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# Assessing herb layer composition under jungle rubber in Sungai Manau Forest, Jambi, Indonesia: indicator species and tree regeneration potential

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**Abstract.** *Siswo, Yun CW, Kim H, Lee J, Atmoko BD, Brahmantya L. 2022. Assessing herb layer composition under jungle rubber in Sungai Manau Forest, Jambi, Indonesia: indicator species and tree regeneration potential. Biodiversitas 23: 5247-5257.* Most of the post-logged forests in Sumatra have been transformed into various land cover types, including plantations and secondary forests. Among plantation systems, rubber agroforestry (jungle rubber) is preferable since it resembles natural forests, which still maintain high biodiversity. While previous studies have been focused on the floristic diversity, composition and structure of jungle rubber, limited research has investigated indicator species and tree regeneration in jungle rubber. This research aimed to compare herb layer composition including species diversity, indicator species and tree regeneration potential between jungle rubber (JF) and the existing natural growing forests, including undisturbed post-logging forest (UF), mixed regrowth forest (MF) and newly regrowth forest (NF), in Sungai Manau Forest, Jambi, Indonesia. We conducted a vegetation survey and subsequently analyzed the data using some comparative analyses, indicator species analysis and regeneration status analysis. Our results showed significant differences in herb layer communities among all land cover types (T= -18.91, $p$=0.000). Although JF and all-natural growing forests showed equal indices of diversity, each land cover type showed its own indicator species, reflecting their environmental conditions. However, indicator species for JF were mostly similar in character to that in MF with non-native semi-shade-tolerant species. Meanwhile, all indicator species for UF were native shade-tolerant species and the indicator species for NF were fully non-native shade-intolerant species. JF is also equal to MF in seedlings availability and tree regeneration potential by showing an equal number of seedling species and the number of individuals where most of the seedlings in both land cover types were pioneer species with "good regeneration "status". Our finding suggested that JF had a similar potential to MF in the succession process. Therefore, jungle rubber can be a good alternative when a plantation system is inevitable in a post-logging forest.

**Keywords:** Indicator species, jungle rubber, regeneration, regrowth, seedling

## INTRODUCTION

A large portion of tropical rainforests in Sumatra have been converted into various land use types (Miettinen et al. 2011; Margono et al. 2014; Abood et al. 2015; Drescher et al. 2016). Forest conversion on the island increased drastically after the end of most logging concession permits in the 2000s since the post-logged forests were left open access with no clear management authority, allowing any parties to easily enter the forest (Tsujino et al. 2016). The post-logged forests in the state of unconverted or without further human disturbances are now only limited to some areas with difficult access and those designated for conservation. In total, Sumatra lost about 2.9 million hectares of forest between 2000 and 2012 (Margono et al. 2014) with only 25% of forest cover (Miettinen et al. 2011; Villamor et al. 2014).

Many post-logged forests with open access status are occupied by communities, either local people, outsiders or both (Suwardi et al. 2013), and converted to agricultural land (Laurance et al. 2014). The post-logged forests occupied by local communities are usually only intensively cultivated with crops (e.g. rice, corn, cassava) for a short period. After the productivity of the land to yield cash crops declined due to the growth of shade trees or infertile soil, some parts of the land were abandoned and gradually recovered into the natural secondary forest, called "mixed regrowth forest". Other post-logged forests have been turned into plantations for oil palm, rubber and many other intensive plantations which are recognized as harmful to biodiversity (Abood et al. 2015; Tarigan and Widyaliza 2015; Drescher et al. 2016). There is also another form of land management type in the post-logged forest managed by smallholders as agroforestry, mostly rubber plantations called "jungle rubber" which is planted together with cash crops at the initial stage of cultivation (Gouyon et al. 1993; Joshi et al. 2002).

Changes in vegetation cover from the forest into other types (e.g. plantation, agriculture) affect herbaceous plants as a response related to changes in sunlight (Abood et al. 2015), microclimate (Meijide et al. 2018) and nutrient content (Osborne 2020). Accordingly, vegetation change, especially by planting monoculture species has been widely recognized as a disturbance since it causes biodiversity decline and leads to the extinction of particular species (Pereira et al. 2012; Braun et al. 2017). One form of such disturbance is the domination of invasive alien species (IAS) driven by anthropogenic factors (Freeman 2015).

Plantation trees are generally exotic or non-native with an invasive character (Valduga et al. 2016), affecting the surrounding environmental conditions and leading to the expansion of non-native/invasive alien species (Wahyuni 2016). At understorey layer, non-native invasive species generally grow and dominate vegetation composition, where their richness increase as the tree layer is reduced, and vice versa (Wahyuni 2016). These species are able to suppress the growth of particular species (especially the native herbaceous species) leading to change in species dominance. Such species also hamper the growth of seedlings and ultimately lead to the loss of tree species regeneration (Fu et al. 2018). Therefore, change in forest stands due to land use changes are commonly becoming large threats to biodiversity and many ecosystem functions.

While the diversity level of monoculture plantation systems is commonly low, some agroforestry systems, such as jungle rubber, still maintain biodiversity (Beukema and van-Noordwijk 2004) and are comparable to forests in terms of preserving biodiversity (Joshi et al. 2002). Böhnert et al. (2016) revealed that jungle rubber provides a favorable environment for epiphytic species diversity, on par with forests. Furthermore, Muhdi et al. (2020) found that jungle rubber has higher species richness than monoculture rubber. Unfortunately, these reports are generally limited to quantitative values of diversity such as species richness, diversity index, dominance index and importance value. Explanation of species composition using such parameters is actually a common way to describe the value of different species for indicating broad ecological patterns (Magurran 2004). Nevertheless, deeper analysis is sometimes needed to analyze indicative species and tree regeneration status of particular areas. Indicator species can be a base consideration for future management/conservation (Siswo et al. 2019). Meanwhile, tree regeneration status is an important aspect to describe forest structure and to illustrate environmental, natural and human factors affecting the vegetation as well as showing the potential for reforestation (Kuma and Shibru 2015; Nur et al. 2016; Saha et al. 2016).

This study explored and compared herb layer composition covering quantitative values of species diversity, indicator species and tree regeneration potential between jungle rubber forest (JF) and other existing forest types including undisturbed post-logging forest (UF), mixed regrowth forest (MF) and newly regrowth forest (NF). We used Sungai Manau forest, Jambi Province, Indonesia as a study area since it provided an excellent context of study which fulfilled the analytical framework of our study (i.e. a landscape with several land cover types to compare).

## MATERIALS AND METHODS

### Study area

We conducted this study in a post-logged forest of a former natural forest concession operated between the 1970s to 2000s (Villamor et al. 2014; Tsujino et al. 2016). The study area was located in Sungai Manau, Merangin District, Jambi Province, Sumatra, Indonesia (PT HAN 2019). Generally, this area is a lowland tropical rainforest with undulating topography variations from flat to sloping with an altitude of 144 - 388 m above sea level (PT HAN 2015). In addition, the region has type A of Schmidt Ferguson climate with an average temperature of around 26.9 - 30°C and high rainfall ranging from 2200 to 3200 mm (BPS Kabupaten Merangin, 2019; climate-data.org (2019).

The study site consisted of various forest cover types and plantation systems due to land occupation and land use conversion after selective logging (Suwardi et al. 2013). As shown in Figures 1 and 2, the land cover types included jungle rubber (JF), undisturbed post-logged forest (UF), mixed regrowth forest (MF), and newly regrowth forest (NF). JF is a post-logged forest experiencing land occupation and cultivation for cash crops planted together with rubber trees under the rubber agroforestry system managed by smallholders (15 years of abandonment after land cultivation planted by cash crops and rubber trees). UF is a post-logged forest that is not occupied and cultivated for agriculture. MF is a post-logged forest experiencing a land occupation and cultivation for cash crops and subsequently abandoned and gradually recovered as a secondary forest (15 years of abandonment after land occupation and cash crop cultivation). NF is an open areas with no tree vegetation cover (newly abandoned areas).

### Sampling design and data collection

We purposively determined the sample sites based on a land cover map for jungle rubber (JF), undisturbed post-logged forest (UF), mixed regrowth forest (MF) and newly regrowth forest (NF). We placed sample plots on each land cover type randomly by considering road access, safety, and social conditions. Sample plots were nested quadratics (Kusmana 1997; Magurran 2004) with a starting point at the same corner. We created the nested plot since we need to investigate tree species density at all layers for tree regeneration status analysis (Sarkar and Devi 2014; Malik and Bhatt 2016; Nelson and Noweg 2021). The nested quadratic plot consisted of a 20 x 20 m plot for tree (mature trees; ≥ 20 cm diameter at breast height), 10 x 10 m plot for pole (young trees; > 10 cm diameter at breast height), 5 x 5 m plot for sapling (small trees, 2-10 cm diameter at breast height) and 2 x 2 m plot for seedling (< 2 cm stem diameter and < 1.5 m height) and herbaceous plant (herb layer species other than seedling). In total, we established 52 nested quadratic plots spread over the four land cover types, where 13 plots were in JF, 15 plots were in UF, 11 plots were in MF, and 13 plots were in NF.

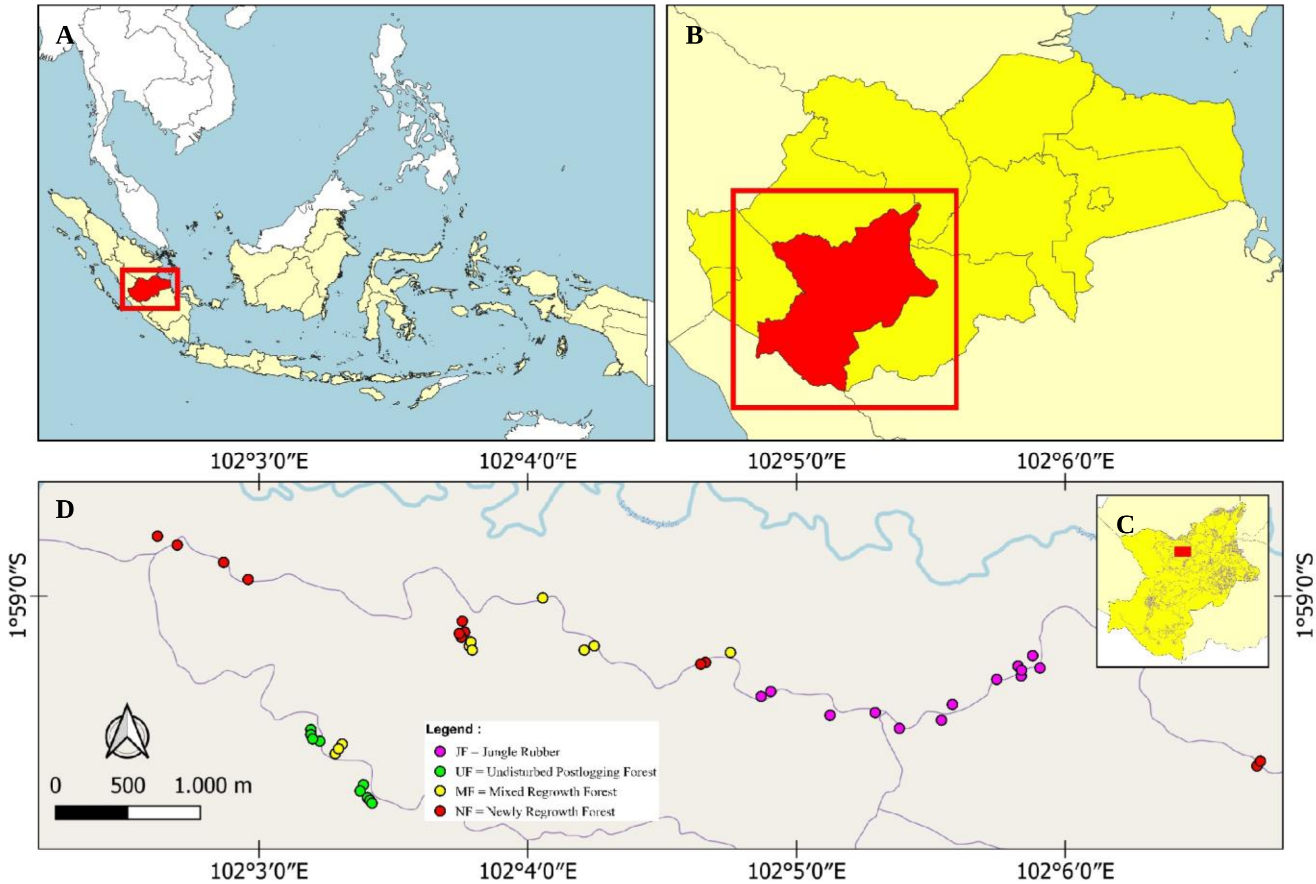



**Figure 1.** Map of the study site: A. Jambi Province, B. Merangin District, C. Sungai Manau Production Forest, D. Study area. Notes: JF: jungle rubber (pink dot markers); UF: undisturbed post-logging forest (green dot markers); MF: mixed regrowth forest (yellow dot markers); NF: newly regrowth forest (red dot markers)


**Figure 2.** Vegetation cover. A. Jungle rubber (JF), B. Undisturbed post-logging forest (UF), C. Mixed regrowth forest (MF), and D. Newly regrowth forest (NF)

We recorded the presence of all species occurring at each vegetation layer including species name, the number of species, and their abundance. Species unable to be identified directly in the field were documented by taking photos for further identification using some determination keys. Within the 2 x 2 m plots, we qualitatively examined the cover-abundance of herb layer species using Braun Blanquet method which we further transformed into a quantitative scale (McCune and Grace 2002). We also estimated the number of individuals of existing seedlings among all herb layer species. Furthermore, we counted the density of saplings, pole and tree at the 5 x 5 m, 10 x 10 m and 20 x 20 m plots, respectively.

**Data processing**

Prior to data analysis, we completed species identification for some unidentified species in the field using a reference book (Yudhoyono and Sukarya 2013) and some websites, such as wikipedia.com, Plantamor.com, and identify.plantnet.org based on the local names and the collected photos. We classified herb layer species as native and non-native species based on some literatures (Kudo et al. 2014; Day et al. 2016; Setyawati et al. 2015; Dar et al. 2019. Thereafter, we calculated herb layer species abundance, including the number of species, frequency, dominance (basal area/coverage) and the importance value (IV). We calculated IV of herb layer species as the average value of relative dominance and relative frequency. According to McCune and Grace (2002), IV is the average of two or more relative values from abundance measures, i.e. among relative frequency, relative density and relative dominance. We then also took into account species diversity in the herb layer represented by species richness, Shannon diversity index, and Evenness index to provide important information reflecting forest structure and function (Singh et al. 2016).

We defined species richness as the number of species and calculated diversity indices by using the following formula (McCune and Grace 2002; Maguran 2004):

$$H' = -\sum\left(\frac{n.i}{N}\right)\ln\left(\frac{n.i}{N}\right)$$

$$E' = \left(\frac{H'}{\ln(N)}\right)$$

Where: $H'$ is the Shannon diversity index, $D'$ is the Simpson dominance index, $E'$ is the Evenness index, $N$ is the total number of individuals and $n.i$ is the number of $i^{th}$ species.

Further, we also prepared abundance data for indicator values calculation including mean abundance, relative abundance and relative frequency (McCune and Grace 2002).

For analysis of regeneration status, we calculated the number of individuals per ha of each tree species at all layers, including seedlings, saplings, poles and mature trees (Sarkar and Devi 2014; Malik and Bhatt 2016; Nelson and Noweg 2021).

**Data analysis**

Based on species abundance per plot, we compared herb layer species composition among land cover types by employing multi-response permutation procedures analysis (MRPP) using PC-ORD software (Peck 2010). We used MRPP as it is a non-parametric analysis that disregards distributional assumption which is appropriate for ecological community data (McCune and Grace 2002).

In addition, we compared diversity indices, the number of species, the number of native or non-native species, and the number of seedlings among land cover types using Kruskal-Wallis analysis followed by Mann-Whitney U-tests for pairwise comparisons. We employed these analyses because our data were non-normally distributed which is common for ecological data (McCune and Grace 2002). Like MRPP, Kruskal-Wallis and Mann-Whitney U-tests are also non-parametric-based analyses that are suitable for non-normally distributed data (Cleophas and Zwinderman 2016).

Furthermore, we assessed indicator species for each forest type by employing Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997; McCune and Grace 2002; Peck 2010). Indicator species are species with indicator values fulfilling the threshold of 25% (Dufrêne and Legendre 1997) and statistically significant at alpha 0.05 of Monte Carlo Significance Test (McCune and Grace 2002).

To support the description of tree regeneration potential, we analyzed the regeneration status of tree species by comparing the density (number of individuals per ha) of seedlings, saplings, poles and mature trees (Malik and Bhatt 2016; Nelson and Noweg 2021). We categorized the regeneration status of tree species as “good regeneration” if seedlings > saplings > poles > mature trees; “fair regeneration” if mature trees > saplings > seedlings; “poor regeneration” if a species survives only in sapling; “none regeneration” if a species is absent in both sapling and seedling stages but present as mature trees; and “new species” if a species has no mature but only sapling and/or seedling stages (Sarkar and Devi 2014; Malik and Bhatt 2016; Nelson and Noweg 2021).

## RESULTS AND DISCUSSION

**Floristic composition**

We identified 134 herb-layer plant species belonging to 57 families from 52 plots distributed across all land cover types. From a total of 134 species, 52 species were non-native and 82 were native species to our study sites. We also identified 46 seedling species among all herb layer species. Some species found in a land cover type were rare and even often absent in other land cover types. Particular species were restricted to specific sites where only 14 species grew in all sites, although most of the species were present in more than one site. Based on the ten most dominant species of each forest type, only a few species in JF had similarities with other forest types, especially UF (Table 1). We found that JF shared only two herb layer species to UF (*Maranta* sp, *Clidemia hirta*), five herb layer species to MF (*Maranta* sp, *Clidemia hirta*, *Thelypteris* sp., *Mikania micrantha, and Costus spicatus)*, and four herb layer species to NF (*Clidemia hirta*, *Thelypteris* sp., *Mikania micrantha, and Costus spicatus*).

MRPP analysis showed significant differences in species composition among herb layer communities (Table 2). This was indicated by *t* statistic values (T) at alpha 0,05 for both general and pairwise comparisons. According to McCune and Grace (2002), the more negative the T, the stronger the separation. Meanwhile, the small value of homogeneity within the group (A) is a common value in community data. McCune and Grace (2002) also stated that the value of A is commonly below 0.1. JF showed the smallest difference to MF (T = -3.19, *p* = 0.005) and appear to have a greater distinction to UF (T = -13.36, *p* = 0.000).

**Table 1.** Herb layer plant species composition at: jungle rubber forest (JF), undisturbed post-logged forest (UF), mixed-regrowth forest (MF) and newly regrowth forest (NF)

| Species name | Family | RF | RDo | IV |
|---|---|---|---|---|
| **UF** | | | | |
| *Maranta* sp. | Marantaceae | 5.13 | 18.18 | 11.66 |
| ***Litsea* sp.** | Lauraceae | 4.03 | 9.86 | 6.94 |
| *Calamus axillaris* | Arecaceae | 4.76 | 6.31 | 5.53 |
| *Thelypteris* sp. | Thelypteridaceae | 5.13 | 5.84 | 5.48 |
| *Elatostema rostratum* | Utricaceae | 3.3 | 5.02 | 4.16 |
| *Clidemia hirta#* | Melastomaceae | 4.03 | 3.58 | 3.8 |
| *Mallotus miquelianus* | Euphorbiaceae | 2.93 | 2.51 | 2.72 |
| *Spathoglottis sp* | Orchidaceae | 2.93 | 2.2 | 2.57 |
| *Tetracera scandens* | Dilleniaceae | 1.1 | 3.98 | 2.54 |
| *Pternandra coerulescens* | Melastomaceae | 2.2 | 2.66 | 2.43 |
| Other (72 species) | | | | 52.13 |
| **JF** | | | | |
| *Clidemia hirta#* | Melastomaceae | 6.19 | 15.12 | 10.65 |
| *Dicranopteris linearis#* | Gleicheniaceae | 3.09 | 8.52 | 5.8 |
| *Thelypteris* sp. | Thelypteridaceae | 4.64 | 6.12 | 5.38 |
| *Mikania micrantha#* | Asteraceae | 2.58 | 7.27 | 4.92 |
| *Maranta* sp. | Marantaceae | 3.61 | 4.98 | 4.29 |
| *Cyrtococcum accrescens#* | Poaceae | 3.09 | 3.83 | 3.46 |
| ***Macaranga hypoleuca#*** | Euphorbiaceae | 4.12 | 2.51 | 3.32 |
| *Curcuma* sp.*#* | Zingiberaceae | 3.09 | 3.2 | 3.14 |
| *Lycopodium* sp. | Lycopodiaceae | 2.06 | 3.92 | 2.99 |
| *Costus spicatus* | Zingiberaceae | 1.55 | 4.02 | 2.78 |
| Other (54 species) | | | | 53.25 |
| **MF** | | | | |
| *Clidemia hirta#* | Melastomaceae | 6.51 | 15.71 | 11.11 |
| *Maranta* sp. | Marantaceae | 4.73 | 11.02 | 7.88 |
| *Thelytpteris* sp. | Thelypteridaceae | 6.51 | 8.37 | 7.44 |
| *Scleira sumatrana* | Cyperaceae | 3.55 | 4.92 | 4.24 |
| *Mikania micrantha#* | Asteraceae | 3.55 | 3.83 | 3.69 |
| *Milletia sericea* | Euphorbiaceae | 2.37 | 4.98 | 3.67 |
| *Costus spicatus* | Zingiberaceae | 2.96 | 3.64 | 3.3 |
| *Piper aduncum#* | Piperaceae | 2.37 | 4.22 | 3.29 |
| *Melastoma candidum#* | Melastomaceae | 3.55 | 2.87 | 3.21 |
| ***Endospermum malaccense****#* | Euphorbiaceae | 2.96 | 3.01 | 2.98 |
| Other (52 species) | | 60.95 | 37.42 | 49.18 |
| **NF** | | | | |
| *Mikania micrantha#* | Asteraceae | 7.79 | 12.67 | 10.23 |
| *Eupatorium inulifolium#* | Asteraceae | 5.84 | 9.27 | 7.56 |
| *Cyrtococcum accrescens#* | Poaceae | 4.55 | 10.28 | 7.41 |
| *Clidemia hirta#* | Melastomaceae | 4.55 | 6.22 | 5.38 |
| *Oriza sativa#* | Poaceae | 1.95 | 8.37 | 5.16 |
| *Milletia sericea* | Euphorbiaceae | 3.25 | 6.45 | 4.85 |
| *Musa* sp. *#* | Musaceae | 4.55 | 4.49 | 4.52 |
| *Eleusine indica#* | Poaceae | 3.25 | 4.86 | 4.05 |
| *Thelypteris* sp. *#* | Thelypteridaceae | 4.55 | 3.11 | 3.83 |
| *Borreria latifolia#* | Rubiaceae | 2.6 | 3.9 | 3.25 |
| Other (43 species) | | | | 43.76 |

Note: RF: relative frequency, RDo: relative dominancy, IV: important value, non-native species were marked by hash marker (#). Bold letters for species names indicated tree species. Species with a bold marker: the most dominant seedling. Non-native species were determined according to some references (Breaden et al. 2012; Kudo et al. 2014; Setyawati et al. 2015; Dar et al. 2019; Day et al. 2019; Siswo et al. 2019; ISSG 2022)

**Table 2.** Summary statistics of multi-response permutation procedure (MRPP) analysis for herb layer plant species communities

| Comparison of Sorensen distance | T | A | *p*-value |
|---|---|---|---|
| General comparison | -18.91 | 0.13 | 0.000 |
| Pairwise comparison: | | | |
| *JF vs UF* | -13.36 | 0.12 | 0.000 |
| *JF vs MF* | -3.19 | 0.02 | 0.005 |
| *JF vs NF* | -8.78 | 0.08 | 0.000 |
| *UF vs MF* | -9.8 | 0.09 | 0.000 |
| *UF vs NF* | -13.81 | 0.15 | 0.000 |
| *MF vs NF* | -6.9 | 0.07 | 0.000 |

Note: T: separation between the group, A: within-group homogeneity, *p*: significance level at alpha 0.05, JF: jungle rubber forest, UF: undisturbed post-logged forest, MF: mixed regrowth forest, NF: newly regrowth forest (open area)

**Species diversity**

In general, our study showed an almost similar number of species between JF and MF with 64 and 62 species, respectively. Although the species richness values in JF and MF were lower than those in UF which reached 82 species, these values were higher than that in NF (Table 1). At plot level, Kruskal Wallis and Mann Whitney U test at alpha 0.05 confirmed that JF had a significantly higher value of species richness compared to NF and showed equal value to MF. We also did not find a significant difference between the values of species richness in JF and UF (Figure 3A). Plot level also exhibited significant differences in the number of native species (Figure 3B). JF had a higher number of native species than that NF. Moreover, the number of native species that occurred in JF was equal to those in MF despite the fewer number compared to those in UF.

Regardless of the differences in species richness and the number of native species, JF and all land cover types including UF, MF and even NF were indistinguishable in abundance distribution pattern as reflected by the IV of each species (Table 1). The ten most dominant species in the four land cover types hold about half of the total proportion in the composition. We found that all land cover types equally showed only one species accounting for about 10% of IV while the IV of the other nine species were evenly distributed between 2% and 9%. Accordingly, we found no significant difference in species diversity indices (Shannon diversity index and Evenness index) among all forest types (Figure 3C, 3D).

**Indicator species**

Based on the 25% indicator value threshold suggested by Dufrêne and Legendre (1997) at alpha 0.05, each land cover type showed a different set of indicator species. Although some species grew dominantly as shared species in more than one land cover type, the indicator species for each land cover type were identified by employing Monte Carlo test of significance in the indicator species analysis (Table 3). From a total of 134 species, we found four indicator species for JF, twelve indicator species for UF, five indicator species for MF, and nine indicator species for NF. Other species were not significant indicators, mostly singleton and infrequent species. Such species had no possibility of being statistically significant indicator species (Dufrêne and Legendre 1997; McCune and Grace 2002).

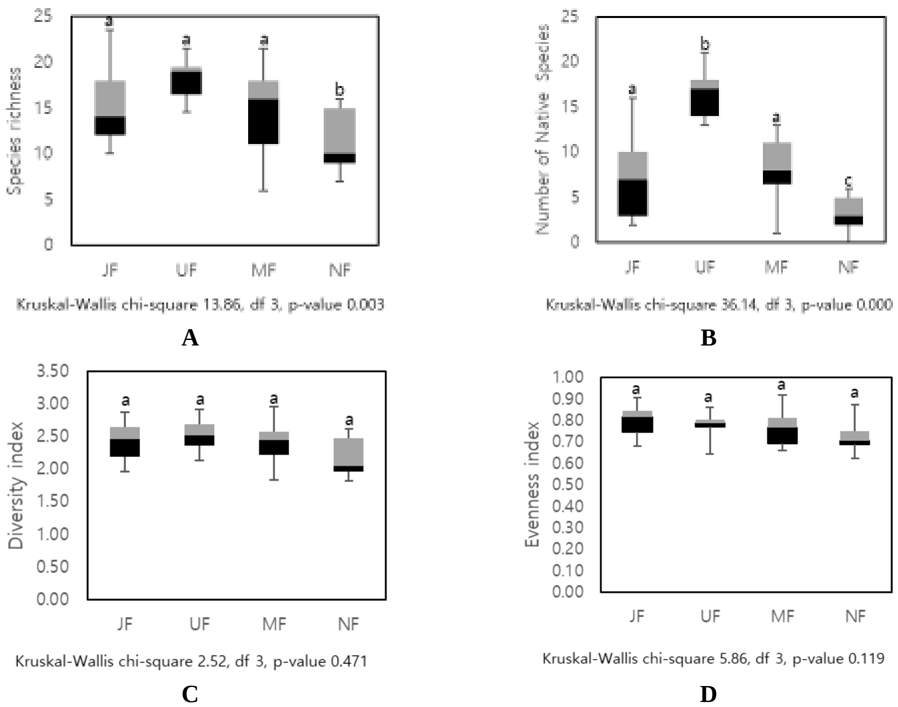



**Figure 3.** Plot-level herb layer species richness (A), number of native species (B), diversity index (C), evenness index (D). Notes: jungle rubber forest (JF), undisturbed post-logged forest (UF), mixed regrowth forest (MF), newly regrowth forest (NF). Black and grey areas of the boxes indicate the second and third quartile, respectively, and whiskers imply the upper and the lower quartile. Different letters (a, b, c) demonstrate significant differences between plot groups (Kruskal-Wallis/Mann-Whitney U test, $p < 0.05$)

We found the different character of species among land cover types (Table 3). Indicator species for UF were native shade-tolerant species. In contrast to UF, indicator species for NF were completely non-native shade-intolerant and light-demanding species. Meanwhile, JF had a similar character of indicator species to MF despite the existence of *Hevea brasiliensis* distinguishing JF. The indicator species for both land cover types were mostly non-native semi-shade-tolerant characters with adaptation ability. Although they were dominant in JF or MF, we also found most of these species in the non-shade area (NF) and full shade area (UF), except *H. brasiliensis.*

**Table 3.** Indicator species distinguishing forest types

| Species | Value | | |
|---|---|---|---|
| | Ival | Max | *p* |
| *Spatologlottis* sp. | 33.9 | UF | 0.0272 |
| *Dyospiros confertiflora* | 46.1 | UF | 0.00 |
| *Palaqium* sp. | 26.7 | UF | 0.01 |
| *Donax cannif* | 33.3 | UF | 0.01 |
| *Mallotus miiq* | 37.5 | UF | 0.00 |
| *Ptenandra canniformis* | 40 | UF | 0.00 |
| *Curculigo capitulata* | 31.9 | JF | 0.01 |
| *Clidemia hirta** | 40.3 | MF | 0.01 |
| *Imperata cylindrica** | 25.7 | MF | 0.07 |
| *Hevea brasiliensis** | 34.3 | JF | 0.01 |
| *Dillenia* sp. | 26.7 | UF | 0.02 |
| *Borreria latifolia*** | 30.8 | NF | 0.01 |
| *Crassocephalum* sp.** | 38.5 | NF | 0.00 |
| *Petunga microcarpa* | 40 | UF | 0.00 |
| *Scleira sumatrana** | 32.3 | MF | 0.03 |
| *Maranta* sp. | 53.9 | UF | 0.00 |
| *Lea indica* | 32.2 | UF | 0.01 |
| *Litsea* sp. | 73.3 | UF | 0.09 |
| *Knema laurina* | 26.7 | UF | 0.01 |
| *Trema orientalis* | 29.1 | NF | 0.02 |
| *Eupatorium inulifolium* | 51.2 | NF | 0.00 |
| *Shorea platyclados* | 46.7 | UF | 0.00 |
| *Musa* sp. | 40.1 | NF | 0.01 |
| *Nephelium* | 29.1 | NF | 0.02 |
| *Mikania micrantha*** | 50.9 | NF | 0.00 |
| *Dicranopteris linearis** | 33.8 | JF | 0.02 |
| *Calamus axillaris* | 66.3 | UF | 0.00 |
| *Eleusina indica*** | 29.2 | NF | 0.03 |
| *Cyrtococcum accrescens*** | 34 | NF | 0.02 |
| *Melastoma cadidum** | 36.9 | MF | 0.01 |
| *Slaginella* sp.* | 26.8 | JF | 0.03 |
| *Piper caducibracteum* | 28.7 | UF | 0.01 |
| *Piper aduncum** | 31.4 | MF | 0.04 |
| *Curcuma* sp.* | 31.5 | JF | 0.03 |
| *Elatostema rostratum* | 53.3 | UF | 0.00 |

Note: Max: maximal value for a group (JF: jungle rubber forest, UF: undisturbed post-logged forest, MF: mixed regrowth forest, NF: newly regrowth forest), IVal: indicator value, *p*: significance of Montecarlo test at alpha 0.05. Species with no asterisk: native shade-tolerant, species with an asterisk: adaptable shade-intolerant (non-native semi-shade-tolerant), species with a double asterisk: non-native shade-intolerant. Only statistically significant indicator species are shown. Non-native species were determined according to some references (Breaden et al. 2012; Kudo et al. 2014; Setyawati et al. 2015; Dar et al. 2019; Day et al. 2019; Siswo et al. 2019; ISSG 2022).

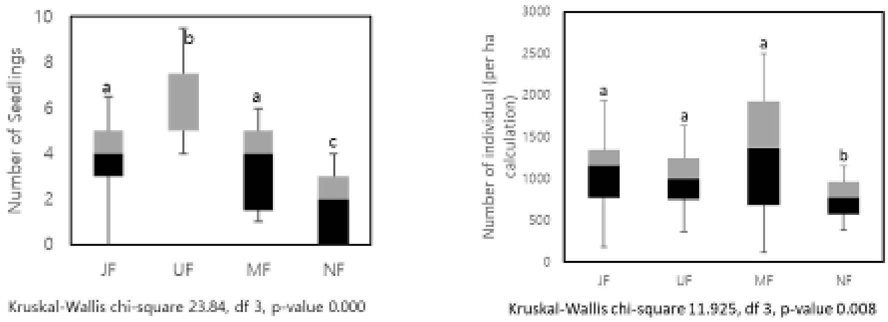
**Seedling availability and tree regeneration status**

Kruskal-Wallis analysis showed a significant difference in the number of seedlings and the number of individuals among land cover types (Figures 4A and 4B). However, similar to the comparison in the number of native species, we found no significant difference between JF and MF in the number of species and seedling individuals. The two land cover types demonstrated a much higher number of seedlings than NF. In addition, JF and MF even exhibited equal seedling individuals to UF although significantly fewer in the number of species. On average, JF and MF similarly exhibited 3 seedling species per plot. Both land cover types also displayed an equal number of individuals per hectare (density) with 14,808 and 14,318 seedling individuals for JF and MF, respectively (Figure 3; Table 3). Different from JF, MF and UF, NF pointed out an average of only 3-5 seedlings per plot with 5,192 seedling individuals per hectare.

A number of tree species in JF had “good regeneration” status, and reached about 50% of total seedlings. This proportion was equal to MF despite the less compared to UF, reaching 87% of the total seedlings. Tree species with good regeneration status in both JF and MF were mostly from Euphorbiaceae and Moraceae families (Table 4). Meanwhile, a number of species from families commonly growing in UF have not regenerated well in JF with “no regeneration” status. However, such species also mostly showed "no regeneration" status in MF.

**Discussion**

Our study showed a significant difference in herb layer community between jungle rubber and the existing natural growing forest (Table 2). As the change in tree vegetation of each land cover type, herb layer species composition seemed to be different where each land cover type was dominated by a different set of species (Table 1). A different set of herb layer species was closely related to the change in forest types. We found that the ten most dominant herb layer species in JF and MF were commonly non-native semi-shade-tolerant species with high adaptabilities, such as *C. hirta* and *Curculigo capitulata*. According to Ismaini (2015) and Breaden et al. (2012), some non-native shade-intolerant species are able to grow with high adaptability, even under shade. For instance, although *C. hirta* is an invasive non-native species commonly found in an open forest (Setyawati et al. 2015; GISD 2022), we found this species across all land cover types, indicating their adaptation ability (Ismaini 2015). *Clidemia hirta* is also known to grow invasively in disturbed forests in various parts of the world (ISSG 2022). Breden et al. (2012) reported that this species is widely distributed in many areas of Australia, even under shade. Furthermore, under a denser canopy of UF, some native species with a shade-tolerant character, such as *Maranta* sp., *Litsea* sp., and *Calamus* sp. were more abundant (Table 1).




A B

**Figure 4.** The number of seedling species (A) and the number of individuals per ha (B) at plot level. Notes: jungle rubber forest (JF), undisturbed post-logged forest (UF), mixed regrowth forest (MF), newly regrowth forest (NF). Black and grey areas of the boxes indicate the second and third quartile, respectively, and whiskers imply the upper and the lower quartile. Different letters (a, b, c) demonstrate significant differences between plot groups (Kruskal-Wallis/Mann-Whitney U test, $p < 0.05$)

**Table 4.** Tree species density and regeneration status

| Forest type | General regeneration | | | | | Regeneration of three most dominant tree species | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Density (n/ha) | | | | RS | Species | Family | Density (n/ha) | | | | RS |
| | Seedling | Sapling | Pole | Tree | | | | Seedling | Sapling | Pole | Tree | |
| UF | 15333 | 2453 | 473 | 213 | Good | *Litsea* sp. | Lauraceae | 2833 | 987 | 73 | 45 | Good |
| | | | | | | *E. tapos* | Urticaceae | 1167 | 187 | 33 | 10 | Good |
| | | | | | | *S. platiclados* | Dipterocarpaceae | 1333 | 27 | 20 | 10 | Good |
| JF | 14808 | 2585 | 523 | 286 | Good | *M. hypoleuca* | Euphorbiaceae | 2269 | 708 | 38 | 0 | Good |
| | | | | | | *H. brasiliensis* | Euphorbiaceae | 1654 | 585 | 277 | 227 | Good |
| | | | | | | *A. scholaris* | Apocynaceae | 1346 | 431 | 62 | 12 | Good |
| MF | 14318 | 2655 | 518 | 159 | Good | *A. odoratisimus* | Moraceae | 682 | 364 | 36 | 34 | Good |
| | | | | | | *E. malacense* | Euphorbiaceae | 2727 | 436 | 118 | 32 | Good |
| | | | | | | *M. gigantea* | Euphorbiaceae | 2182 | 218 | 82 | 36 | Good |
| NF | 5192 | - | - | - | New | | | | | | | |

Note: RS: Regeneration status

These species are widely distributed in the tropics (Brown 2014). On the other hand, NF with no tree stand was almost completely dominated by non-native species with light demanding character, mostly invasive species such as *Mikania micranta* (Day et al. 2016) and *Eupatorium inulifolium* (Kudo et al. 2014). Some previous studies also indicated similar findings that different tree vegetation cover changes the understory diversity especially in the herb layer. Rembold et al. (2017) reported that alien species are almost absent in forests but present in various converted land. Meanwhile, Wahyuni et al. (2016) revealed that many pioneer species dominantly grow in an open forest.

Despite the loss of many native species with shade-tolerant character in open forests, some non-native species with shade-intolerant character rapidly take the place of herb layer (Wahyuni 2016; Rembold et al. 2017). According to Beukema and van Noordwijk (2004) and Su et al. (2019), besides leading to the loss of particular species, changes in the tree vegetation cover also provide opportunities for the growth of other particular species. In some cases, open forest with decreased tree vegetation cover provides higher diversity indices than denser forest. For example, undergrowth on *Acacia nilotica* stands in Baluran National Park showed that the diversity index in open parts was higher than that of shaded ones (Djufri and Wardiah 2017). Therefore, the equal diversity indices in our study were unsurprising as the herb layer species in the four land cover types were similarly diverse despite the change in the species list. In addition, although there was a significant difference in the number of species, especially for NF, our study showed that herb layer composition among all land cover types had similar patterns in species domination and distribution as shown by IVI (Table 1). According to Indriyanto (2008), IVI reflects species domination in a community which determines the diversity and evenness indices.

The similarity in the distribution pattern of IVI in the four land cover types led to the similarity in the quantitative values of diversity (diversity index and evenness index) since the abundance of individual species is an important component in the calculation of diversity indices (McCune and Grace 2022; Magurran 2004). The diversity index will be high if a community is composed of many species with low dominance of particular species (Indriyanto 2008). In relation to the similarity in the indices of diversity, the diversity index for all forest types was between 2 and 3. This range of diversity index is still categorized as moderate but approaching the high category (Oddum 1993). Furthermore, all forest types showed an even distribution of species as indicated by the evenness index in the range of 0.7 and 0.8. According to Magurran (2004), evenness index ≥ 0.6 indicates evenly distributed individuals distribution.

Besides similarity in the diversity indices, equal value in species richness between JF and MF, even and UF (Figure 2a) might reflect the type of tropical areas as having high species richness (Brown 2014). Joshi et al. (2002) revealed that the species abundance of jungle rubber in Jambi is approaching species abundance in a secondary forest and reached about half of the natural forest. Furthermore, Böhnert et al. (2016) found a similarity in epiphyte species in terms of species richness, diversity and evenness. Similarly, Rembold et al. 2017) showed equality between jungle rubber and forest in terms of the richness and density of species in the herb layer. This fact also supported some statements that jungle rubber maintains biodiversity as the extensive management (traditional agroforestry) commonly implemented by smallholders (Joshi et al. 2002; Böhnert et al. 2016). In addition, wild colonizing species are growing as companion species alongside rubber trees (Beukema and van-Noordwijk 2004) after the shade of rubber plants hampered the growth of some other crops (Gouyon et al. 1993; Joshi et al 2002).

In relation to changes in the species list, our study found significant differences in the number of native species and seedlings. A significant difference between JF and UF in terms of the number of native species was relevant to the loss and the emergence of particular species (non-native species) as the changes in tree vegetation cover (Wahyuni 2016; Rembold et al. 2017). Land occupation and cultivation for rubber plantations in the early stage of jungle rubber development removed the native species and gave rise to the non-native species. Meanwhile, no significant difference in the number of native species and seedlings between JF and MF (Figure 2B; Figure 3A; Figure 3B) reflected a similar stage of the succession process under the change in tree vegetation cover between both forest types. As shown in Table 1, JF and MF also similarly exhibited only one seedling in the ten most dominant species. These species were pioneer species with the fast-growing character from Euphorbiaceae. Species from this family were common species in a secondary forest (Aoyagi et al. 2013; Yassir 2014). Therefore, some pioneer species other than *H. brasiliensis* growing in JF reflected a secondary forest condition as seen in MF (Table 3, Appendix A Table A2).

In more detail, indicator species differentiated JF from other forest types reflecting its specific environment (Magurran 2004; Siswo et al. 2019). As shown in Table 3, some species clearly became indicator species for particular land cover types. The indicator species of JF were significantly different from UF as the change in the environment in the jungle rubber stand. All indicator species of UF clearly explain the more natural condition compared to other land cover types (Table 3). Indicator species such as *Shore* sp., *Litsea* sp., *Palaqium* sp., *Diospyros confertiflora*, and *Calamus* sp. are the common species usually explored in a tropical rainforest (Brown 2014). Meanwhile, in spite of the similarities in herb layer species diversity indices, richness, number of native species between JF and MF, both land cover types also displayed different lists of indicator species (Table 3). However, we did not find species preferences to the specific environments between JF and MF because most of the indicator species from both land cover types similarly belong to pioneer species and with identical characteristics as non-native semi-shade-tolerant species. (Table 3). In addition, there were no tree species (seedlings) explored as significant indicator species for both JF and MF as they were similar in species and abundance. Seedling species from pioneer groups such as Euphorbiaceae were equally distributed in both land cover types with the below threshold of indicator values. According to McCune and Grace (2002), such condition has no possibility of being indicator species with significant statistical results. Both land cover types similarly exhibited optimal conditions for pioneer seedlings and the indicator species categorized non-native semi shade-intolerant species although these species were actually able to grow in various shade levels. Moreover, different from other land cover types, indicator species for NF were completely non-native shade-intolerant and light-demanding species characterizing open areas including *M. micranta* (Day et al. 2016), *Eupathorium inuliufolium* (Dar et al. 2019) and *Cyrtococcum accrescens* (Setyawati et al. 2015).

Looking further at seedlings availability, we found good potential for tree species regeneration in JF. Indeed, JF did not exhibit the same environmental conditions as UF. However, the equal number of seedling species and seedling individuals between JF and MF indicated that JF provided an opportunity for the natural succession process as a secondary forest. The structure of tree species found in both land cover types resembled inverted "J" shapes where seedlings > saplings > poles and trees (Table 4). Inverted “J” shape is a common form to describe a forest stand approaching the structure of natural forests (Magurran 2004), mainly tropical forests (Aigbe and Omokhua 2014). Such condition also illustrates the ongoing process of regeneration and succession (Suwardi et al. 2013; Malik and Bhatt 2016).

Regeneration is a vital process for forest biodiversity and sustainability. The regeneration of species within a community might vary from one to another. Sometimes the most dominant tree species do not have a good regeneration status (Nelson and Noweg 2021). However, our study found that the most dominant seedlings in JF regenerated with ‘good regeneration” status as in MF and UF (Table 4). Overall, JF was similar to MF by displaying a comparable number of species with “good regeneration” and “new species”, mostly from Euphorbiaceae and Moraceae families (Table 4). This fact confirmed some previous findings that although *H. brasiliensis* was dominant in the species composition at tree layer, extensive management of jungle rubber still provides space for other species to grow and regenerate, especially pioneer species

(Joshi et al. 2002; Meijide et al. 2018). Tree species from pioneer groups with fast-growing characters such as species from the Euphorbiaceae family (Aoyagi et al. 2013; Yassir 2014) and Moraceae family (Yassir 2014) were the common species in a secondary forest or succession forest.

In conclusion, quantitative values of species diversity sometimes do not explain differences among species communities. Accordingly, indicator species were important to describe more detailed condition of the communities. Our results found no significant difference in species diversity of herb layer communities among land cover types. However, we found differences in species characteristics, indicator species and tree regeneration potential, especially between jungle rubber and undisturbed post-logging forest and between jungle rubber and newly regrowth forest. In spite of the significant difference compared to an undisturbed forest, the number and character of herb layer species and the potential for tree regeneration in jungle rubber were better than those in newly regrowth forests. Meanwhile, jungle rubber exhibited an equal number of native species, similarity in the character of indicator species, number of seedlings and tree regeneration status to mixed regrowth forest, indicating a similar stage of forest succession as a secondary forest. Thus, jungle rubber can be a good alternative when a plantation system is inevitable in a post-logging forest as a good solution in resolving conflicts of interest between biodiversity and local people's dependence on forests.

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