

A COMPARISON OF FOREST REGENERATION IN AN ABANDONED RUBBER PLANTATION AND LOGGED-OVER FOREST WITH IMPLICATIONS FOR FOREST-ECOSYSTEM RESTORATION IN SOUTHEAST THAILAND[†]

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ABSTRACT

Rubber plantations have been encroaching into upland areas in Southeast Asia for many decades. Such monocultural expansion is a major driver of deforestation in many countries. In Thailand, illegal rubber plantations are subject to government forfeiture and most have been abandoned, allowing subsequent forest regeneration. In Rayong Province, Southeast Thailand, rubber has expanded into upland forest areas since 1987. Here, we report on tree regeneration and ground flora in a rubber plantation abandoned 20 years ago in semi-evergreen forest in the province and compare it with a regenerating forest that was selectively logged prior to 1978. We also surveyed mammals and birds at each site, to determine the potential for zoochorous seed dispersal. The tree flora (≥ 10 cm DBH) of the abandoned rubber plantation was dominated by *Leucaena leucocephala* (Leguminosae, Mimosoideae), and the sapling layer (1–5 cm DBH) by *Streblus ilicifolius* (Moraceae). The non-native *L. leucocephala* had been introduced by the plantation owner to enrich the soil. Rubber trees (up to 33 years old) still dominated the upper canopy. Native small-tree density (5–10 cm DBH) was 66% higher and native large-tree density (≥ 10 cm DBH) was 24% lower in the abandoned rubber plantation (ARP) than in the logged evergreen forest (LEF), indicating an earlier successional status in the former. Species richness and diversity of woody plants were higher in the LEF than in the ARP in most strata, except for tree and shrub species ≥ 5 cm DBH, of which 73 species had re-established in the ARP (despite competition from the alien *L. leucocephala*), compared with 63 species in the LEF. Native liana species were common in both plots (22 species in the ARP; 24 in the LEF). Of all native trees and shrubs ≥ 5 cm in DBH in the ARP 73% were known to be dispersed by animals, in comparison with 79% for the LEF. Longterm research is needed to determine if native species, recruiting into the ARP from nearby logged natural forests, will be able to outcompete the alien species and become dominant.

Keywords: forest restoration, invasive species, *Leucaena leucocephala*, rubber plantation, colonization, semi-evergreen forest

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[†] This paper is dedicated to our colleague and friend J. F. Maxwell who passed away in 2015 while conducting this field survey.

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INTRODUCTION

Rubber plantations (*Hevea brasiliensis*) have high economic value and cover enormous areas of the landscape in Southeast Asia, where over 75% of the world's natural rubber was harvested during the period 2009–2019 (FAO, 2021). By 2050, the area under rubber plantations of the major producers, Thailand, Malaysia, and Indonesia, is predicted to increase fourfold (FOX *ET AL.*, 2014). Rubber monocultures have expanded into natural forest in many parts of the region and compete for area with nature reserves, which are important for biodiversity conservation and preserving ecological functions. Plantations are expanding into marginal areas, resulting in conversion of high-biodiversity secondary forests into economically unsustainable plantations with unstable rubber market prices (AHRENDS *ET AL.*, 2015).

In Thailand, logged-over forests are often converted to rubber plantations, which may subsequently be abandoned when they become unproductive or economically unsustainable. Current governmental policy is to seize illegal or abandoned rubber plantations, and allow the forest to recover. Therefore, an understanding of forest regeneration in abandoned plantations is vital to justify this policy and adjust it if necessary. Restoration of disturbed areas through planting of selected species is widely recommended to improve their productive capacity, environmental functions, and biodiversity value (ELLIOTT *ET AL.*, 2003; SHONO *ET AL.*, 2007; STANTURF *ET AL.*, 2014; PARROTTA, 2000), but may not be feasible over the entire landscape.

In this study, we recorded the structure and species composition of regenerating forest in a rubber plantation, which had been abandoned 20 years before in Southeast Thailand and compared its composition with partly degraded forest nearby, subjected to selective logging from 1967 to 1977, but not burned. The rubber plantation had undergone more severe disturbance than the logged forest and was colonized by the non-native species *Leucaena leucocephala*, which is classified as an invasive species by the World Conservation Union (LOWE *ET AL.*, 2000). The effect of such species on native plant communities is of great concern (CAMPBELL *ET AL.*, 2019; KUO, 2003; GISD, 2021; RICHARDSON & REJMÁNEK, 2011). This species readily establishes in abandoned areas and develops dense stands in a few years, preventing or delaying natural forest regeneration (CHEN *ET AL.*, 2012; HATA *ET AL.*, 2007; MAROD *ET AL.*, 2012; YOSHIDA & OKA, 2000).

We carried out a detailed inventory of plant species (trees, saplings, and seedlings) within 100 circular plots, covering totally one-hectare in each of the logged forest and abandoned rubber plantation. Both forest areas were in a state of succession, and we hypothesized, due to the previous conversion of the rubber plantation to agriculture, that the pathways of succession in these two areas would be different. Unfortunately, there was no undisturbed natural forest at similar altitude in the local area that would have enabled us to measure the success of succession.

We also carried out an inventory of birds and mammals, to evaluate the potential for seed dispersal from nearby forest into both study sites.

METHODS

Study Areas

The Khun-In Mountains (12°1.491'–13°56.044'N, 101°23.680'–101°27.311'E) in the Panomsart Mountain Range were once covered by tropical dry evergreen forest, which has recently been reclassified (at least the lowland areas) as semi-evergreen forest by ASHTON (2014). However, the forest becomes more evergreen at altitudes above about 300 m a.s.l. and appears similar to the seasonal evergreen forest farther to the southeast (personal observations). The study area (altitude 90–300 m a.s.l.) is located in Pah Yup Nai Sub-district of Wangchan District in Rayong Province, Southeast Thailand (Figure 1), where rubber plantations have been introduced and expanded into upland forest areas since 1987. At present, the upland hill areas are covered by active rubber plantations, abandoned rubber plantations (ARP) and logged semi-evergreen or evergreen forest (LEF). The ARP site is 91–167 m in altitude and the LEF 202–335 m. The ARP site lies less than 300 meters from natural forest, whereas LEF site is surrounded by natural forest on three sides. Both sites are near the facility of the Petroleum Authority of Thailand Public Company Limited (PTT). The LEF is 1 km to the southwest, whereas the ARP is 1.5 km to the south (Figure 2). The climate is seasonally humid with an average annual temperature of 28.9°C, 1,267 mm mean annual rainfall and mean relative humidity of 77.5% (TMD, 2015). Rainfall is concentrated between May and October. The topography is undulating terrain. Soils are colluvium and residuum from granite.

Soil type was analyzed from 24 sample plots at the PTT facility and classified as coarse-loamy, siliceous, subactive isohyperthermic, typic Paleudalfs. We did not analyze soil in the study areas but the presence of bedrock outcrops suggests that the soil of the ARP might have become degraded by repeated burning.

Interventions

Both sites were selectively logged during 1967–1977. The ARP site then underwent intensive agriculture. In the ARP, cassava (*Manihot esculenta*) was grown for five years in 1977–1982, cashew nuts (*Anacardium occidentale*) were grown for seven years during 1982–1989 and rubber plantation (*Hevea brasiliensis*) for 12 years during 1989–2001, after which the site was abandoned until the present. *Leucaena leucocephala* seeds were obtained from the Rayong provincial forestry office to be planted along with rubber trees to enrich the soil. Fire was used during clearance and later for controlling understory regrowth. In the LEF, most economic trees of the family Dipterocarpaceae were logged during 1967–1977. The LEF has not been burned to our knowledge. The area has been remained free of further disturbance until the start of the study.

Commercial use of both study areas is now illegal. Located (at least partly) in a zone of steep slopes and classified as a protected watershed, the land is under the responsibility of the Chawae Cooperative Estate of Rayong Province, Cooperative Promotion Department, Ministry of Agriculture and Cooperatives. The local community has recently applied to convert the land to community forest status, following Thailand's Community Forest Act, B.E. 2562 (2019). The application is still being processed. Therefore, the management aim of these areas is ecological restoration and eco-tourism, according to interviews of local leaders.

Data Collection

Plants

Field work was carried out in April–June 2015. One hundred circular plots of 100 m² (5.64-m radius) area each were used to collect data on forest tree species composition in the ARP and another set of 100 circular plots in the LEF, which was 2.7 km to the west. Total study area was approximately 200 ha in each environment and the total area contained within all circular sample plots was 1 ha per site. The plots were established along line transects 80 m apart extending in a north–south direction. Plots were placed 20 m to the east and west of each transect at 40-m intervals along each transect. The length of the transects varied depending on terrain: they extended up the hill to about 300 m in altitude in LEF, and through to the north edge of the rubber plantation in ARP. There were 10 transects in the LEF and five in the ARP. Transects varied up to 530 m in length in ARP and 280 m in LEF. The location of the initial plot on each transect was randomized.

Trees with diameter at breast height (DBH at 1.3 m) of ≥ 5 cm were identified and recorded in all plots. Saplings (DBH 1.0–4.9 cm) and shrubs were identified and recorded in 10-m² subplots (1.78-m radius) in the centers of the 100-m² circular plots, and seedlings (height <1.3 m) and other ground flora were identified and recorded in 1-m² subplots (0.56-m radius) in the centers of the 10-m² circular plots. Thus, the combined area of the tree samples in each site was 1 ha, that of the sapling samples was 0.1 ha, and that of the seedling samples was 0.01 ha.

Voucher specimens of many species were stored in herbaria in Chiang Mai University (Biology), BIOTEC in Science Park, Pathum Thani, and other herbaria in Thailand. A list of all species of plants found in the plots is compiled in the Appendix. Here we have also tabulated the known or suspected mode of seed dispersal for all woody species, using information taken from the Mo Singto plot (BROCKELMAN *ET AL.*, 2017), the Flora of Thailand, and other sources on the internet.

Soil type was collected and analyzed from 24 sample plots at the PTT facility, but not in our study sites. Physical soil property included bulk density and texture. Chemical property included soil carbon, suspended organic carbon, total nitrogen, pH, electrical conductivity, organic matter, available P, exchangeable K, % base saturation, Ca, Mg, Na and Cation Exchange Capacity.

Species richness and diversity

In each study site, we calculated species richness (no. species/ha), density (no. stems/ha), and dominance (basal area/ha) of each species in each plot for all size classes except saplings and seedlings. Frequency was the number of plots out of 100 in which a given species was found. The contribution of each species to the forest community in relation to other species was determined by relative density (density/combined density of all species), relative dominance (basal area/basal area of all species), and relative frequency (frequency/sum of frequencies of all species). Species richness (SR) was compared between sites, on the basis of number of individuals sampled, rather than area (CONDIT *ET AL.*, 1996). Rarefaction and extrapolation were employed to remove the effect of uneven sampling of tree numbers, using EstimateS and iNEXT (COLWELL, 2013; CHAO *ET AL.*, 2014; 2016). Rarefaction involves reduction of the abundance of the more abundant sample to the size of the less abundant one by use of the multinomial probability distribution. A method of comparison by “extrapolation” of the abundance of the smaller sample to the size of the larger one, thus making use of more data,

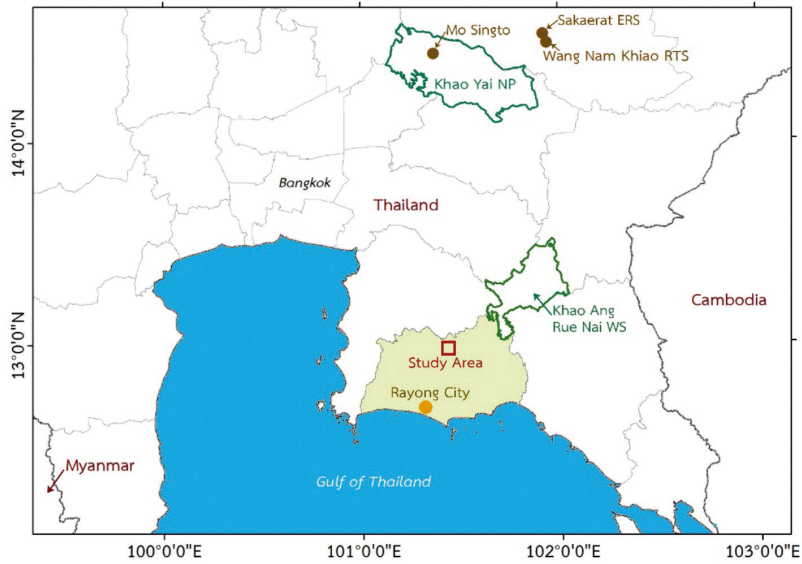


Figure 1. Map showing location of the study area in Southeast Thailand. Rayong Province is shaded light green (NP = National Park, WS = Wildlife Sanctuary, ERS = Environmental Research Station, RTS = Forestry Research and Student Training Station).

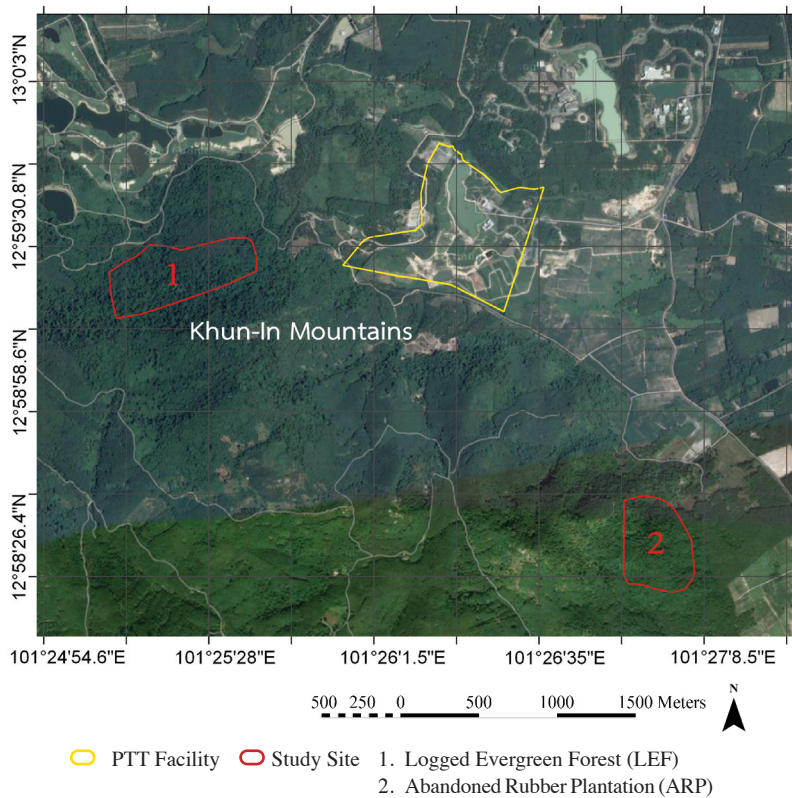


Figure 2. Google Earth image of the study area dated 31 Dec. 2020, 0700 h.

has also been developed by GOTELLI & COLWELL (2001), and COLWELL *ET AL.* (2012), and rarefaction and extrapolation are conveniently used in combination (CHAO & JOST, 2012; CHAO *ET AL.*, 2014).

An additional, and more recent, method for comparing species richness is by standardizing to a common “coverage” (CHAO & JOST, 2012; CHAO *ET AL.*, 2014). Coverage measures the extent to which the community is adequately sampled. Coverage is measured by the relation between the number of individuals sampled in the community and the number required to detect virtually all, or some very high percentage (ca., 99.5%), of the species present. A sample of individuals with low coverage will have a relatively high number of species represented by only single individuals (singletons). Therefore, the proportion of singletons can be used to estimate the coverage of a sample. The website iNEXT Online provides non-technical explanations and procedures for estimating and graphing coverage along with sample-size based diversity estimation parameters (CHAO *ET AL.*, 2016).

Diversity was measured using the Shannon-Wiener Index or $H' = -\sum [(p_i) \ln(p_i)]$, where p_i is the proportion of individuals of species i . Species evenness was measured using the J' index of Pielou, $J' = H/H_{\max} = H'/\ln S$. To compare species composition between the two sites, Renkonen's index of percentage similarity was used (RENKONEN, 1938; SCHOENER, 1968), $D(P_x, P_y) = 1 - 1/2\sum |P_{xi} - P_{yi}|$, where P_{xi} and P_{yi} are the probabilities of occurrence of species x and y in the i th quadrat, respectively. We use Jaccard's Index to compare the similarity of two habitats. The index is $A/(A + B + C)$, where A = number of species shared by two assemblages, B = number of species unique to assemblage x , and C = number of species unique to assemblage y ; and the abundance-based Jaccard similarity indices (CHAO *ET AL.*, 2005).

Seed-dispersing animals

In each study area, mammals and birds were recorded along three 500-meter-long transects, passing through important habitats. Along each transect, bird and mammal surveys were conducted separately within one hour in the morning after sunrise, over three days in each study site. One bird mist net and 15 small-mammal live traps were placed in each study area. Traps were placed 100 meters apart along each transect. One bat mist net was placed and monitored every 15–20 minutes between 7 and 10 p.m. each day. All animals caught were released after identification and photographing. Diversity was measured using the Shannon-Wiener Index and species evenness was measured using the J' index of Pielou.

RESULTS

Species Diversity

Statistical summaries of the top ten species of woody plants in the large stem (≥ 5 cm in DBH), sapling, and seedling strata are presented in Tables 1 and 2 and Figure 3. Figure 4 illustrates aspects of the canopy structure and ground vegetation of the sites. The ARP was dominated by the alien species, *Leucaena leucocephala*, where it constituted 30.6% of the number of trees ≥ 5 cm DBH. It also dominated the seedling layer but was the fifth most abundant species in the sapling layer. Rubber trees still comprised about 6% of tree individuals and 15% of basal area among trees ≥ 5 cm in DBH. There was only one species in common between ARP and LEF, *Pterocymbium tinctorium*, the most abundant tree in the LEF.

Overall, the LEF had higher total species richness and diversity than the ARP forest in most categories. Comparison of species richness showed no statistical differences in species density of native tree species ≥ 5 cm in DBH between ARP (73) and LEF (63), nor for species 10 cm DBH (ARP 48 vs LEF 53) (Table 3). Richness values for both sites were well within each other's 95% confidence limits. For saplings, seedlings, and herbaceous ground plants, the LEF had significantly higher species density than the ARP. This is also clear by inspection of the abundance/numbers curves, shown in Figures 5 and 6 (left side).

Further evidence of the similarity in tree species richness between the two sites was provided by abundance-based rarefaction and extrapolation of our data (Table 3, Figures 5 and 6, left side), which reduced difference in tree species richness between ARP and LEF. The extrapolated number for ARP increased species richness of trees ≥ 10 cm from the observed value of 48 to 51.6, closer to the observed value of 53 in the LEF. The two curves nearly coincide up to 300 individuals and beyond (Figure 5A). For all trees ≥ 5 cm DBH, extrapolation reduced the difference between ARP and LEF, from 10 to 7.4 (73–65.6) species (Table 3). The confidence intervals between the ARP and LEF overlap substantially. For saplings (Figure 5C) and seedlings (Figure 6A), however, rarefaction accentuated differences in species richness between the sites. LEF was markedly more species-rich than ARP. After extrapolating the lower sample size of the LEF to the size of the ARP sample, species richness increased in LEF to 65.4% above that in ARP for saplings, and 63.6% above that in ARP for seedlings (Table 3). For herbaceous plants (Figure 6B), the observed sample size for the LEF is more than three times that for ARP, and species richness is 85.6% above the extrapolated value for the ARP. For saplings, seedlings, and ground flora, the confidence envelopes did not overlap, indicating differences between LEF and ARP were highly significant.

Using species richness-coverage curves, Figures 5 and 6 (right sides) compare ARP with LEF for the five life form categories, and Table 3 presents estimated coverages for our observed data. Species diversity is not linearly related to coverage, but tends to increase much faster at high coverage values. This is because the species left to be sampled at high coverage tend to be rare species, represented by singletons. Hence, coverage curves tend to be more nonlinear when species abundance distributions are less even. Differences in coverage between ARP and LEF, were small, ranging from zero (for herbaceous plants) to 4% (for seedlings) and 5% (for saplings). Extrapolating species diversity values for saplings and seedlings in the LEF to equal coverage markedly increased difference between the habitats. In fact, for all tree stages, coverage for LEF was lower than for ARP, which means that in general, our survey samples underestimated species richness in LEF more than in ARP.

Shannon-Wiener diversity was higher in LEF than in ARP (Table 4). A higher index indicates a relatively greater frequency of rare species, as evidenced by the lower coverage values reported above. This difference was lowest for large trees; consistent with the lack of difference in species richness of trees.

Below we document and compare the floras of the ARP and LEF in more detail, and then present our evidence and reasons for the differences found.

Flora of the Abandoned Rubber Plantation (ARP)

There were 1,038 woody plant stems ≥ 5 cm in DBH per ha of 85 species, 745 woody sapling stems of 69 species per 0.10 ha of circular plots, and 894 woody plant seedlings of 59 species in 0.01 ha of plots in the ARP (Table 1 and Figure 3). As indicated in the Appendix, these totals include 22 species of woody climbers (lianas) for the ARP, including 12 species

Table 1. Density, frequency and basal area of 10 top species of woody plants, including trees, shrubs, palms and woody climbers (lianas), in abandoned rubber plantation (ARP) in three size classes. CT = Canopy Tree, UT = Understory Tree, S = Shrub, P = Palm, WC = Woody Climber.

Botanical name (family)	Density (stem/ha)	Relative density (%)	Frequency (no. of plots)	Basal area (m ² /ha)	Relative basal area (%)
Stems with DBH ≥5 cm					
<i>Leucaena leucocephala</i> (Fabaceae), UT	322	31.02	67	4.61	32.08
<i>Streblus asper</i> (Moraceae), CT	125	12.04	51	1.09	7.59
<i>Microcos paniculata</i> (Tiliaceae), CT	71	6.84	34	0.54	3.76
<i>Hevea brasiliensis</i> (Euphorbiaceae), CT	62	5.97	27	2.12	14.75
<i>Pterocymbium tinctorium</i> (Sterculiaceae), CT	44	4.24	22	1.15	8.00
<i>Lagerstroemia cochinchinensis</i> (Lythraceae), CT	37	3.56	22	0.38	2.64
<i>Bauhinia bracteata</i> (Fabaceae), UT	35	3.37	29	0.34	2.37
<i>Sterculia pexa</i> (Sterculiaceae), UT	19	1.83	15	0.42	2.92
<i>Lepisanthes rubiginosa</i> (Sapindaceae), UT	18	1.73	14	0.11	0.77
<i>Stereospermum fimbriatum</i> (Bignoniaceae), CT	17	1.64	9	0.15	1.04
Other N = 75 species	288	27.75		3.46	24.08
Total N = 85 species	1,038	100		14.37	100
Stems with DBH 1–4.9 cm					
<i>Streblus ilicifolius</i> (Moraceae), UT	2,140	28.72	49		
<i>Polyalthia sp.</i> (Annonaceae), CT	1,210	16.24	35		
<i>Streblus asper</i> (Moraceae), CT	580	7.79	37		
<i>Diospyros ferrea</i> (Ebenaceae), CT	310	4.16	20		
<i>Leucaena leucocephala</i> (Fabaceae), UT	270	3.62	18		
<i>Microcos paniculata</i> (Tiliaceae), CT	250	3.36	19		
<i>Antidesma japonicum</i> (Euphorbiaceae), UT	220	2.95	14		
<i>Hevea brasiliensis</i> (Euphorbiaceae), CT	150	2.01	4		
<i>Bauhinia bracteata</i> (Fabaceae), UT	150	2.01	11		
<i>Mallotus peltatus</i> (Euphorbiaceae), UT	130	1.74	6		
Other N = 59 species	2,040	27.38			
Total N = 69 species	7,450	100			
Seedlings					
<i>Leucaena leucocephala</i> (Fabaceae), UT	16,300	18.23	22		
<i>Bauhinia bracteata</i> (Fabaceae), UT	9,000	10.07	42		
<i>Caryota urens</i> (Arecaceae), P	9,000	10.07	7		
<i>Streblus ilicifolius</i> (Moraceae), UT	6,900	7.72	32		
<i>Caryota mitis</i> (Arecaceae), P	6,200	6.94	2		
<i>Secamone elliptica</i> (Asclepidaceae), WC	6,200	6.94	15		
<i>Diospyros filipendula</i> (Ebenaceae), S	3,800	4.25	9		
<i>Erythralum scandens</i> (Olacaceae), WC	2,600	2.91	10		
<i>Ichnocarpus frutescens</i> (Apocynaceae), WC	2,400	2.68	10		
<i>Streblus asper</i> (Moraceae), CT	1,900	2.13	11		
Other N = 49 species	25,100	28.08			
Total N = 59 species	89,400	100			

Table 2. Density, frequency and basal area of 10 top species of woody plants, including trees, palms and woody climbers, in three size classes in the logged evergreen forest (LEF). CT = Canopy Tree, UT = Understory Tree, P = Palm, WC = Woody Climber.

Botanical name (family)	Density (stem/ha)	Relative density (%)	Frequency (no. of plots)	Basal area (m ² /ha)	Relative basal area (%)
Stems with DBH ≥5 cm					
<i>Pterocymbium tinctorium</i> (Sterculiaceae), CT	94	16.85	42	1.17	5.01
<i>Macaranga tanarius</i> (Euphorbiaceae), UT	85	15.23	56	5.78	24.69
<i>Arenga westerhoutii</i> (Arecaceae), P	78	13.98	50	6.97	29.77
<i>Cleidion javanicum</i> (Euphorbiaceae), CT	25	4.48	16	0.45	1.91
<i>Caryota urens</i> (Arecaceae), P	23	4.12	12	0.11	0.47
<i>Artocarpus gomezianus</i> (Moraceae), CT	21	3.76	17	0.32	1.39
<i>Picrasma javanica</i> (Simaroubaceae), CT	14	2.51	12	0.35	1.50
<i>Nephelium melliferum</i> (Sapindaceae), CT	14	2.51	11	0.23	0.96
<i>Mallotus philippensis</i> (Euphorbiaceae), UT	14	2.51	11	0.11	0.45
<i>Ficus vasculosa</i> (Moraceae), CT	11	1.97	11	3.19	13.63
Other N = 59 species	179	32.08		4.74	20.20
Total N = 69 species	558	100		23.42	100
Stems with DBH 1–4.9 cm					
<i>Mallotus peltatus</i> (Euphorbiaceae), UT	840	18.03	34		
<i>Pterocymbium tinctorium</i> (Sterculiaceae), CT	540	11.59	29		
<i>Trevesia palmata</i> (Araliaceae), UT	190	4.08	9		
<i>Nephelium melliferum</i> (Sapindaceae), CT	180	3.86	11		
<i>Quisqualis indica</i> (Combretaceae), WC	170	3.65	13		
<i>Casearia flexuosa</i> (Flacourtiaceae), UT	150	3.22	9		
<i>Leea indica</i> (Leeaceae), UT	140	3.00	7		
<i>Ardisia ionantha</i> (Myrsinaceae), UT	130	2.79	10		
<i>Cleidion javanicum</i> (Euphorbiaceae), CT	120	2.58	11		
<i>Arenga westerhoutii</i> (Arecaceae), P	100	2.15	9		
Other N = 75 species	2,100	45.06			
Total N = 85 species	4,660	100			
Seedlings					
<i>Ventilago denticulata</i> (Rhamnaceae), WC	12,200	19.00	8		
<i>Caryota mitis</i> (Arecaceae), P	6,200	9.66	6		
<i>Arenga westerhoutii</i> (Arecaceae), P	4,000	6.23	23		
<i>Mallotus peltatus</i> (Euphorbiaceae), UT	2,600	4.05	17		
<i>Byttneria aspera</i> (Sterculiaceae), WC	2,500	3.89	9		
<i>Macaranga tanarius</i> (Euphorbiaceae), UT	2,100	3.27	8		
<i>Picrasma javanica</i> (Simaroubaceae), CT	1,800	2.80	4		
<i>Connarus semidecandrus</i> (Connaraceae), WC	1,700	2.65	9		
<i>Pterocymbium tinctorium</i> (Sterculiaceae), CT	1,600	2.49	8		
<i>Quisqualis indica</i> (Combretaceae), WC	1,500	2.34	8		
Other N = 66 species	28,000	43.62			
Total N = 76 species	64,200	100			

Table 3. Comparison of species richness of native tree and shrub species and ground herb flora between abandoned rubber plantation (ARP) and logged evergreen forest (LEF). Stem numbers have been rarefied or extrapolated to facilitate comparison between ARP and LEF, according to CHAO ET AL. (2014, 2016).

Growth-form	Habitat	Species richness	95 % confidence limits	Stem count	Rarefied/ Extrapolated species richness	Coverage	Total stems/ ha
Trees, shrubs ≥ 10 cm	ARP	48	38.3, 57.7	243	E 51.6	0.94	243
	LEF	53	34.5, 71.5	318	R 46.9	0.92	318
Trees, shrubs ≥ 5 cm	ARP	73	61.0, 85.0	618	R 70.4	0.97	618
	LEF	63	54.0, 72.0	544	E 65.6	0.96	544
Saplings	ARP	54	44.0, 64.0	667	R 47.2	0.98	6,670
	LEF	77	64.8, 89.2	431	E 89.3	0.93	4,310
Seedlings	ARP	42	29.7, 54.3	546	R 37.1	0.98	54,600
	LEF	55	27.5, 82.5	347	E 68.7	0.93	34,700
Ground flora	ARP	13	6.8, 19.2	93	E 16.7	0.96	9,300
	LEF	31	19.5, 42.5	334	R 21.6	0.98	33,400

≥ 5 cm in DBH). Tables 5 and 6 present summaries of the numbers, basal areas, and maximum sizes of trees 10 cm in DBH and over, the size most often used in comparisons of forest stands and types.

In terms of general forest structure, the most common tree species in the top canopy layer were *Leucaena leucocephala*, *Hevea brasiliensis*, *Streblus asper*, *Pterocymbium tinctorium*, and *Lagerstroemia cochinchinensis* (Table 5 and Figure 4). *L. leucocephala* dominated in both numbers and basal area, but the largest species was *P. tinctorium*, reaching a DBH of 83 cm. The small tree stratum was dominated by *Microcos paniculata* and *Sterculia pexa*, and the understory (sapling) layer by *L. leucocephala* and *S. asper*. *L. leucocephala* also dominated the seedling layer with 18% of all stems. The ARP was dominated by relatively few tree species, with three comprising 58% of stems ≥ 10 cm, and only three species comprising 57.5% of basal area (Table 5). In the sapling layer (1–4.9 cm DBH), three species comprised more than half (53%) of stems, and in the seedling layer, the top three species made up 38% of stems (Table 1). The seedling layer included 42 native species of trees, and the ground herbaceous flora included only 13 species (Table 3).

The basal area and density of rubber trees were negatively correlated with the density of other tree species ($N = 100$, $r = -0.265$, $p = 0.008$; and $r = -0.245$, $p = 0.014$, respectively). However, both basal area and density of rubber trees were significantly and positively correlated with the number of species ≥ 5 cm DBH regenerating in sample plots, although the relationship was weak ($N = 100$, $r = 0.247$, $p = 0.013$; and $r = 0.244$, $p = 0.015$, respectively). The density of *L. leucocephala* also had a negative correlation with the density of all other tree species ($r = -0.297$, $p = 0.003$). The negative relationship between the occurrence of the two alien species and the numbers of other species ≥ 5 cm DBH in the 100 tree plots in the ARP is illustrated in Figure 7. This relation suggests that the alien species are competing against the native species.

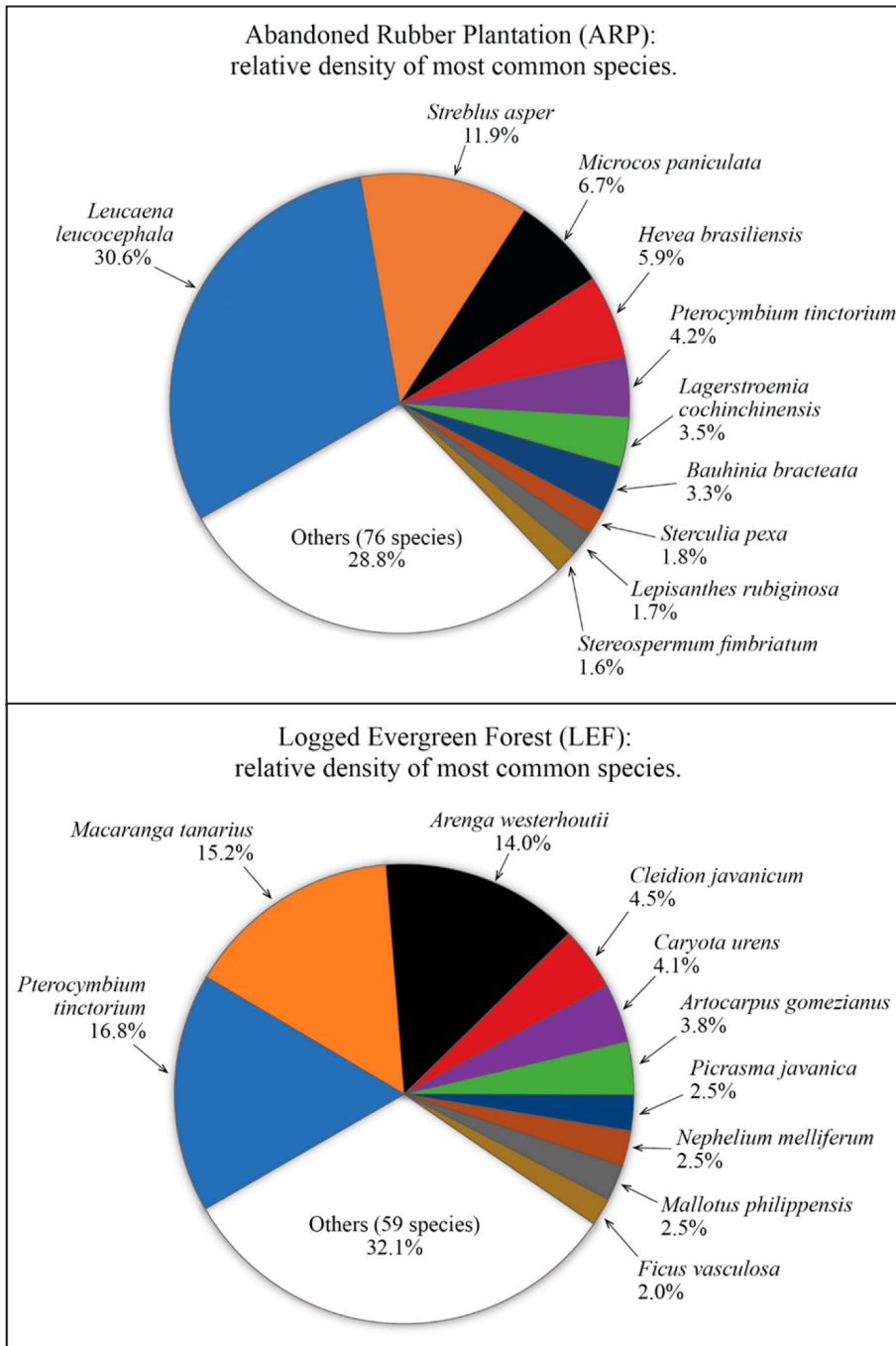


Figure 3. Relative density of common tree species with >5 cm DBH in abandoned rubber plantation (ARP) and logged evergreen forest (LEF).

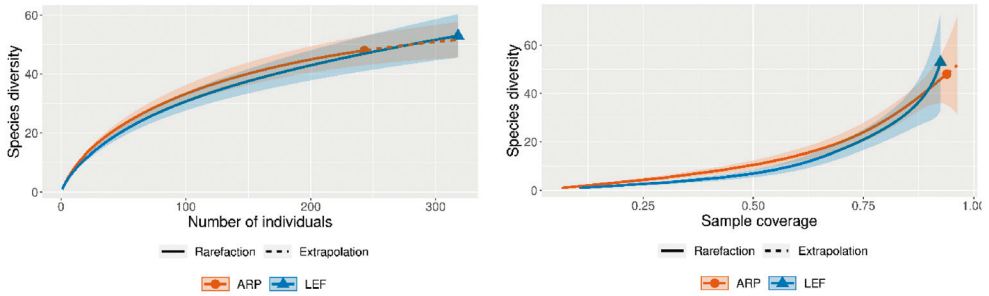


Figure 4. Photos of study site. (a) Abandoned rubber plantation. Canopy in ARP is lower than that in LEF. Note the presence of a liana in ARP. (b) *Hevea brasiliensis*, the dominant species in the abandoned rubber plantation. (c) Logged but regenerating dry evergreen forest. (d) High diversity of ground vegetation of logged dry evergreen forest.

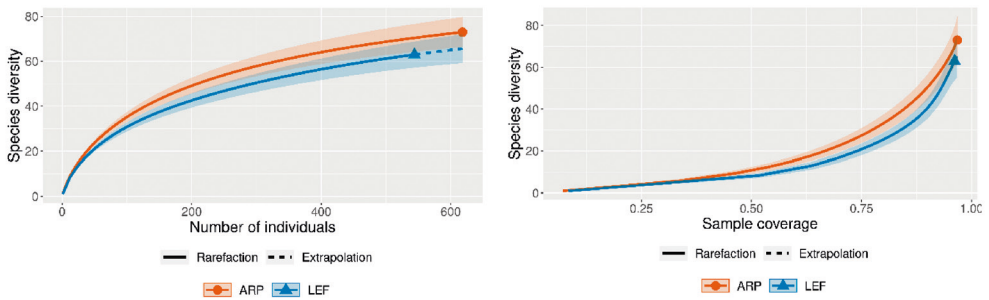
Table 4. Comparison of diversity and similarity indices between abandoned rubber plantation (ARP) and logged evergreen forest (LEF) habitats.

Growth-form	Habitat	Shannon-Wiener diversity index	Jaccard similarity index	Abundance-based Jaccard similarity index	Percentage similarity index
Trees	ARP	3.01	0.34	0.40	0.17
	LEF	3.17			
Saplings	ARP	2.97	0.24	0.44	0.15
	LEF	3.59			
Seedlings	ARP	3.09	0.27	0.47	0.19
	LEF	3.29			
Ground flora	ARP	1.77	0.16	0.12	0.12
	LEF	2.60			

A Trees ≥ 10 cm in DBH



B Trees ≥ 5 cm in DBH



C Saplings 1–4.9 cm in DBH

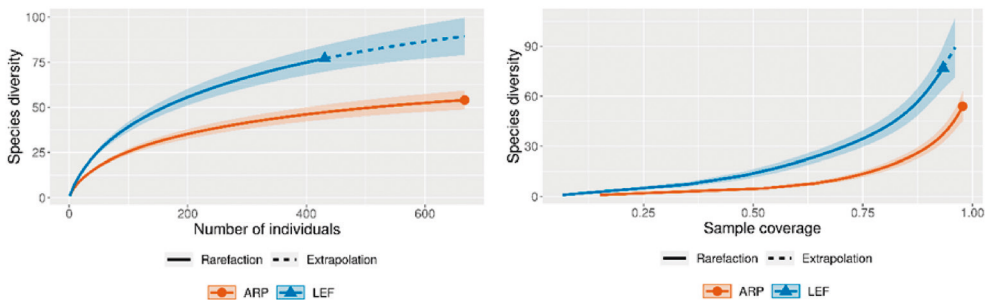
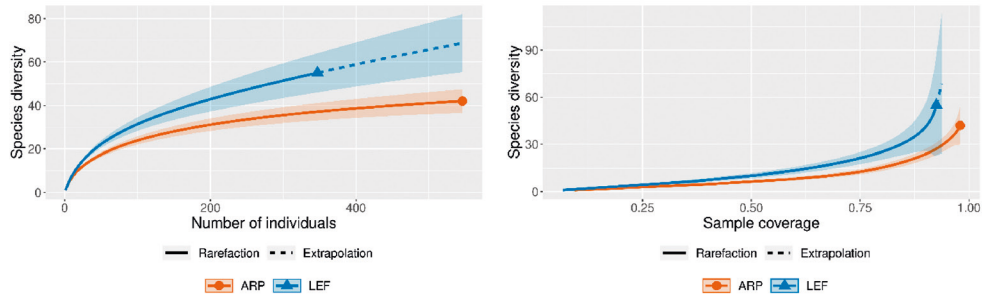


Figure 5. Sample-size-based (left) and coverage-based (right) rarefaction or extrapolation curves for ARP and LEF, for A, trees ≥ 10 cm; B, trees ≥ 5 cm in DBH; and C, saplings 1–4.9 cm DBH. Alien species are excluded from the ARP. Shaded areas indicate approximate 95% confidence limits with 200 bootstrap replications. See Table 3 for species richness values and other data.

A Seedlings <1 cm in DBH



B Ground flora

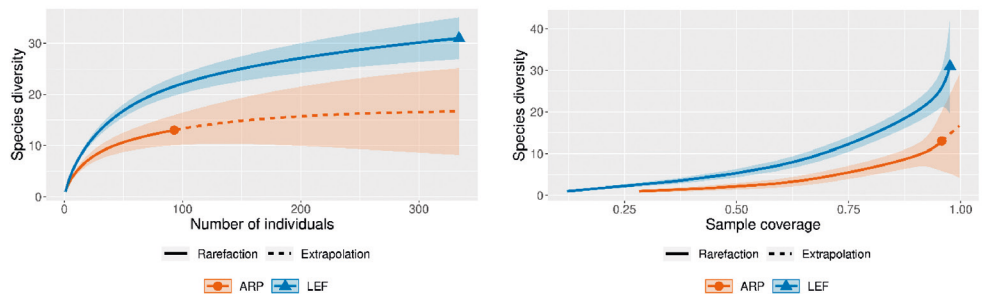


Figure 6. Sample-size-based (left) and coverage-based (right) rarefaction or extrapolation curves for ARP and LEF, for A, seedlings; and B, ground herb vegetation. Shaded areas indicate approximate 95% confidence limits with 200 bootstrap replications. Alien species are excluded from ARP. See Table 3 for species richness values and other data.

Flora of the Logged Dry Evergreen Forest (LEF)

In the LEF, there were 558 woody plant stems of 69 (including six liana) species, 466 sapling stems of 85 species in 0.10 ha of circular quadrats, and 642 stems of 76 species of seedlings in 0.01 ha of circular plots (Table 2 and Figure 3). Since commercial hardwood tree species had been logged during 1967–1977, it is not surprising that few stems of such large trees remained. Only *Dipterocarpus dyeri* was found (two trees, five seedlings; Table 6, Appendix). The common pioneer tree, *Macaranga tanarius* was the most abundant tree ≥ 10 cm DBH with 79 stems/ha, closely followed by *Arenga westerhoutii* (55 stems), a large palm which dominated the slopes above 200 m in elevation (Table 6), followed by the deciduous tree *Pterocymbium tinctorium*. *P. tinctorium*, however, was the most numerous of the small trees (5–10 cm in DBH). In the sapling layer, *Mallotus peltatus* had the highest density (84 stems/0.1 ha). The seedling layer was relatively rich with 76 woody plant species represented (Table 2).

Comparison of the ARP and LEF

The total number of trees of native species ≥ 5 cm DBH did not differ significantly between the sites ($P > 0.05$; Mann Whitney U test comparing 100 samples in each area). Table 4 compares the similarity in species composition between sites, using both presence/absence and percentage similarity indices. Similarity in species present ranged from 16% to 34%, and percentage similarity from 12% (herbaceous ground flora) to 19% (seedlings). Saplings had lower similarities than did trees. The similarity between ARP and LEF in species composition depended on the test used and on the stratum being compared. Overall, 89 species were found in both habitats, whereas 86 species were found only in the LEF and 48 species only in the ARP. Jaccard's similarity index revealed highest similarity in the tree stratum, followed by seedlings, saplings and ground herbs (Table 4). The abundance-based similarity index of CHAO *ET AL.* (2005) ranked the strata differently, with the seedlings showing highest similarity, followed by saplings. We believe this discrepancy is due to relatively low sample sizes and the relatively high sample variation in counts of singletons and doubletons (species with only one or two stems in the samples) in the species counts. High sample error is especially common in communities with many rare species (CHAO *ET AL.*, 2005), and is a major reason why virtually all similarity indices have strong downward bias. The value of 0.47 for seedling similarity seems high, but it is a sign that much larger sample sizes are needed, to measure true similarity in such a high-diversity landscape. The percentage similarity index also ranked seedlings as having highest similarity between habitats.

Burning in ARP had probably diminished the seed bank there, compared with the LEF. However, resprouts from underground roots and stumps were a source of tree stems of ten mostly canopy species in the ARP; a source of regeneration not observed in the LEF (Table 7).

A final comparison between the habitats was made in the size distributions (cm DBH) of trees and saplings (Figure 8). In both categories, the LEF distribution was more even (relatively more large trees and fewer small trees). Although the overall density of trees was lower in LEF, the LEF tended to have relatively more old trees indicative of a more mature size structure, or less severe disturbance.

Finally, we compare the species in the ARP and LEF with respect to seed dispersal mechanisms. The frequency of seed-dispersal mechanisms was similar in both sites. Of the 120 native, woody species recorded in the ARP, 80 (66.7%) were animal-dispersed, 21 (17.5%) were wind-dispersed and 20 (16.7%) were gravity-dispersed or unknown. For the LEF, of 140 non-vine woody species recorded, 92 (65.7%) were animal-dispersed, 19 (13.6%) were wind-dispersed and 29 (20.7%) were gravity-dispersed or unknown. For only trees and shrubs ≥ 5 cm in DBH, however, 73% of species in the ARP were animal dispersed, compared with 79% in the LEF.

Mammal and Bird Faunas

Mammals and birds were substantially more abundant in LEF than in ARP by 167% and 87%, respectively. Species richness in LEF was also much higher (by 54% and 37%), compared with ARP, although species diversity was only marginally higher (17% and 8%) (Table 8). Twenty mammal species representing 13 families were recorded in the LEF

Table 5. Woody plant species with DBH ≥ 10 cm in abandoned rubber plantations (ARP). Maximum DBH, Density (stem/ha), Frequency (no. of plots), and Basal area (BA in m²/ha).

Botanical name (family)	Max. DBH	Density (relative den., %)	Frequency	Basal area (relative BA, %)
<i>Leucaena leucocephala</i> (Fabaceae)	40.9	194 (38.8)	60	4.03 (33.6)
<i>Hevea brasiliensis</i> (Euphorbiaceae)	53.0	52 (10.4)	24	2.07 (17.3)
<i>Streblus asper</i> (Moraceae)	36.6	44 (8.8)	26	0.79 (6.6)
<i>Pterocymbium tinctorium</i> (Sterculiaceae)	83.1	22 (4.4)	13	1.04 (8.7)
<i>Microcos paniculata</i> (Tiliaceae)	18.9	21 (4.2)	16	0.29 (2.5)
<i>Bauhinia bracteata</i> (Fabaceae)	19.7	17 (3.4)	14	0.27 (2.3)
<i>Lagerstroemia cochinchinensis</i> (Lythraceae)	24.0	16 (3.2)	12	0.29 (2.4)
<i>Sterculia pexa</i> (Sterculiaceae)	27.7	15 (3.0)	12	0.40 (3.3)
<i>Adenantha microsperma</i> (Fabaceae)	30.6	9 (1.8)	8	0.32 (2.7)
<i>Pterospermum grande</i> (Sterculiaceae)	24.4	7 (1.4)	4	0.14 (1.2)
<i>Azelia xylocarpa</i> (Fabaceae)	14.0	6 (1.2)	4	0.08 (0.6)
<i>Vitex peduncularis</i> (Verbenaceae)	16.6	6 (1.2)	3	0.08 (0.7)
<i>Artocarpus gomezianus</i> (Moraceae)	31.3	5 (1.0)	4	0.18 (1.5)
<i>Stereospermum fimbriatum</i> (Bignoniaceae)	21.8	5 (1.0)	5	0.10 (0.9)
<i>Wrightia arborea</i> (Apocynaceae)	17.6	5 (1.0)	5	0.07 (0.6)
<i>Hymenodictyon orixense</i> (Rubiaceae)	15.0	4 (0.8)	4	0.05 (0.4)
<i>Lepisanthes rubiginosa</i> (Sapindaceae)	15.0	4 (0.8)	4	0.05 (0.4)
<i>Aglaiia elaeagnoidea</i> (Meliaceae)	12.4	3 (0.6)	2	0.03 (0.3)
<i>Dimocarpus longan</i> (Sapindaceae)	24.8	3 (0.6)	2	0.08 (0.6)
<i>Diospyros ferrea</i> (Ebenaceae)	16.3	3 (0.6)	3	0.04 (0.4)
<i>Erythrina subumbrans</i> (Fabaceae)	52.0	3 (0.6)	3	0.31 (2.6)
<i>Harrisonia perforata</i> (Simaroubaceae)	17.5	3 (0.6)	2	0.05 (0.4)
<i>Hibiscus macrophyllus</i> (Malvaceae)	19.1	3 (0.6)	2	0.05 (0.4)
<i>Sphenodesme pentandra</i> (Verbenaceae)	15.0	3 (0.6)	3	0.04 (0.3)
<i>Bridelia stipularis</i> (Euphorbiaceae)	16.9	2 (0.4)	1	0.04 (0.3)
<i>Bridelia tomentosa</i> (Euphorbiaceae)	20.1	2 (0.4)	2	0.04 (0.3)
<i>Capparis micracantha</i> (Capparaceae)	14.7	2 (0.4)	1	0.03 (0.3)
<i>Caryota urens</i> (Arecaceae)	12.1	2 (0.4)	2	0.02 (0.2)
<i>Mallotus philippensis</i> (Euphorbiaceae)	11.9	2 (0.4)	2	0.02 (0.2)
<i>Nephelium melliferum</i> (Sapindaceae)	37.2	2 (0.4)	2	0.18 (1.5)
<i>Picrasma javanica</i> (Simaroubaceae)	35.3	2 (0.4)	2	0.15 (1.2)
<i>Pterospermum cinnamomum</i> (Sterculiaceae)	23.2	2 (0.4)	1	0.06 (0.5)
<i>Sandoricum koetjape</i> (Meliaceae)	15.5	2 (0.4)	2	0.03 (0.3)
<i>Sterculia balanghas</i> (Sterculiaceae)	19.9	2 (0.4)	2	0.04 (0.3)
<i>Streblus ilicifolius</i> (Moraceae)	25.2	2 (0.4)	2	0.06 (0.5)
<i>Toona ciliata</i> (Meliaceae)	16.4	2 (0.4)	2	0.04 (0.3)
<i>Ventilago denticulata</i> (Rhamnaceae)	12.0	2 (0.4)	2	0.02 (0.2)
<i>Alangium salvifolium</i> (Alangiaceae)	20.5	1 (0.2)	1	0.03 (0.3)
<i>Alchornea rugosa</i> (Euphorbiaceae)	53.0	1 (0.2)	1	0.22 (1.8)
<i>Artocarpus heterophyllus</i> (Moraceae)	11.6	1 (0.2)	1	0.01 (0.1)
<i>Artocarpus rigidus</i> (Moraceae)	12.4	1 (0.2)	1	0.01 (0.1)
<i>Beilschmiedia</i> aff. <i>intermedia</i> (Lauraceae)	19.0	1 (0.2)	1	0.03 (0.2)
<i>Cassia fistula</i> (Fabaceae)	13.0	1 (0.2)	1	0.01 (0.1)

Table 5 (continued).

Botanical name (family)	Max. DBH	Density (relative den., %)	Frequency	Basal area (relative BA, %)
<i>Chisocheton cumingianus</i> (Meliaceae)	14.6	1 (0.2)	1	0.02 (0.1)
<i>Delonix regia</i> (Fabaceae)	10.4	1 (0.2)	1	0.01 (0.1)
<i>Desmos chinensis</i> (Annonaceae)	12.1	1 (0.2)	1	0.01 (0.1)
<i>Diospyros glandulosa</i> (Ebenaceae)	11.3	1 (0.2)	1	0.01 (0.1)
<i>Erismanthus sinensis</i> (Euphorbiaceae)	18.5	1 (0.2)	1	0.03 (0.2)
<i>Erycibe elliptilimba</i> (Convolvulaceae)	10.2	1 (0.2)	1	0.01 (0.1)
<i>Heteropanax fragrans</i> (Araliaceae)	20.2	1 (0.2)	1	0.03 (0.3)
<i>Litsea</i> sp. (Lauraceae)	11.1	1 (0.2)	1	0.01 (0.1)
<i>Macaranga siamensis</i> (Euphorbiaceae)	12.7	1 (0.2)	1	0.01 (0.1)
<i>Mallotus peltatus</i> (Euphorbiaceae)	17.8	1 (0.2)	1	0.02 (0.2)
<i>Suregada multiflora</i> (Euphorbiaceae)	11.5	1 (0.2)	1	0.01 (0.1)

Table 6. Woody plant species with DBH ≥ 10 cm in logged evergreen forest (LEF). Maximum DBH, Density (stem/ha), Frequency (no. of plots), and Basal area (BA in m²/ha).

Botanical name (family)	Max. DBH	Density (relative den., %)	Frequency	Basal area (relative BA, %)
<i>Macaranga tanarius</i> (Euphorbiaceae)	54.9	79 (24.5)	54	5.76 (41.4)
<i>Arenga westerhoutii</i> (Arecaceae)	58.6	55 (17.1)	40	2.73 (19.6)
<i>Pterocymbium tinctorium</i> (Sterculiaceae)	37.4	27 (8.4)	21	0.92 (6.6)
<i>Picrasma javanica</i> (Simaroubaceae)	31.5	12 (3.7)	10	0.34 (2.5)
<i>Artocarpus gomezianus</i> (Moraceae)	27.4	10 (3.1)	8	0.27 (2.0)
<i>Ficus vasculosa</i> (Moraceae)	36.9	10 (3.1)	10	0.52 (3.8)
<i>Cleidion javanicum</i> (Euphorbiaceae)	28.5	9 (2.8)	8	0.19 (1.4)
<i>Macaranga siamensis</i> (Euphorbiaceae)	38.4	9 (2.8)	8	0.38 (2.7)
<i>Horsfieldia irya</i> (Myristicaceae)	28.9	8 (2.5)	7	0.26 (1.8)
<i>Nephelium melliferum</i> (Sapindaceae)	26.7	7 (2.2)	7	0.21 (1.5)
<i>Sterculia pexa</i> (Sterculiaceae)	25.0	7 (2.2)	5	0.17 (1.3)
<i>Alstonia scholaris</i> (Apocynaceae)	21.1	6 (1.9)	5	0.13 (0.9)
<i>Stereospermum fimbriatum</i> (Bignoniaceae)	21.2	6 (1.9)	4	0.11 (0.8)
<i>Mallotus philippensis</i> (Euphorbiaceae)	20.0	5 (1.6)	5	0.07 (0.5)
<i>Heteropanax fragrans</i> (Araliaceae)	12.9	4 (1.2)	4	0.05 (0.3)
<i>Semecarpus albescens</i> (Anacardiaceae)	15.9	4 (1.2)	1	0.05 (0.4)
<i>Sterculia balanghas</i> (Sterculiaceae)	22.0	4 (1.2)	3	0.08 (0.6)
<i>Toona ciliata</i> (Meliaceae)	35.9	4 (1.2)	4	0.21 (1.5)
<i>Xerospermum noronhianum</i> (Sapindaceae)	14.3	4 (1.2)	4	0.04 (0.3)
<i>Baccaurea ramiflora</i> (Euphorbiaceae)	18.0	3 (0.9)	3	0.05 (0.4)
<i>Caryota urens</i> (Arecaceae)	12.1	3 (0.9)	3	0.03 (0.2)
<i>Ficus fistulosa</i> (Moraceae)	22.5	3 (0.9)	3	0.06 (0.5)
<i>Hibiscus macrophyllus</i> (Malvaceae)	30.9	3 (0.9)	3	0.14 (1.0)
<i>Aglai lawii</i> (Meliaceae)	21.2	2 (0.6)	2	0.05 (0.3)
<i>Castanopsis</i> sp. (Fagaceae)	26.7	2 (0.6)	2	0.07 (0.5)
<i>Dipterocarpus dyeri</i> (Dipterocarpaceae)	28.5	2 (0.6)	2	0.10 (0.8)
<i>Eugenia cerasoides</i> (Myrtaceae)	16.4	2 (0.6)	2	0.03 (0.2)
<i>Mallotus peltatus</i> (Euphorbiaceae)	13.4	2 (0.6)	2	0.03 (0.2)

Table 6 (continued).

Botanical name (family)	Max. DBH	Density (relative den., %)	Frequency	Basal area (relative BA, %)
<i>Pterospermum grande</i> (Sterculiaceae)	18.8	2 (0.6)	2	0.04 (0.3)
<i>Alchornea rugosa</i> (Euphorbiaceae)	10.3	1 (0.3)	1	0.01 (0.1)
<i>Aphanamixis polystachya</i> (Meliaceae)	11.1	1 (0.3)	1	0.01 (0.1)
<i>Dasydaschalon acuminatum</i> (Annonaceae)	24.8	1 (0.3)	1	0.05 (0.4)
<i>Diospyros malabarica</i> (Ebenaceae)	10.4	1 (0.3)	1	0.01 (0.1)
<i>Duabanga grandiflora</i> (Sonneratiaceae)	25.0	1 (0.3)	1	0.05 (0.4)
<i>Elaeocarpus sphaericus</i> (Elaeocarpaceae)	12.6	1 (0.3)	1	0.01 (0.1)
<i>Erycibe elliptilimba</i> (Convolvulaceae)	10.2	1 (0.3)	1	0.01 (0.1)
<i>Erythrina subumbrans</i> (Fabaceae)	27.7	1 (0.3)	1	0.06 (0.4)
<i>Ficus callosa</i> (Moraceae)	23.9	1 (0.3)	1	0.04 (0.3)
<i>Ficus hispida</i> (Moraceae)	13.1	1 (0.3)	1	0.01 (0.1)
<i>Garcinia xanthochymus</i> (Guttiferae)	14.6	1 (0.3)	1	0.02 (0.1)
<i>Gonocaryum lobbianum</i> (Icacinales)	10.5	1 (0.3)	1	0.01 (0.1)
<i>Gouania leptostachya</i> (Rhamnaceae)	10.4	1 (0.3)	1	0.01 (0.1)
<i>Irvingia malayana</i> (Irvingiaceae)	53.8	1 (0.3)	1	0.23 (1.6)
<i>Knema lenta</i> (Myristicaceae)	22.6	1 (0.3)	1	0.04 (0.3)
<i>Knema tenuinervia</i> (Myristicaceae)	19.8	1 (0.3)	1	0.03 (0.2)
<i>Lithocarpus polystachyus</i> (Fagaceae)	19.1	1 (0.3)	1	0.03 (0.2)
<i>Litsea</i> sp. (Lauraceae)	15.3	1 (0.3)	1	0.02 (0.1)
<i>Microcos paniculata</i> (Tiliaceae)	10.7	1 (0.3)	1	0.01 (0.1)
<i>Mitrephora vandaeflora</i> (Annonaceae)	24.5	1 (0.3)	1	0.05 (0.3)
<i>Palaquium</i> sp. (Sapotaceae)	11.8	1 (0.3)	1	0.01 (0.1)
<i>Phoebe lanceolata</i> (Lauraceae)	14.4	1 (0.3)	1	0.02 (0.1)
<i>Quisqualis indica</i> (Combretaceae)	12.1	1 (0.3)	1	0.01 (0.1)
<i>Sandoricum koetjape</i> (Meliaceae)	10.7	1 (0.3)	1	0.01 (0.1)
<i>Streblus asper</i> (Moraceae)	22.1	1 (0.3)	1	0.04 (0.3)
<i>Ventilago denticulata</i> (Rhamnaceae)	13.9	1 (0.3)	1	0.02 (0.1)
<i>Walsura trichostemon</i> (Meliaceae)	12.0	1 (0.3)	1	0.01 (0.1)
<i>Wrightia arborea</i> (Apocynaceae)	10.4	1 (0.3)	1	0.01 (0.1)

(Table 9). Rodentia was the most speciose order with seven species recorded: three squirrels, three rats and a porcupine. Chiroptera (bats) was represented by five species, two of them fruit eaters. Civets (Viverridae) were represented by two species, which are omnivorous. Of particular importance was the presence of the long-tailed macaque (*Macaca fascicularis*), which has a broad diet including diverse fruits.

Mammals in ARP were a smaller subset of the same species recorded in LEF, missing seven species. Thirteen species in eight families were recorded (Tables 8 and 9). Rodentia was represented by the most species, including all the species recorded in LEF except the bandicoot rat. Civets (Viverridae) included the same two species. Only two of the five bat species recorded in LEF were also recorded in ARP: the fruit bat *Cynopterus sphinx* and critically important pollinator, *Eonycteris spelaea* was found in the ARP as well as in LEF.

The LEF yielded 93 species of birds in 40 families (Tables 8 and 10). Of particular importance were fruit eaters, potential seed dispersal agents, which included three species of barbets, the parrot *Loriculus vernalis*, three doves/pigeons, one oriole, one forest myna (the fruit-eating hill myna), six species of bulbuls, and four species of flowerpeckers.

Birds in the ARP included 68 species in 29 families (Tables 8 and 10). Fruit eaters and possible seed dispersers included the same four species of barbets, the parrot *L. vernalis*, two doves, the oriole, the hill myna, six species of bulbuls and two flowerpeckers.

DISCUSSION

The Return of Species Diversity

The species diversity of both study sites has been reduced, although in strikingly different ways. The clearing and burning of the former rubber plantation must have reduced the original species diversity to zero, except perhaps for a few weeds. All native species that exist there now are colonists from nearby environments. Logging reduced species diversity in the LEF by an unknown amount, and the species there now are survivors of the logging era or colonizers from the surrounding forest matrix. Neither forest area is expected to have attained the species diversity and structure of its predisturbance form, which, unfortunately, can no longer be precisely determined due to lack of primary forest in the local region. First, we discuss factors affecting succession of the abandoned rubber plantation. The logged forest site serves as a partial control since it was not completely destroyed and converted.

By nearly all measures, the LEF supported higher species richness and diversity (Shannon-Wiener diversity) than the ARP, an expected result given the total destruction of the latter. Clearing and burning of forest change soil-nutrient cycles and the physical, chemical, and biological properties of soil (GIARDINA *ET AL.*, 2000; NORRGROVE & HAUSER, 2015; HATTORI *ET AL.*, 2019). Rubber tree cultivation likely changed the soil so that only a small subset of species could establish and persist under the changed conditions. Forest conversion to rubber plantations negatively impacts soil fertility by changing carbon stocks and microbial biomass (MONKAI *ET AL.*, 2018; DRESCHER *ET AL.*, 2016; ZHANG & ZHANG, 2003, 2005; ZHANG *ET AL.*, 2007). It is well known that the trajectory of ecological succession can be drastically altered by repeated fires (e.g., UHL & JORDAN, 1984; UHL & KAUFFMAN, 1990; COCHRANE & SCHULTZ, 1999; CHAZDON, 2014). Further research is needed to compare those soil and microclimate conditions that define the niches of the species that grow in the two sites and thus explain differences in species composition.

The higher species richness of the LEF compared with the ARP was most pronounced in the sapling and seedling categories, and the ground herb stratum. The tree strata of the two sites were about equally species-rich, a result which is difficult to explain. We speculate that the very dense ground vegetation of the LEF, including an abundance of grasses (which we did not sample) repressed recruitment of young trees. Alternatively, the severity of logging may have reduced overall tree diversity, although it should not have affected the rate of recolonization by the exploited species.

In spite of continued dominance of introduced nonnative species, the ARP is being colonized by native species, as is evident from the long list of species in the sapling and seedling layers. These colonizers, though mostly still uncommon, attest to the importance of

the mammal and bird communities that inhabit both sites. The proportion of zoochorous tree and shrub species was above 70% and virtually the same in both sites. The available species pool of immigrants is determined by the surrounding communities from which seeds carried by wind and animals colonize the area (ZOBEL, 1997; PRACH & WALKER, 2020), and hence the surrounding landscape is an important factor in predicting the path of succession (CHAZDON *ET AL.*, 2009; MELO *ET AL.*, 2013; PRACH *ET AL.*, 2015). The proximity of the ARP to natural forest, even if degraded, was probably a factor in its relatively rapid succession.

Both the ARP and the LEF have become dominated by early successional species; in the LEF these include *Macaranga tanarius*, *Mallotus* spp., *Cleidion javanicum*, *Trevesia palmata* and *Ardisia ionantha*. The ARP succession involves species not found in the LEF, led by *Leucaena leucocephala*, and including *Streblus asper* and *Aphanamixis polystachya*. Interestingly, these same three species were found to be increasing in abundance during succession on the dry evergreen forest plot at Wang Nam Khiao Forestry Research and Training Center, Nakhon Ratchasima Province, between surveys conducted in 2002 and 2016 (PHUMPHUANG *ET AL.*, 2018). *Streblus ilicifolius*, which dominated the ARP sapling layer, was also common in the sapling layer of the Wang Nam Khiao site. There are numerous other floristic resemblances between these two sites.

Comparison with Other Forests

It is of interest to know how similar the species richness and diversity, and forest structure, are to other undisturbed forests of similar type in the region. Forest attributes should be compared with continental lowland forests of similar latitude and climate. Such forests in Thailand are variously referred to as dry evergreen, seasonal evergreen (of at least two subtypes), seasonal dry evergreen, and semi-evergreen forests. There are no precise definitions of these overlapping types, which appear to grade into one another. We compare our forest stands with several others in Central and Southeast Thailand that have been studied using the same methods of measuring trees, and reported quantitative data per hectare.

BUNYAVEJCHEWIN (1999) reported on the structure, species richness, and dynamics of two 1-ha stands of “seasonal dry evergreen forest” at the Sakaerat Environmental Research Station in Nakhon Ratchasima Province, just east of Khao Yai National Park at 14°30′N latitude. The area received annual rainfall of 1,240 mm, similar to our site, but the plots were slightly higher in altitude (460–540 m.s.l.). The two plots were dominated by different species of dipterocarps: the lower one by *Hopea ferrea*, and the upper one by *Shorea henryana*, along with *Hydnocarpus ilicifolius* (none of these species was present in our plots). The two plots were inventoried during two periods (1987 and 1997) 10 years apart. Species richness of stems ≥ 4.5 cm in DBH of the lower plot had declined from 76 to 65 species, and had increased from 100 to 111 species in the upper plot. The numbers from the lower *Hopea ferrea* plot are in a range similar to the LEF (63 species) and ARP (73 species) plots. The average stem densities, however, in the *Hopea ferrea* plot (1,142) and the *Shorea henryana* plot (1,253) were about twice as high as the densities on the LEF plot (544) and ARP plot (618). The basal areas of the Sakaerat plots averaged around 29 m²/ha, higher than the LEF plot (23.4) and ARP plot (14.3). This is to be expected, as average tree sizes were larger on the more mature Sakaerat plots. Thus, although the species compositions of the Sakaerat plots differed greatly from ours, species richness was not very dissimilar and differences in other characteristics suggested the younger successional status of our plots. The relatively low native stem density of the ARP plot reflects competition from *Leucaena leucocephala* which had 322 stems.

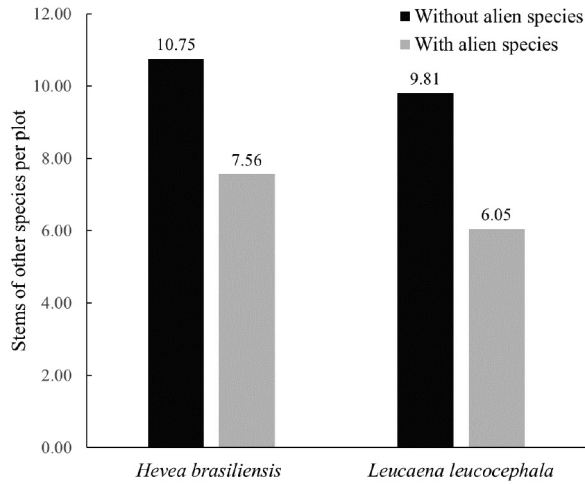


Figure 7. Number of stems of other tree species with >5 cm DBH per plot with and without *Hevea brasiliensis* and with and without *Leucaena leucocephala*.

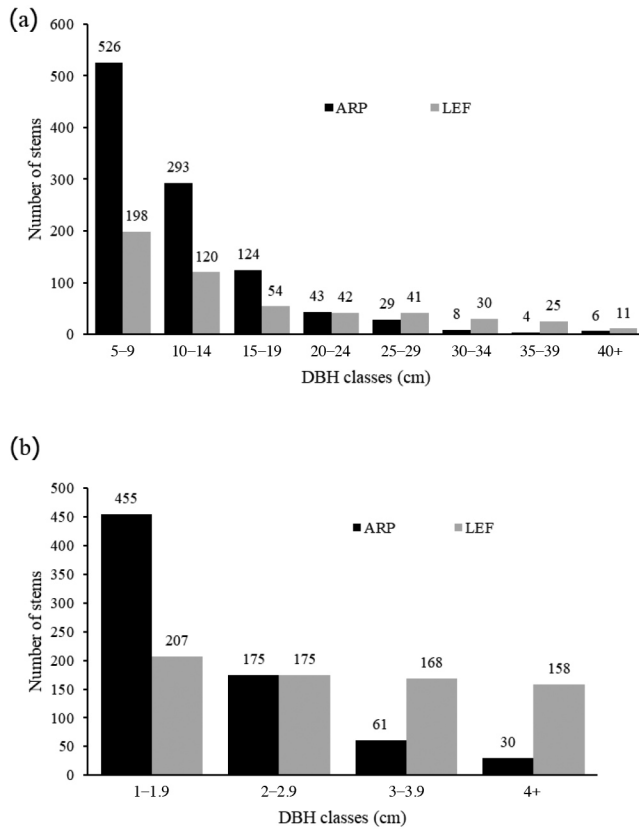


Figure 8. Frequency of stems of trees (a) and saplings (b) in different DBH classes compared between abandoned rubber plantation (ARP) and logged evergreen forest (LEF).

Table 7. Tree species sprouting from stumps (CT = Canopy Tree, UT = Understory Tree).

Species	N (stumps)	DBH of sprouts (cm)
<i>Hevea brasiliensis</i> (Euphorbiaceae), CT	3	1.0, 1.2, 2.5
<i>Streblus ilicifolius</i> (Moraceae), UT	3	1.0, 1.1, 1.9
<i>Leucaena leucocephala</i> (Fabaceae), UT	2	2.3, 5.9
<i>Microcos paniculata</i> (Tiliaceae), CT	1	1.0
<i>Ellipanthus tomentosus</i> (Connaraceae), UT	1	1.5
<i>Irvingia malayana</i> (Irvingiaceae), CT	1	1.7
<i>Polyalthia</i> sp. (Annonaceae), CT	1	1.9
<i>Diospyros malabarica</i> (Ebenaceae), CT	1	2.1
<i>Streblus asper</i> (Moraceae), CT	1	3.1
<i>Diospyros ferrea</i> (Ebenaceae), CT	1	4.1

Table 8. Diversity of mammal and bird faunas in logged evergreen forest (LEF) and abandoned rubber plantation (ARP).

Habitats	Mammals				Birds			
	N	Species	H'	Evenness	N	Species	H'	Evenness
LEF	120	20	2.59	0.86	561	93	4.30	0.95
ARP	45	13	2.21	0.88	300	68	3.99	0.94

Table 9. Number of mammals found in the abandoned rubber plantation (ARP) and logged evergreen forest (LEF).

Order	Family	Scientific name	ARP	LEF
Polidota	Manidae	<i>Manis javanica</i> (Desmarest, 1822)	0	4
Insectivora	Soricidae	<i>Suncus etruscus</i> (Savi, 1822)	0	3
Scandentia	Tupaiaidae	<i>Tupaia belangeri</i> (Wagner, 1841)	5	10
Primates	Cercopithecidae	<i>Macaca fascicularis</i> (Raffles, 1821)	0	4
Chiroptera	Pteropodidae	<i>Cynopterus sphinx</i> (Vahl, 1797)	2	4
		<i>Eonycteris spelaea</i> (Dobson, 1871)	2	3
		<i>Pteropus lylei</i> (Andersen, 1908)	0	2
	Vespertilionidae	<i>Kerivoula picta</i> (Pallas, 1767)	0	1
	Hipposideridae	<i>Hipposideros pomona</i> (Andersen, 1918)	0	2
	Carnivora	Viverridae	<i>Viverricula indica</i> (Desmarest, 1817)	2
<i>Paguma larvata</i> (Smith, 1827)			1	3
Herpestidae		<i>Herpestes javanicus</i> (Geoffroy, 1818)	1	3
Artiodactyla	Suidae	<i>Sus scrofa</i> (Linnaeus, 1758)	2	2
Rodentia	Sciuridae	<i>Callosciurus finlaysonii</i> (Horsfield, 1823)	5	8
		<i>Menetes berdmorei</i> (Blyth, 1849)	9	24
		<i>Tamiops rodolphei</i> (Milne-Edwards, 1867)	10	16
	Muridae	<i>Rattus rattus</i> (Linnaeus, 1758)	4	19
		<i>Bandicota savilei</i> (Thomas, 1916)	0	3
		<i>Rattus losea</i> (Swinhoe, 1871)	1	1
		<i>Hystrix brachyura</i> (Linnaeus, 1758)	1	4

Table 10. Number of birds in study trails in abandoned rubber plantation (ARP) and logged evergreen forest (LEF).

Order	Family	Scientific names of birds	ARP	LEF
Galliformes	Phasianidae	<i>Arborophila chloropus</i> (Blyth, 1859)	0	5
		<i>Gallus gallus</i> (Linnaeus, 1758)	2	3
Piciformes	Megalaimidae	<i>Megalaima lineata</i> (Vieillot, 1816)	8	12
		<i>Megalaima faiostricta</i> (Temminck, 1831)	7	11
		<i>Megalaima australis</i> (Horsfield, 1821)	6	12
		<i>Megalaima haemacephala</i> (Muller, 1776)	3	2
Coraciiformes	Alcedinidae	<i>Alcedo atthis</i> (Linnaeus, 1758)	0	1
Coraciiformes	Meropidae	<i>Merops orientalis</i> (Latham, 1801)	3	6
		<i>Merops leschenaulti</i> (Vieillot, 1817)	17	13
Cuculiformes	Cuculidae	<i>Cacomantis merulinus</i> (Scopoli, 1786)	3	1
		<i>Cacomantis sonneratii</i> (Latham, 1790)	1	3
		<i>Phaenicophaeus tristis</i> (Lesson, 1830)	5	6
		<i>Eudynamys scolopacea</i> (Linnaeus, 1758)	2	1
		<i>Centropus sinensis</i> (Stephens, 1815)	2	5
Psittaciformes	Psittaculidae	<i>Loriculus vernalis</i> (Sparman, 1787)	3	6
Apodiformes	Apodidae	<i>Cypsiurus balasinensis</i> (Gray, 1829)	0	4
		<i>Apus affinis</i> (Gray, 1830)	0	2
		<i>Collocalia germani</i> (Oustalet, 1876)	0	8
Strigiformes	Tytonidae	<i>Phodilus badius</i> (Horsfield, 1821)	1	3
	Strigidae	<i>Glaucidium cuculoides</i> (Vigors, 1831)	4	7
		<i>Otus lettia</i> (Pennant, 1769)	3	4
		<i>Ninox scutulata</i> (Raffles, 1822)	1	5
Caprimulgiformes	Caprimulgidae	<i>Caprimulgus macrurus</i> (Horsfield, 1821)	0	1
Columbiformes	Columbidae	<i>Streptopelia chinensis</i> (Scopoli, 1786)	2	1
		<i>Chalcophaps indica</i> (Linnaeus, 1758)	5	13
		<i>Treron curvirostra</i> (Gmelin, 1789)	0	8
Gruiformes	Rallidae	<i>Amaurornis phoenicurus</i> (Pennant, 1769)	0	3
Accipitriformes	Accipitridae	<i>Spilornis cheela</i> (Latham, 1790)	2	4
		<i>Accipiter badius</i> (Gmelin, 1788)	3	8
		<i>Butastur indicus</i> (Gmelin, 1788)	0	1
Falconiformes	Falconidae	<i>Falco tinnunculus</i> (Linnaeus, 1758)	0	1
Pelecaniformes	Ardeidae	<i>Ardeola bacchus</i> (Bonaparte, 1855)	0	1
		<i>Ardeola speciosa</i> (Horsfield, 1821)	0	3
Passeriformes	Eurylaimidae	<i>Serilophus lunatus</i> (Gould, 1834)	0	6
		<i>Corydon sumatranus</i> (Raffles, 1822)	0	5
	Pittidae	<i>Pitta moluccensis</i> (Muller, 1776)	2	13
		<i>Pitta sordida</i> (Statius Müller, 1776)	0	8
	Laniidae	<i>Lanius cristatus</i> (Linnaeus, 1758)	3	5
	Corvidae	<i>Crypsirina temia</i> (Daudin, 1800)	7	11
		<i>Corvus macrorhynchos</i> (Wagler, 1827)	0	2
		<i>Cissa chinensis</i> (Boddaert, 1783)	1	3

Table 10 (continued).

Order	Family	Scientific names of birds	ARP	LEF
	Artamidae	<i>Artamus fuscus</i> (Vieillot, 1817)	2	6
	Oriolidae	<i>Oriolus chinensis</i> (Linnaeus, 1766)	5	8
	Chloropseidae	<i>Chloropsis aurifrons</i> (Temminck, 1829)	0	7
	Rhipiduridae	<i>Rhipidura javanica</i> (Sparrman, 1788)	4	8
	Dicruridae	<i>Dicrurus leucophaeus</i> (Vieillot, 1817)	5	10
		<i>Dicrurus hottentottus</i> (Linnaeus, 1766)	3	4
		<i>Dicrurus paradiseus</i> (Linnaeus, 1766)	7	13
	Monarchidae	<i>Hypothymis azurea</i> (Boddaert, 1783)	5	7
	Aegithinidae	<i>Aegithina tiphia</i> (Linnaeus, 1758)	5	6
	Muscicapidae	<i>Muscicapa sibirica</i> (Gmelin, 1789)	3	1
		<i>Muscicapa dauurica</i> (Pallas, 1811)	4	8
		<i>Ficedula parva</i> (Bechstein, 1792)	4	5
		<i>Eumyias thalassina</i> (Swainson, 1838)	0	2
		<i>Cyornis tickelliae</i> (Blyth, 1843)	9	11
		<i>Copsychus saularis</i> (Linnaeus, 1758)	1	1
		<i>Copsychus malabaricus</i> (Scopoli, 1788)	5	5
	Sturnidae	<i>Gracula religiosa</i> (Linnaeus, 1758)	7	10
	Hirundinidae	<i>Hirundo rustica</i> (Linnaeus, 1758)	0	2
	Pycnonotidae	<i>Pycnonotus aurigaster</i> (Vieillot, 1818)	5	5
		<i>Pycnonotus melanicterus</i> (Gmelin, 1789)	15	6
		<i>Pycnonotus finlaysoni</i> (Strickland, 1844)	6	8
		<i>Pycnonotus blanfordi</i> (Jerdon, 1862)	6	6
		<i>Pycnonotus atriceps</i> (Temminck, 1822)	6	7
		<i>Pycnonotus goiavier</i> (Scopoli, 1786)	1	0
		<i>Alophoixus ochraceus</i> (Moore, 1854)	0	1
	Cisticolidae	<i>Orthotomus sutorius</i> (Pennant, 1769)	3	10
		<i>Orthotomus atrogularis</i> (Temminck, 1836)	1	7
	Acrocephalidae	<i>Acrocephalus orientalis</i> (Temminck and Schlegel, 1847)	0	3
		<i>Acrocephalus aedon</i> (Pallas, 1776)	0	3
	Phylloscopidae	<i>Phylloscopus fuscatus</i> (Blyth, 1842)	2	3
		<i>Phylloscopus schwarzi</i> (Radde, 1863)	4	5
		<i>Phylloscopus nornatus</i> (Blyth, 1842)	3	6
		<i>Phylloscopus borealis</i> (Blasius, 1858)	3	8
		<i>Phylloscopus trochiloides</i> (Sundevall, 1837)	1	5
		<i>Phylloscopus plumbeitarsus</i> (Swinhoe, 1861)	6	10
		<i>Phylloscopus tenellipes</i> (Swinhoe, 1860)	3	6
	Timaliidae	<i>Macronous gularis</i> (Horsfield, 1822)	6	16
	Leiotrichidae	<i>Garrulax leucolophus</i> (Hardwicke, 1815)	19	27
		<i>Garrulax pectoralis</i> (Gould, 1836)	3	8
	Pellorneidae	<i>Pellorneum ruficeps</i> (Swainson, 1832)	7	12
		<i>Malacopteron cinereum</i> (Eyton, 1839)	2	3
	Dicaeidae	<i>Dicaeum cruentatum</i> (Linnaeus, 1758)	2	3
		<i>Dicaeum concolor</i> (Jerdon, 1840)	0	5

Table 10 (continued).

Order	Family	Scientific names of birds	ARP	LEF
		<i>Dicaeum agile</i> (Tickell, 1833)	4	5
		<i>Dicaeum chrysorrheum</i> (Temminck and Laugier, 1829)	0	1
	Nectariniidae	<i>Anthreptes singalensis</i> (Gmelin, 1788)	4	5
		<i>Nectarinia jugularis</i> (Linnaeus, 1766)	6	6
		<i>Anthreptes malacensis</i> (Scopoli, 1786)	2	2
		<i>Aethopyga siparaja</i> (Raffles, 1822)	0	5
		<i>Cinnyris asiaticus</i> (Latham, 1790)	0	4
		<i>Arachnothera longirostra</i> (Latham, 1790)	5	9
	Motacillidae	<i>Dendronanthus indicus</i> (Gmelin, 1789)	2	3
	Estrildidae	<i>Lonchura striata</i> (Linnaeus, 1766)	8	17

An even more interesting comparison can be made with the Wang Nam Khiao plot mentioned above, in “dry evergreen” forest. This plot is a few kilometers west of the Sakaerat plots, and has a slightly drier climate with 1,100 mm average annual rainfall. The plot was established as a 1-ha plot in 2002 (EIADTHONG, 2000) and resurveyed and expanded to 3 ha in 2016 (PHUMPHUANG *ET AL.*, (2018). In 2003, a severe rainfall and flooding event caused blowdowns of canopy species of *Dipterocarpus alatus* and *Melia azedarach* which produced forest gaps and facilitated the invasion of the successional species mentioned above. The number of species ≥ 4.5 cm DBH per ha averaged somewhat higher (79 to 90 species) than in the LEF (73 species) and ARP (63 species) plots. Tree density was also slightly higher (average 789, range 763–783 stems/ha). Floristic resemblance to our plots was also greater than for the Sakaerat plots: of the top 10 species of trees and saplings in the Wang Nam Khiao plot, 40% were also present on one of our plots. BUNYAVECHEWIN (1999) presented lists of the top 20 species in each of his two plots at Sakaerat; on average, only 20% of these occurred on one of our plots.

Our final comparison is with two well-documented plots in the ForestGEO large plot network of the Center for Tropical Forest Science, Smithsonian Institution, that are considered to be continental seasonal evergreen forests. The first to be established was the 50-ha plot in Huai Kha Khaeng Wildlife Sanctuary (HKK), western Thailand (BUNYAVEJCHEWIN *ET AL.*, 2001, 2002), and the second was the 30-ha Mo Singto (MS) plot later established in Khao Yai National Park (BROCKELMAN *ET AL.*, 2017). The MS plot, at an altitude of 725–815 m a.s.l., has a moister climate (annual rainfall about 2,100 mm) than the HKK plot (550–640 m a.s.l. and 1,475 mm of annual rainfall). The MS plot has an average of 4,416 stems of 135 species ≥ 1 cm DBH per ha, a total basal area of 31.8 m²/ha, and an average of 1,142 stems of 101 species ≥ 5 cm DBH. The HKK plot has approximately 1,609 stems ≥ 1 cm DBH per ha and a basal area of 30.1 m²/ha. Stem densities and species richness of ForestGEO plots are usually given for trees ≥ 10 cm DBH. BUNYAVECHEWIN *ET AL.* (2011) have estimated the average species richness of dry seasonal evergreen forests in Thailand (including HKK) as 83 species/ha, slightly higher than 80 species (range 63–98)/ha on the MS plot. The HKK and MS plots are dominated by different canopy species: the HKK plot by *Hopea odorata*, and the MS plot by *Dipterocarpus gracilis*, *Sloanea sigun* and *Ilex chevalieri*, in terms of basal area.

To summarize these comparisons, the ARP and the LEF lie at the lower end of the seasonal or dry evergreen forests of central Thailand in terms of tree abundance, basal

area, and species richness, as we would expect from elevation and climate data. In terms of species composition, however, no two forests in the plots we have reviewed have the same dominant canopy species, and species composition varies greatly among these plots from the limited amount of published data. The main conclusion to be drawn from this is that seasonal evergreen and semi-evergreen forests of central Thailand cannot easily be characterized by species composition. Their overlapping floras share species from the large number (more than a thousand) available in the regional landscape, with local species sample plot floras determined by local climate and environmental conditions as well as by chance and dispersal ability. A fundamental sampling problem exists because the number of species in the landscape of Central Thailand greatly exceeds the number that may occur together in any reasonable-sized study plot (and one hectare is a relatively large botanical sample plot for a species inventory). Even random 1-ha samples from a single tropical forest ecosystem will have low species similarity just by chance, and the smaller the samples are relative to the available species pool, the lower their similarity will be (PLOTKIN & MULLER-LANDAU, 2002; CHAO *ET AL.*, 2005).

The species present in the ARP and LEF plots are best compared with locally similar stands which, unfortunately, may not be available. The nearest relatively undisturbed forests of similar composition most likely lie in Khao Ang Rue Nai Wildlife Sanctuary in Chachoengsao and Rayong Provinces about 40 km to the northeast, but we are aware of no tree census plots that have been established there.

Effects of Alien Species on Succession

The differences in the successional communities are, in part, a reflection of the unpredictability of the successional pathway due to variation in site conditions and history (MESQUITA *ET AL.*, 2001; FERGUSON *ET AL.*, 2003; CHAZDON, 2008; WALKER *ET AL.*, 2010; LARKIN *ET AL.*, 2012; WILLIAMSON *ET AL.*, 2014). However, the path of succession in the ARP is being diverted, and possibly suppressed, by the dominance of its two alien species, the rubber tree *Hevea brasiliensis* and the fire-tolerant *Leucaena leucocephala*. The effect of the rubber trees is probably declining and will eventually disappear as the species is not recruiting in the plot. Latex was still being harvested from many trees. The effects of rubber trees on other tree species may be both positive and negative. The basal area as well as density of rubber trees had a significant positive correlation with the number of regenerating tree species ≥ 5 cm DBH, which shows the possible catalytic effect of rubber trees in the development of a new plant community (BUMRINGSRI *ET AL.*, 2006). However, the basal area and density of rubber trees had significant negative correlations with the density of other trees ≥ 5 cm DBH, which suggests that the surviving rubber trees still competed with other species.

Our study has provided evidence that the introduced *L. leucocephala* has also repressed the numbers of recruiting native species. To prove this effect would require an experiment in which *L. leucocephala* was removed from a series of replicated plots, along with monitoring of native species in control plots without removal of *L. leucocephala*. There is evidence from other studies documenting allelopathic effects of *L. leucocephala* on native species (CHATURVEDI & JHA, 1992; CHEN *ET AL.*, 2018; CHOU & KUO, 1986). In the case of the ARP, it appears likely that the existing larger tree species became established before the introduced *L. leucocephala* became dominant, and that the effects of the alien species on species richness have been felt mostly by saplings and seedlings. Rubber trees are now still the dominant species in the top canopy layer but are expected to be largely replaced by *L. leucocephala*, which is represented

by five times more stems (>5 cm DBH) than rubber. This will also make it difficult for other large species such as *Pterocymbium tinctorium* and *Lagerstroemia cochinchinensis* to become established in the upper canopy.

Natural and Novel Forest Ecosystems

Restoration ecologists have sometimes been accused of setting unattainable objectives, i.e., restoration of the original set of species on human-disturbed sites (HOBBS *ET AL.*, 2006, 2011). The objective, or “target” community (VAN ANDEL & ARONSON, 2012), or “potential vegetation” (PRACH & WALKER, 2020), are restoration concepts developed largely in the Temperate Zone and may be less applicable to more species-rich tropical forest landscapes. SER (2004), however, refers to the target as the “reference ecosystem” that “could have been manifested as any one of many potential states that fall within the historic range of variation of that ecosystem.” A more flexible and realistic definition of forest restoration is “Directing and accelerating ecological succession towards an indigenous reference forest ecosystem of the maximum biomass, structural complexity, biodiversity and ecological functioning that can be self-sustained within prevailing climatic and soil limitations” (ELLIOTT, 2020), although monitoring all these ecosystem characteristics presents a challenge. Without more detailed surveys of the landscape, we can only speculate that succession will lead to a variety of species in all strata typical of the regional semi-evergreen forest. “Typical” species may be defined as those that have relatively high frequencies over the landscape.

A new ecosystem or forest community may, after severe disturbance, develop a new and unforeseen combination of species, which has been branded a “novel ecosystem” by HOBBS *ET AL.* (2006, 2011). A novel ecosystem may involve “the invasion of new species that prevent the growth and regeneration of pre-existing species by competition” (HOBBS *ET AL.*, 2006), a qualification that applies to what has happened in the ARP. We regard a para-rubber orchard invaded by *L. leucocephala* as a novel ecosystem and by implication undesirable from a restoration standpoint. However, this novel ecosystem might possibly transition unaided to an acceptable, non-novel, natural forest community. The native species colonizing the sapling and seedling layers — at least 70% of them animal-dispersed — offer hope that unaided succession will allow the forest ecosystem to escape its “novel” status, but it will probably take several more decades. The problem of *L. leucocephala* invading the landscape is not likely to be solved by intervention — removing it from every area where it occurs. Our study asks the general question, will recolonization of an abandoned rubber plantation from nearby natural forest allow native species to reclaim the forest, or at least coexist with the alien species as a naturally functioning ecosystem?

Due to rapid land degradation, the Thai government has promoted commercially available fast-growing species such as *L. leucocephala*, *Acacia mangium* and *Acacia auriculiformis* for restoring forests (e.g., JAIYASUK *ET AL.*, 2015; ORDGPB, 2020). Recent restoration programs, however, have tended to avoid planting *L. leucocephala*, and instead have selected non-exotic species. In 2022 the Ministry of Agriculture and Cooperatives encouraged the owners of rubber plantations to grow useful native species of trees together with rubber trees in mixed plantations, so that the native species would provide added economic value as well as facilitate restoration if desired (PROJECT TO SUPPORT PLANTING NATIVE SPECIES IN RUBBER PLANTATIONS AND AGRICULTURAL AREAS—2020 FISCAL YEAR, 2022).

CONCLUSIONS AND RECOMMENDATIONS

Our study was a classic ecological “natural experiment”, i.e., an empirical observational study, in which “treatments” (2 disturbance regimes) were determined by previous land use already in place, rather than deliberately applied by the investigators. Although, ideally, it would have been useful to have included plot replication, other natural treatments (e.g., ARP without *L. leucocephala*, and plots at various distances from natural forest seed sources) and a proper control (i.e., survey of the reference forest type), these were precluded by landscape configuration and time limitations. Nevertheless, the detailed inventory of species—both plant and animal—presented above provides useful clues as to how restoration of logged-over forest and former rubber plantations might be improved.

Our first suggestion is that before interventions are planned, the designated areas, and the natural forest ecosystems surrounding them, should be mapped using remote sensing by high-resolution satellite and by drones. The purposes of such mapping are several: to map the size, shape and condition of the designated areas, to determine their proximity to and relation with local communities, and to determine their proximity to natural forests which are potential sources of colonizing species. Such data should be useful to any administrative bodies tasked with coordinating the selection and monitoring of areas for intervention.

Our study showed that forest regeneration was proceeding adequately in the logged over forest without the need for interventions other than prevention of fires and encroachment, since it is located near natural sources of propagules. Tree planting is needed only where natural regeneration falls below levels needed to outcompete herbaceous weeds and establish a closed canopy within a desirable timeframe, and becomes essential where natural colonization may be lacking due to extirpation of seed dispersers or excessive distance from seed sources (ELLIOTT *ET AL.*, 2013). Restoration of degraded or encroached forest at the borders of or within protected areas such as national parks will most likely occur naturally without direct intervention. Indirect intervention in such areas is recommended, consisting of improved border protection and the recruitment of local villagers to help protect the forest.

A second suggestion is that the “target” of succession should consist of species indigenous to the reference forest type, since they are genetically adapted to local conditions. A survey of the reference forest type is desirable to determine availability of seed sources and to set goals for restoration. There are, however, numerous environments in which a reference forest is not available, such as in urban and suburban developments, intensive agricultural areas or totally deforested landscapes that are common in most areas of Thailand. In such cases the species composition of the primeval vegetation might be derived indirectly climate-niche modelling, old herbarium records and studies of scattered remnant vegetation (TIANSAWAT *ET AL.*, 2022). However, recreating original forest in degraded areas, cleared of forest long ago, and within landscapes without reference forest remnants may be unfeasible and too expensive. On such sites, “novel” species mixes, with high biomass accumulation, biodiversity and ecological functioning that meet the practical and aesthetic needs of local communities may become the most acceptable restoration outcomes. Ultimately, forest restoration and subsequent management will not be successful unless it meets the needs and aspirations of local stakeholders. If local residents need community forests to provide economic benefits (such as the villagers at our study sites), or recreational benefits, then a novel forest community incorporating as many useful native species as possible becomes the target. Such fine-scale planning will require intensive site preparation and care, as well as removal of undesired species such as alien vines, which we see smothering trees along most of our roadways.

Above all, we should not divert succession by planting non-native species, particularly aggressive, invasive ones such as *L. leucocephala*. Such intervention carries more risks than benefits, and results in vegetation of reduced species diversity and biomass. The objectives of landscape planning and forest restoration are not merely to create more green areas and increase biomass, but to achieve the maximum recovery of biodiversity, ecological function and human-use value as possible within the limits imposed by prevailing climatic and soil conditions.

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DATA AVAILABILITY

The data summary in the Appendix is available as an Excel file upon request from the first two authors.

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Appendix (continued).

Botanical name (family)	Habit	Dispersal mode	Number of stems															
			Logged Evergreen Forest						Abandoned Rubber Plantation									
			≥10 cm	5-10 cm	1-5 cm	<1 cm	Ground flora	≥10 cm	5-10 cm	1-5 cm	<1 cm	Ground flora						
<i>Ficus fistulosa</i> Reinw. ex Bl. var. <i>fistulosa</i> (Moraceae)	UT	B, M	3	3	10	1												
<i>Ficus heterophylla</i> L. f. (Moraceae)	S	B, M				17												
<i>Ficus hispida</i> L. f. (Moraceae)	UT	A	1	1	9													
<i>Ficus pumila</i> L. (Moraceae)	WC	B, M				2												
<i>Ficus vasculosa</i> Wall. ex Miq. (Moraceae)	CT	B, M	10	1	1													
<i>Fluggea virosa</i> (Roxb. ex Willd.) Voigt (Euphorbiaceae)	S	B															2	
<i>Garcinia gracilis</i> Pierre (Guttiferae)	CT	M				2												
<i>Garcinia xanthochymus</i> Hk. f. ex T. And. (Guttiferae)	CT	M	1	1	1							3						
<i>Globba kerrii</i> Craib (Zingiberaceae)	H	G								1								
<i>Glycosmis pentaphylla</i> (Retz.) DC. var. <i>pentaphylla</i> (Rutaceae)	UT	B, M				6	1						1	1				
<i>Goniothalamus laoticus</i> (Fin. & Gagnep.) Ban (Annonaceae)	CT	G				2												
<i>Goniothalamus marcanii</i> Craib (Annonaceae)	UT	G				2	1							12	7			
<i>Gonocaryum lobbianum</i> (Miers) Kurz (Icacinaeae)	UT	U	1	1	2													
<i>Gouania leptostachya</i> DC. var. <i>leptostachya</i> (Rhamnaceae)	WC	W	1			2								8	2			
<i>Gynostemma pentaphyllum</i> (Thunb.) Mak. forma <i>pentaphyllum</i> (Cucurbitaceae)	H	G								8								
<i>Harpullia arborea</i> (Blanco) Radlk. (Sapindaceae)	CT	B, M				2												
<i>Harrisonia perforata</i> (Blanco) Merr. (Simaroubaceae)	S	M					1								3	2		
<i>Heteropanax fragrans</i> (Roxb. ex DC.) Seem. (Araliaceae)	UT	G	4	2	3	1									1			
<i>Hevea brasiliensis</i> Müll. Arg. (Euphorbiaceae)	CT	W				1									52	10	15	7

Appendix (continued).

Botanical name (family)	Habit	Dispersal mode	Number of stems													
			Logged Evergreen Forest						Abandoned Rubber Plantation							
			≥10 cm	5-10 cm	1-5 cm	<1 cm	Ground flora	≥10 cm	5-10 cm	1-5 cm	<1 cm	Ground flora				
<i>Macaranga siamensis</i> S. J. Davies (Euphorbiaceae)	CT	B	9	6	1			1	3	2						
<i>Macaranga tanarius</i> (L.) M.-A. var. <i>tomentosa</i> (Bl.) (Euphorbiaceae)	UT	B	79	6	5	21					1					
<i>Maclura cochinchinensis</i> (Lour.) Corn. (Moraceae)	UT	M				1										
<i>Maesa montana</i> A. DC. (Myrsinaceae)	UT	G			1	1									1	
<i>Mallotus peltatus</i> (Geisel.) M.-A. (Euphorbiaceae)	UT	B	2	7	84	26			1	3	13	4				
<i>Mallotus philippensis</i> (Lmk.) M.-A. (Euphorbiaceae)	UT	B	5	9	8				2	1						
<i>Mammea siamensis</i> (Miq.) T. And. (Guttiferae)	CT	B, M			1					1	1					
<i>Melochia umbellata</i> (Houtt.) Stapf (Sterculiaceae)	UT	W			1										1	
<i>Memecylon tilacinum</i> Zoll. & Mor. (Melastomataceae)	UT	M									1	3				
<i>Memecylon umbellatum</i> Burm. f. (Melastomataceae)	UT	M									1	3	4			
<i>Merremia vitifolia</i> (Burm. f.) Hall. f. (Convolvulaceae)	WC	G					4								1	
<i>Microcos paniculata</i> L. (Tiliaceae)	CT	M	1								21	50	25	4		
<i>Micromelum falcatum</i> (Lour.) Tana. (Rutaceae)	UT	M											1			
<i>Mikania cordata</i> (Burm. f.) B. L. Rob. forma <i>undulata</i> Kost. (Compositae)	H	G												5		2
<i>Millettia lineata</i> (Craib) Ast (Annonaceae)	CT	M						3	1							
<i>Millettia Leucantha</i> Kurz var. <i>leucantha</i> (Fabaceae)	UT	G								2						
<i>Mitrephora vandaeiflora</i> Kurz (Annonaceae)	CT	M	1							5						
<i>Murraya paniculata</i> (L.) Jack (Rutaceae)	UT	B, M												1		
<i>Musa acuminata</i> Colla ssp. <i>siamica</i> Simm. (Musaceae)	H	G												10		

