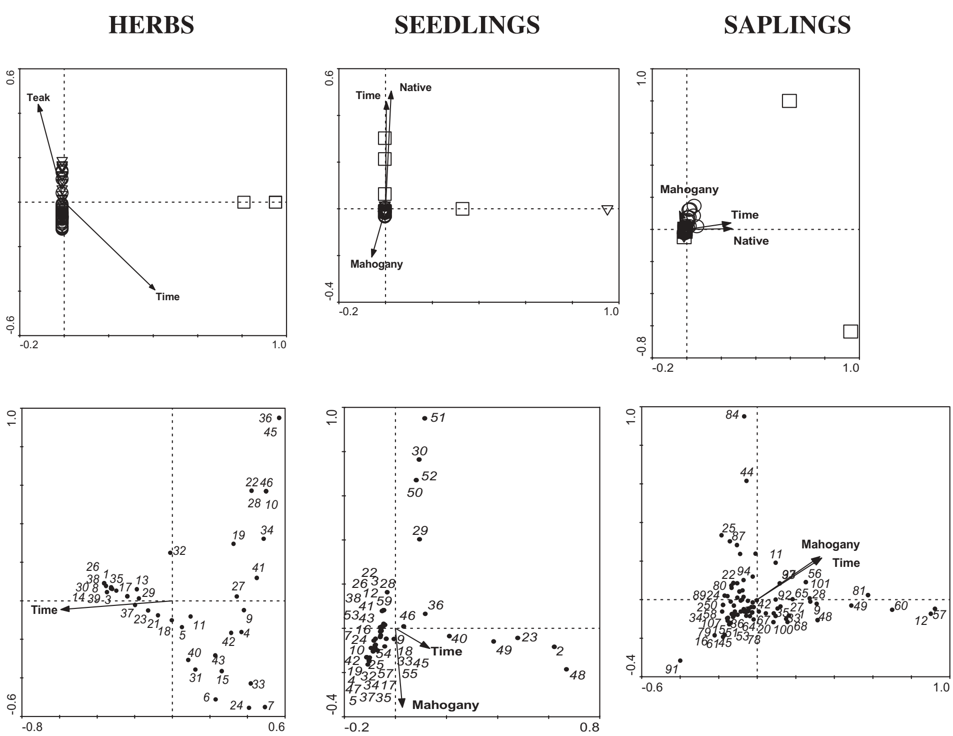

Figure 3. Ordinations with Correspondence Analyses for herbs, seedlings, and saplings. Top three graphs show plots for teak stands (triangles, N = 36), mahogany stands (circles, N = 36) and native forest (squares, N = 9). Bottom three graphs are only for rehabilitated stands and show species as points 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.

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, $p < .002$), native forests (F = 3.17, $p < .002$), and mahogany (F = 1.50, $p = .018$) 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, $p < .002$) and mahogany (and teak) (F = 1.87, $p < .002$) 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 more similar to 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 ($p = .073$) 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 leasing 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, possibly 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 was 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 & 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 yr after planting than in *Pinus merkusii* Jungh. & de Vriese, *Peronema canescens* Jack, and *Schima wallichii* (DC.) Korth. Forest (Kunarso & Azwar, 2013). Teak stands in our study were, on average, younger than mahogany stands, 39 ± 4 versus 50 ± 3 yr, 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 & Das, 2016; Manimegalai, 2012). Even though Wolfe, Dent, Deago, and 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 & Gara, 2003; Nikmah, Jumari, & Wiryani, 2016). In contrast, a study in northern Thailand, where teak is indigenous, showed that a 37-yr-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 the density of plants only increased in mahogany stands.

Martin, Moloney, and 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 the 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 & 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 & Brown, 2010; Campos-Arceiz & 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 yr, and whether they would with time achieve a larger proportion of species also occurring in the native forests is uncertain (Guariguata & 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 is 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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