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**Phylogenetic structure of understorey plant
communities in four different land-use systems
in Sumatra (Indonesia)**

**Phylogenetische Struktur der Unterwuchs Pflanzengesellschaften in
vier verschiedenen Landnutzungssystemen auf Sumatra (Indonesien)**

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List of Abbreviations

ANITA	Amborella, Nymphaeales and Illiciales, Trimeniaceae-Austrobaileya
ANOVA	Analysis of Variance
APG	Angiosperm Phylogeny Group
BLADJ	Branch Length Adjuster
EFForTS	Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems
IUCN	The International Union for Conservation of Nature
MNTD	Mean Nearest Distance
MoE	Ministry of Environment
MoF	Ministry of Forestry
MPD	Mean Pairwise Distance
NRI	Net Relatedness Index
NTI	Nearest Taxon Index
PD	Phylogenetic Diversity
PS	Phylogenetic Structure
SEAMEO BIOTROP	Southeast Asian Regional Centre for Tropical Biology
SES	Standardized Effect Size
SR	Species Richness
TD	Taxonomic Diversity
TPI	<i>Tebang Pilih Indonesia</i> (Indonesian Selective Logging System)
TPTI	<i>Tebang Pilih Tanam Indonesia</i> (Indonesian Selective Logging with Replanting System)
Tukey's HSD	Tukey's Honest Significant Different

Summary

Tropical lowland forests in Southeast Asia are considered to be one of the most diverse ecoregions in the world, yet simultaneously face a huge threat of biodiversity loss, primarily due to forest conversion into human-dominated landscapes such as agricultural areas. Along with deforestation and land-use change, the invasion of alien plant species also alters native plant communities, particularly the understorey communities. Understorey communities contribute significantly to the diversity of tropical habitats and play an important role in forest succession and ecosystem functioning. Hence, understanding the impact of forest conversion and alien species invasion on the understorey communities will provide more information on biodiversity maintenance and ecosystem functioning. Additionally, this study will provide new insights on the impact of extensive plantation systems on native plant communities.

In this study, I had three main objectives: (1) analyzing phylogenetic diversity (PD) and correlating PD with taxonomic diversity (TD), (2) analyzing phylogenetic structure, and (3) investigating the role of alien plant species on the phylogenetic structure of understorey plant communities across four land-use systems.

The study is based on a complete vascular plant inventory that was carried out by Katja Rembold in the context of subproject B06 of the EFForTS project (*Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems in Sumatra (Indonesia)*). I used the data from 32 core plots in four land-use systems (tropical lowland rainforest, jungle rubber, rubber plantations and oil palm plantations) and in two landscapes (Harapan, Bukit Duabelas) in Jambi Province (Sumatra). I combined taxonomic (species richness (SR), Simpson's index) and phylogenetic metrics (phylogenetic diversity and structure) as the main variables to achieve my three main objectives.

I used a total of 151,728 individuals, of which 1,533 comprised of morphologically identified species and 135 plant families for the analysis. My results demonstrated that PD (Faith's PD and weighted-Faith's PD) was significantly different among land-use systems ($F = 41.39$, $df = 3$, $p < 0.001$ and $F = 26.3$, $df = 3$, $p < 0.001$). PD (Faith's PD and weighted-Faith's PD) was highest in forest ($22,820.70 \pm 5,231$ and $22,451.70 \pm 7,048$ million years) and lowest in rubber and oil palm plantations ($8,377.54 \pm 1,817$ and $7,548.66 \pm 2,271$ million years, and $7,006.40 \pm 3,091$ and $6,803.49 \pm 1,699$ million years). TD (SR and Simpson's index) was likewise significantly different among land-use systems ($F = 35.73$, $df = 3$, $p < 0.001$ and $F = 26.63$, $df = 3$, $p < 0.001$). SR was highest in forest (238.50 ± 71 species per plot) and lowest in rubber and oil palm plantations (58.65 ± 21 and 65.5 ± 18 species per plot). Simpson's index was highest in forest (0.95 ± 0.04) and other land-use systems had similar values.

Hence, forest conversion evidently leads to decreased PD and TD towards more intensively managed land-use systems.

Other PD metrics, namely MPD (Mean Pairwise Distance) and MNTD (Mean Nearest Taxon Distance), also showed significant differences among the land-use systems ($F = 15.89$, $df = 3$, $p < 0.001$ and $F = 14.96$, $df = 3$, $p < 0.001$). MPD was highest in oil palm plantations (551.08 ± 20 million years) and MNTD was the lowest in forest (150.74 ± 11 million years). Thus, MPD and MNTD showed a reverse pattern than PD (Faith's PD and weighted-Faith's PD) and SR. Moreover, species richness had a strong positive correlation with PD ($R^2 = 0.98$, $df = 30$, $P < 0.001$) and a negative correlation with MPD and MNTD ($R^2 = 0.34$, $df = 30$, $P < 0.001$ and $R^2 = 0.72$, $df = 30$, $P < 0.001$).

Analyses on phylogenetic structure (NRI (Net Relatedness Index) and NTI (Nearest Taxon Index)) also showed significant differences among land-use systems ($F = 14.3$, $df = 3$, $p < 0.001$ and $F = 3.05$, $df = 3$, $p < 0.01$). Forest had the highest NRI (0.63 ± 1), while oil palm plantations had the lowest NRI (-3.17 ± 1). Forest, rubber and oil palm plantations had similar NTI, while in jungle rubber, NTI (0.15 ± 1) was the lowest of all land-use systems. In more detailed observations, most plots (>50%) in forest, jungle rubber and rubber had a randomly distributed phylogenetic structure in overall phylogeny. In contrast, most plots (87.5%) in oil palm plantations had overdispersed structures. These results were slightly different for terminal phylogeny. Half of the forest plots had clustered phylogenetic structures, but more than 50% of the plots in jungle rubber, rubber and oil palm plantations had randomly distributed phylogenetic structures.

The existence of alien plant species in each land-use system evidently influenced the phylogenetic structure of understorey plant communities. Excluding alien species from the community reduced the mean NRI in jungle rubber, rubber and oil palm plantations ($t = -2.96$, $df = 7$, $p < 0.05$, $t = -2.68$, $df = 7$, $p < 0.01$ and $t = -4.32$, $df = 7$, $p < 0.01$), but not in forest. Conversely, excluding alien plant species in the communities reduced NTI only in agricultural systems, namely rubber ($t = -2.9$, $df = 7$, $p < 0.05$) and oil palm plantations ($t = -4.64$, $df = 7$, $p < 0.01$). In more detailed observations, the exclusion of alien plant species increased the number of plots with an overdispersed phylogenetic structure (12.5-25%) in all land-use systems in the overall phylogeny (NRI). Conversely, in the terminal phylogeny (NTI), the exclusion led to randomly distributed phylogenetic structures, especially in all oil palm plantations.

In the individual-based metrics (weighted metrics), the exclusion of alien plant species only reduced the weighted NRI, particularly in jungle rubber ($t = -8.42$, $df = 7$, $p < 0.001$) and oil palm plantations ($t = 3.74$, $df = 7$, $p = 0.007$), while in the other land-use systems the exclusion had apparently no influence. Furthermore, this exclusion increased the number of plots (25 - 37.5%) with overdispersed phylogenetic

structure in jungle rubber and oil palm plantations. However, the exclusion had no effect on the terminal phylogeny (weighted NTI).

In conclusion, forest conversion into more intensively managed systems negatively affects understorey plant diversity both at taxonomic and phylogenetic level. PD has strong correlation with TD. Furthermore, forest conversion generates increasing random and overdispersed phylogenetic structures along an intensification gradient. Invasion of alien plant species evidently plays a strong role in changing the phylogenetic structure of the plant communities. Instead of creating more overdispersed community structures, the presence of alien plant species leads to a less overdispersed and a more random phylogenetic structure. Therefore, I recommend that future studies should give more attention to the invasion of alien plant species in the local plant communities, and investigate not only the impact upon species loss, but also the change in overall community composition caused by forest conversion.

Zusammenfassung

Die tropischen Tieflandregenwälder Südostasiens gehören zu den Ökoregionen mit der größten biologischen Vielfalt weltweit. Dieser Reichtum ist heutzutage stark bedroht auf Grund der Umwandlung tropischer Wälder in Siedlungen bzw. Landwirtschaftliche Anbauflächen und durch die Einwanderung invasiver Pflanzenarten. Letztere konkurrieren mit der Verbreitung heimischer Pflanzenarten, insbesondere mit Unterwuchsarten, die einen wesentlichen Beitrag zur Vielfalt der tropischen Lebensräume leisten und für die sukzessive Entwicklung der Wälder sowie das Ökosystem eine entscheidende Rolle spielen. In dieser Arbeit wird untersucht, welche Auswirkung invasive Pflanzen auf den Unterwuchs tropischer Wälder haben um einen Beitrag zum Schutz von biologischer Vielfalt sowie Ökosystemen zu liefern.

Zunächst wird in dieser Arbeit die phylogenetische Vielfalt (PD) analysiert und mit taxonomischer Vielfalt (TD) korreliert (1). Zudem wird die phylogenetische Struktur untersucht (2) und die Wirkung der invasiven Pflanzenarten auf die phylogenetische Struktur des Unterwuchses innerhalb der vier Landnutzungssysteme ermittelt (3).

Die vorliegende Arbeit entstand im Rahmen des Teilprojekt B06 des Projektes „Ecological and socioeconomic functions of tropical lowland rainforest transformation systems (Sumatra, Indonesia)“ (EFForTS). Diese Studie basiert auf einer umfassenden Vegetationsaufnahme durchgeführt von Katja Rembold. Zwei Landschaften in der Provinz Jambi (Harapan und Bukit Duabelas) und 32 Kernflächen (Plots) wurden für die Vegetationsaufnahmen ausgewählt. In jeder Landschaft wurden je vier Flächen in vier verschiedenen Landnutzungssystemen gewählt: Tieflandregenwald, Kautschuk-Agroforstsysteme, Kautschukplantagen und Ölpalmpflanzungen. Es wurden taxonomische (Artenreichtum, Simpson-Index) und phylogenetische Maße (phylogenetische Diversität und Struktur) verwendet, um meine Hauptziele zu erreichen.

Der Datensatz umfasst insgesamt 151.728 Individuen von 1.533 morphologisch identifizierten Arten und 135 Pflanzenfamilien. Die Ergebnisse zeigen, dass es signifikante Unterschiede in der PD aller Landnutzungssysteme gibt ($F = 41.39$, $df = 3$, $p < 0,001$ und $F = 26,3$, $df = 3$, $p < 0,001$). Wald hat die höchste PD ($22,820.70 \pm 5231$ und $22,451.70 \pm 7.048$ Millionen Jahren), während Kautschuk- und Ölpalmpflanzungen die niedrigste PD aufweisen ($8,377.54 \pm 1.817$ und $7,548.66 \pm 2.271$ Millionen Jahren, und $7,006.40 \pm 3091$ und $6,803.49 \pm 1.699$ Millionen Jahre). Die TD der Landnutzungssysteme ist ebenfalls unterschiedlich ($F = 35.73$, $df = 3$, $p < 0,001$ und $F = 26.63$, $df = 3$, $p < 0,001$). Wald hat die höchsten Artenzahlen ($238,50 \pm 71$ Arten pro Plot) und Kautschuk- und Ölpalmpflanzungen die niedrigsten (58.65 ± 21 und $65,5 \pm 18$ Arten pro Plot). Die Diversität (Simpson-Index) war im Wald ebenfalls am höchsten ($0,95 \pm 0,04$), in den anderen Landnutzungssystemen jedoch

ähnlichen. Diese Ergebnisse zeigen, dass sich sowohl PD als auch TD durch die Umwandlung von Wald zu Agrarflächen verringern.

Weitere PD-Maße wie MPD (mittlere paarweise Distanz) und MNTD (mittlere Distanz zum nächsten Verwandten) zeigten ebenfalls deutliche Unterschiede zwischen den Landnutzungssystemen ($F = 15.89$, $df = 3$, $p < 0,001$ und $F = 14.96$, $df = 3$, $p < 0,001$). Ölpalmlantagen hatten die höchste MPD ($551,08 \pm 20$ Millionen Jahren) und Wald die niedrigste MNTD ($150,74 \pm 11.000.000$ Jahre). MPD und MNTD weisen also ein umgekehrtes Muster auf als PD (Faith PD und gewichtet-Faith PD) und Artenreichtum. Der Artenreichtum korreliert stark positiv mit PD ($R^2 = 0,98$, $df = 30$, $p < 0,001$) und negativ mit MPD und MNTD ($R^2 = 0,34$, $df = 30$, $p < 0,001$ und $R^2 = 0,72$, $df = 30$, $p < 0,001$).

Die phylogenetische Struktur (NRI (Net Relatedness Index) und NTI (Nearest Taxon Index)) wies ebenfalls deutliche Unterschiede zwischen den Landnutzungssystemen auf ($F = 14,3$, $DF = 3$, $p < 0,001$ und $F = 3,05$, $df = 3$, $p < 0,01$). Wald hatte die höchste NRI ($0,63 \pm 1$) und Ölpalmlantagen die niedrigste NRI ($-3,17 \pm 1$). Wald, Kautschuk- und Ölpalmlantagen hatten eine vergleichbare NTI, während Kautschuk-Agroforst die niedrigste NTI ($0,15 \pm 1$) unter den vier Landnutzungssystemen hatte. Die meisten Plots ($> 50\%$) im Wald, im Kautschuk-Agroforst und in den Kautschukplantagen hatten eine zufällig verteilte phylogenetische Struktur während die Strukturen der meisten Ölpalmlots ($87,5\%$) „overdispersed“ war. Bezüglich der NTI sah die strukturelle Verteilung anders aus: die phylogenetischen Strukturen der Hälfte der Waldplots war „clustered“, während mehr als 50% der Plots im Kautschuk-Agroforst, Kautschuk- und Ölpalmlantagen zufällig verteilte phylogenetische Strukturen hatten.

Das Vorkommen invasiver Pflanzen beeinflusste die phylogenetische Struktur des Unterwuchses in allen Landnutzungssystemen. Der Ausschluss der invasiven Pflanzen aus der Gemeinschaft verringerte den mittleren NRI im Kautschuk-Agroforst, Kautschuk- und Ölpalmlantagen ($t = -2,96$, $df = 7$, $p < 0,05$, $t = -2,68$, $df = 7$, $p < 0,01$ und $t = -4,32$, $df = 7$, $p < 0,01$), nicht aber im Wald. Im Gegensatz dazu verringerte der Ausschluss von invasiven Pflanzen die NTI nur in den intensiv genutzten landwirtschaftlichen Anbauflächen, nämlich Kautschuk- ($t = -2,9$, $df = 7$, $p < 0,05$) und Ölpalmlantagen ($t = -4,64$, $df = 7$, $p < 0,01$). Darüber hinaus steigert der Ausschluss invasiver Pflanzen die Zahl der Plots mit „overdispersed“ phylogenetischer Struktur ($12,5$ bis 25%) in allen Landnutzungssystemen in der gesamten Phylogenie (NRI). Im Gegensatz dazu führte der Ausschluss invasiver Pflanzen zu einer zufällig verteilten phylogenetischen Struktur bezüglich der NTI, insbesondere in allen Ölpalmlots.

Der Ausschluss von invasiven Pflanzen reduzierte die gewichtete NRI, besonders im Kautschuk-Agroforst ($t = -8,42$, $df = 7$, $p < 0,001$) und Ölpalmlantagen ($t = 3,74$, $df = 7$, $p = 0,007$), während in den anderen Landnutzungssystemen der Ausschluss

offenbar keinen Einfluss hatte. Darüber hinaus erhöhte der Ausschluss die Anzahl der Plots (25 bis 37,5%) mit „overdispersed“ PD in Kautschuk- und Ölpalmplantagen, hatte jedoch keine Auswirkung auf die gewichtete NTI.

Die Umwandlung von Wald in intensiver bewirtschaftete Systeme hat eine negative Auswirkung sowohl auf die phylogenetische als auch auf die taxonomische Diversität der Unterwuchspflanzen. Darüber hinaus erzeugt die Umwandlung zunehmend zufällig und „overdispersed“ phylogenetische Strukturen entlang eines Intensivierungsgradienten. Invasive Pflanzen spielen eine sehr wichtige Rolle bei der Veränderung der phylogenetischen Struktur der Pflanzengesellschaften in den verschiedenen Landnutzungssystemen. Anstatt mehr „overdispersed“ Gesellschaftsstrukturen zu erzeugen, führt das Vorhandensein invasiver Pflanzen zu einer zufällig Struktur. Diese Ergebnisse zeigen, dass zukünftige Studien sich nicht nur auf die Auswirkungen von Artverlust konzentrieren sollten, sondern auch die Auswirkung invasiver Pflanzen auf die einheimischen Pflanzengesellschaften berücksichtigen sollten.

1. Introduction

1.1. Background

Tropical lowland forests in Southeast Asia are considered to be one of the most diverse ecoregions in the world (Brooks et al., 2006; Koh et al., 2013; Sodhi et al., 2010a). This region is also placed second in regards to proportion of endemic vascular plant species (25%) (Sodhi et al., 2010b). Furthermore, four of 25 biodiversity hotspots worldwide are identified in this region where both high number of endemic species and massive habitat loss coincide (Myers et al., 2000). The unique geological history combined with a stable tropical climate and numerous insular biotas has produced a high level of species richness and high levels of endemism (Sodhi et al., 2004). It has been estimated that 59.6% of the 29,375 recorded vascular plant species in Indonesia do not occur anywhere else (Sodhi et al., 2004).

Recent loss of habitat mainly due to deforestation has put thousands (8,343–48,043) of vascular plant species at risk of extinction in Southeast Asian countries (Sodhi et al., 2010b). Southeast Asia has also been described to have the highest proportion of threatened species across taxa such as vascular plants, birds, mammals and reptiles (Sodhi et al., 2010b). Indonesia is listed in the top ten countries worldwide with the highest number of threatened plant species, with approximately 426 species (IUCN, 2015). Based on current deforestation rates in Southeast Asia, Sodhi and Brook (2011) estimated that around 24-26% of the existing endemic taxa or 859-4,815 vertebrate species and 8,343–48,043 species of vascular plants are at risk of extinction due to habitat loss.

Human populations have converted natural habitats for agriculture, forestry and other uses since many centuries ago (Ellis and Ramankutty, 2008; Hurtt et al., 2011), but large-scale deforestation in particular in Southeast Asia began around the 1800s (Sodhi et al., 2004). Today, more than three quarters of native terrestrial biosphere habitats have been transformed into human modified land-use systems or anthropogenic biomes (Ellis and Ramankutty, 2008; Ellis et al., 2012).

In 2012, Indonesia had an annual forest loss of around 0.84 million ha, which makes it a country among the highest deforestation rates worldwide (Margono et al., 2014). Furthermore, most of this loss occurred in the lowland forests which often hold high levels of biodiversity (Margono et al., 2014).

There has been a long history of forest degradation and conversion into human modified land-use systems in Indonesia. In Sumatra in particular, forest conversion into large-scale monoculture plantations such as oil palm (*Elaeis guineensis*), industrial timber (*Acacia mangium*) and rubber (*Hevea brasiliensis*) plantations occurred rapidly since the 1970s (Beukema et al., 2007). Old growth forests were used extensively and unrestrictedly for timber production, until the Indonesian government initiated the Indonesian selective logging system (*TPI = Tebang Pilih Indonesia*) to sustainably manage the forests in the 1970s. Later on in the 1990s, a new system known as Indonesian selective logging with replanting system (*TPTI= Tebang Pilih Tanam Indonesia*) was introduced and is still implemented until today (Rimbawanto, 2006).

Rubber trees were introduced from Brazil in the second half of the 19th century. After successful introduction, the species became an important commercial crop due to the high demand of rubber for industrial uses and consumer goods in the last part of 19th century (Byerlee, 2014). Rubber then started to flourish as “jungle rubber”, agroforest crop, in Sumatra in the beginning of the 20th century (Gouyon et al., 1993; Murdiyarto et al., 2002). By definition, jungle rubber is a complex agroforestry system where woody perennials (native woody plants) are purposely planted with agricultural crops (rubbers) in some form of spatial arrangement or temporal sequence (Gouyon et al., 1993). In this study the jungle rubber is a secondary forest enriched with rubber trees.

Oil palm is native to West and Central Africa. The introduction to Indonesia began in 1848 when the first four trees were received and planted in Bogor Botanic Gardens in Java. These four trees later on became the main seed source for all Southeast Asian oil palm plantations in Sumatra. The development of commercial oil palm plantations began in 1911 under the Dutch administration (Henderson and Osborne, 2000). Since

then, the plantations developed rapidly and since 2005 Indonesia has been the world's largest palm oil producer (Henderson and Osborne, 2000). This development did not come without environmental consequences: during the period of 1990-2005, more than 55% of oil palm plantations in Indonesia were established on formerly forested areas. In 2010 only a quarter of Sumatra's forests remained as reported by Miettinen et al. (2011).

Along with deforestation, the invasion of alien plant species also alters native plant communities. Alien or non-native plant species are plant taxa that occur in a given area due to intentional or accidental introduction as a result of human activities (Richardson et al., 2008). Alien plants can become invasive and outcompete the native ones which indirectly causes the loss of the native species (Peh, 2010). Invasive alien species cause enormous economic losses and costs in Southeast Asia. The total annual loss attributed to agriculture, human health and environment was estimated to be US\$33.5 billion in this region, nearly 90% of which are associated with the agricultural sector, for instance damaged crops due to weeds and pathogens (Nghiem et al., 2013).

Additionally, the introduction of alien species can cause biotic homogenization in the areas in which they are introduced (Winter et al., 2009). Biotic homogenization means increasing species similarity across space over time due to species invasions and extinctions (Olden, 2006). This essentially means that native species in a given area are replaced by alien species. Therefore, this process will probably lead to biotic simplification, which is caused by extirpation of local species being replaced by newly arriving widespread alien species (Olden et al., 2004).

Indonesia among other Southeast Asian countries harbored the largest number of invasive plant and animal species (Peh, 2010). But the information about the ecology of invasive species and its impact on local biodiversity is limited. Currently, our knowledge of invasive plant species in Indonesia is mainly based on the work of Tjitrosoedirdjo et al. (2007a, 2005) and MoE and SEAMEO BIOTROP (2006). Sumadijaya (2012) additionally focuses on the distribution of invasive grass species. Apart from these country wide reports, there are also some small scale reports that

focus on certain areas (Kudo et al., 2014; Sunaryo et al., 2012; Zuhri and Mutaqien, 2013).

Those aforementioned threats such as forest conversion and alien plant invasion will have enormous impacts not only on tree communities but also on understorey plant communities. Understorey plant communities play an important role in forest succession and ecosystem functioning since tree seedlings or regeneration is found in this layer of the community. Furthermore, understorey plants, in particular herbaceous species, have higher natural extinction rates than plant species in other strata (Gilliam, 2007). Some studies also reported that understorey plant species are relatively more vulnerable to alien species plant invasion. Once the alien invasive species is established in the herb layer, they can rapidly dominate the communities and reduce the species diversity (Gilliam, 2007; Lorenzo et al., 2012). These alien species also benefit from their higher competitive ability and allelopathy which helps to facilitate their persistence and dominance (Hernández et al., 2014).

There are many studies related to the biodiversity status of tropical countries. Notably, many of them are concentrated in well-conserved and protected areas with low levels of human activities or influence (Chazdon et al., 2009; Schulze et al., 2004; Waltert et al., 2011). In order to understand the current status of our forest and understand possible future trajectories, investigating the biodiversity pattern across scale and within multi land-use systems is crucial. Some studies in this context have shown that human modified land-use systems such as rubber agroforests are able to combine rich biodiversity and ecosystem functions, as well as livelihood benefits for people (Beukema and van Noordwijk, 2004; Beukema et al., 2007; Villamor et al., 2014). Several other studies comparing faunal biodiversity between forests and agricultural areas (e.g. rubber plantation, jungle rubber and oil palm plantations) have shown that human modified land-use systems significantly reduce biodiversity (Danielsen et al., 2009; Fitzherbert et al., 2008; Joshi et al., 2002). The loss of biodiversity has considerable impact on ecological functions (Cardinale et al., 2006) such as vulnerability to fire, induced droughts, elevated CO₂ among many other impacts (Tilman et al., 2014).

There has been a rapid increase of incorporating evolutionary history in understanding community composition and diversity (Cavender-Bares et al., 2009; Faith, 2002; Vamossi et al., 2009; Webb et al., 2002). A meta-analysis study on biodiversity-plant productivity relationship even showed that evolutionary history represented by phylogenetic diversity provided critical information for understanding and predicting the effects of biodiversity loss (Cadotte et al., 2008). This indicates that evolutionary history is an important supplement to revealing a complete picture of biodiversity structure (Devictor et al., 2010; van Meerbeek et al., 2014). Moreover, incorporating evolutionary history will also provide increased understanding of the influence of invasive species on community structure. It has been shown that two communities of equal taxonomic diversity may be composed of species with either highly similar or different phylogenetic histories leading to clustered or overdispersed phylogenetic community composition (Devictor et al., 2010; Webb, 2000; Webb et al., 2002). Therefore, incorporating evolutionary history in the examination of biodiversity will help in gaining a better understanding of the impact of forest conversion into human modified land-use systems and provide more insights on the influence of alien species upon the local communities.

1.2. Objectives of study

This study had three main objectives: (1) analyzing phylogenetic diversity (PD) of vascular understorey plants from 32 core plots within four different land-use systems and comparing PD with taxonomic diversity (TD), (2) analyzing phylogenetic structure (PS) of vascular understorey plant communities in four land-use systems (3) investigating the role of alien plant species in determining the phylogenetic structure. These objectives support the main goal of the study, which is to examine the impact of forest conversion and alien plant invasion on native plant diversity.

To achieve these objectives, three main hypotheses were investigated:

- 1) Forest conversion into more intensively managed land-use systems has a negative impact on PD.
 - a. PD is highest in forest and lowest in the more intensively managed systems.
 - b. PD is correlated with TD.
- 2) Forest conversion into more intensively managed land-use systems alters PS.

- a. PS in forest is clustered; indicating that closely related species with similar traits co-occur.
 - b. Forest conversion leads to more random or over-dispersed PS.
- 3) Alien plant invasion contributes to creating overdispersed PS in agricultural areas.

2. Methods

2.1. Study area

Sumatra is the second largest island in Southeast Asia with an area of 475,000 km², and lies in the westernmost part of Indonesia. It stretches from 95° to 107° longitude East and from 5° N to 5° S latitude (Laumonier, 1997; Murdiyarso et al., 2002). The highest places in Sumatra are located in the Barisan Mountains with the highest peak at Mt. Kerinci at 3,805 m above mean sea level (Barber et al., 2005). The soils were formed from various parent materials. The Eastern lowland parts of Sumatra where major rivers are located are mainly dominated by hydromorphic soil. The peatland areas of Eastern Sumatra, mostly around the provinces Riau and Jambi, are composed of organosols. In the lowland as well as in the mountainous areas, yellow podzolic soils cover most of the areas. In the western part, sandy regosols dominate (Whitten et al., 2000).

The climatic conditions of Sumatra are typical for an equatorial island with abundant and evenly distributed rainfall through the year (Laumonier, 1997; Whitten et al., 2000). The rainfall in the mountains is very variable with some areas in the eastern Barisan Range receive less than 1,500 mm, while rainfall in the western part of this mountain range may reach 6,000 mm. In average the rainfall in Sumatra including lowland areas is approximately 2,500 mm per year (Whitten et al., 2000). Generally, most rainfall occurs from November to March, due to a strong influence of the wet northwest monsoon. The driest months are between May to September which is associated with the prevalence of the dry southeast monsoon (Aldrian and Dwi Susanto, 2003). Mean monthly temperatures are more or less uniform.

In the case of Jambi province and most northern areas, two peaks of rainfall were identified between October to November and March to May, which are associated with the southward and northward movement of the inter-tropical convergence zone (Aldrian and Dwi Susanto, 2003). In this province, the annual rainfall is $2,235 \pm 385$ mm and the mean annual temperature is 26.7 ± 1.0 °C. The dominant soil in this area is categorized as loam and clay Acrisol soils (Allen et al., 2015).

Due to its geological history and climatic condition, Sumatra supports a wide range of vegetation types and high species richness. The natural vegetation is distributed from coastal mangroves up to mountainous areas and from sandy soils to peat swamps. The biota itself is also unique, from a parasitic plant of *Rafflesia* spp. to the tallest flower of *Amorphophallus titanum*. Not to mention the dominant Dipterocarp tree species such as *Shorea* spp. and *Dipterocarpus* spp. in the lowland forest areas (Whitten et al., 2000).

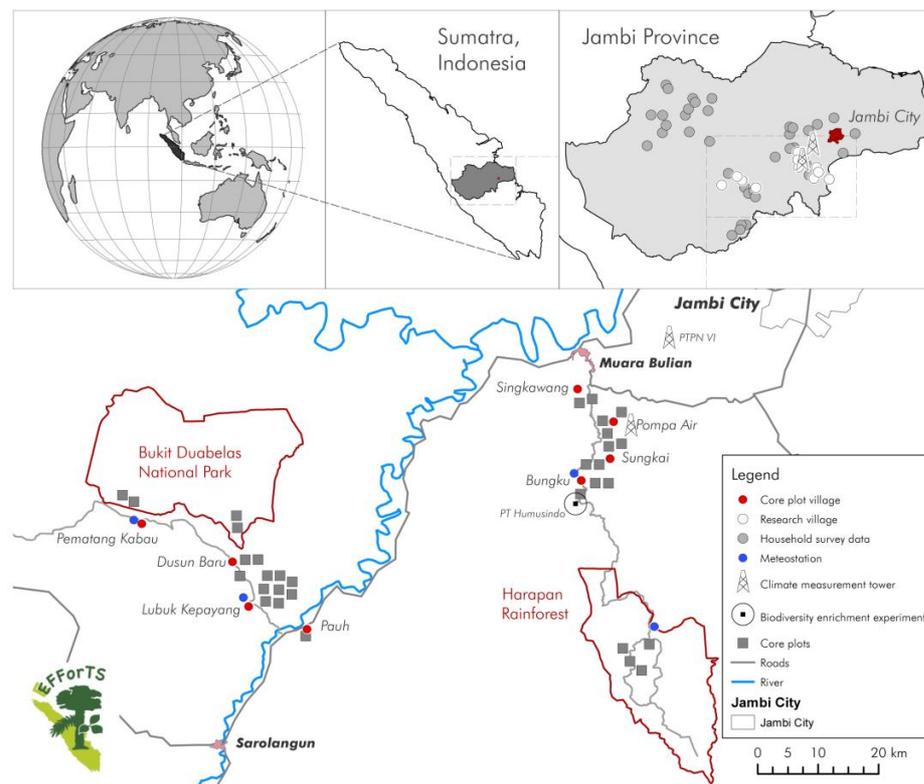


Figure 1. Map of the study area in Jambi province (Sumatra). Two lowland forest areas were delineated with red lines. Three human modified land-use systems (jungle rubber, rubber and oil palm plantations) occurred in mosaics located between forest areas and the city of Jambi. Core plots (grey colour) were located in all four land-use systems. (Source: Drescher et al. in prep.)

This study is part of the EFForTS project (*Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems' in Sumatra (Indonesia)*), a collaborative research project between the University of Göttingen and several institutions in Indonesia. The project region of the EFForTS project is located in Jambi Province, Sumatra (Indonesia) where two remaining lowland rainforests,

namely Bukit Duabelas National Park and Harapan Rainforest, are situated representing two landscapes (Figure 1).

Bukit Duabelas National Park is a lowland forest with an area of 60,500 hectares and had been designated since 2000. Prior to designation as a national park, this forest was a productive forest managed by private concession. In the northern part of the area, an old growth tropical lowland forest can still be found. The topography ranges from 50 to 400 meter above sea level with annual temperature between 20° and 30° C. The average daily temperature ranges from 24°C to 29°C and with relative humidity about 72-100% (Kusuma et al., 2011). Interesting biota that can be found in this area are dipterocarp trees, a commercially important species of rattan (*Calamus manan*) and some enigmatic fauna for instance siamang (*Symphalangus syndactylus*) and Sunda clouded leopard (*Neofelis diardi*) (MoF, 2013).

Harapan Rainforest is a new initiative for ecosystem restoration concession in Sumatra. With an area of 98,455 hectares it stretches the boundary between Jambi and South Sumatra Province. The mean monthly rainfall varies from 79 to 385 mm, with a mean annual rainfall of 2,390 mm. The topography is undulating with an elevation range between 30 and 120 m above sea level (Harrison and Swinfield, 2015).

Mosaics of various anthropogenic land-use systems surround both of the lowland protected forests. The dominant intensively managed systems that are found and typical are jungle rubber (extensive rubber plantations), intensive rubber and oil palm plantations. These are also the land-use systems that were investigated in this study. Thus, any term regarding to each system will refer to these land-use systems.

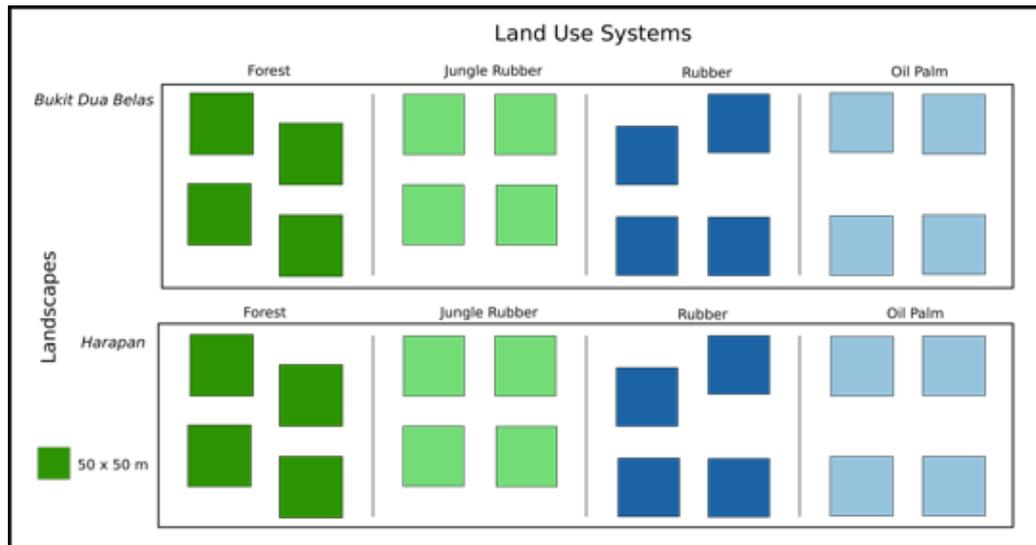


Figure 2. Schematic representation of the plot design of the four land-use systems located in two landscapes (Bukit Duabelas and Harapan). (Source: modified from Kreft (2012).

2.2. Study design

Four land-use systems (forest, jungle rubber, rubber plantations and oil palm plantations) are located in each landscape. In every land-use system, four replicates of 50 x 50 m core plots were established in each of the four land-use systems (Figure 2). Nested inside each core plot, a total of five 5 x 5 m plots were placed randomly (Figure 3). In total 32 core plots (8 plots for each land-use system) were investigated. Each core plot had to fulfill certain requirements such as an elevation below 100 m above sea level, identical soil condition, similar age of oil palm trees (average age of 14 years) and rubber trees (average age of 13 years) and similar jungle rubber conditions (contain remaining old forest trees).

2.3. Data collection

The present study is based on a complete vascular plant inventory that was already carried out within all 32 core plots by Katja Rembold. All vascular plant individuals (including herbaceous terrestrial plants, seedlings, shrubs and small trees with dbh up to 10 cm) growing within the five subplots of each core plot were identified and counted. Whenever possible, herbarium specimens were prepared of three individuals per species for identification and later deposition at several Indonesian herbaria

(Herbarium Bogoriense, SEAMEO BIOTROP Herbarium, UNJA Herbarium, and Harapan Rainforest Herbarium).

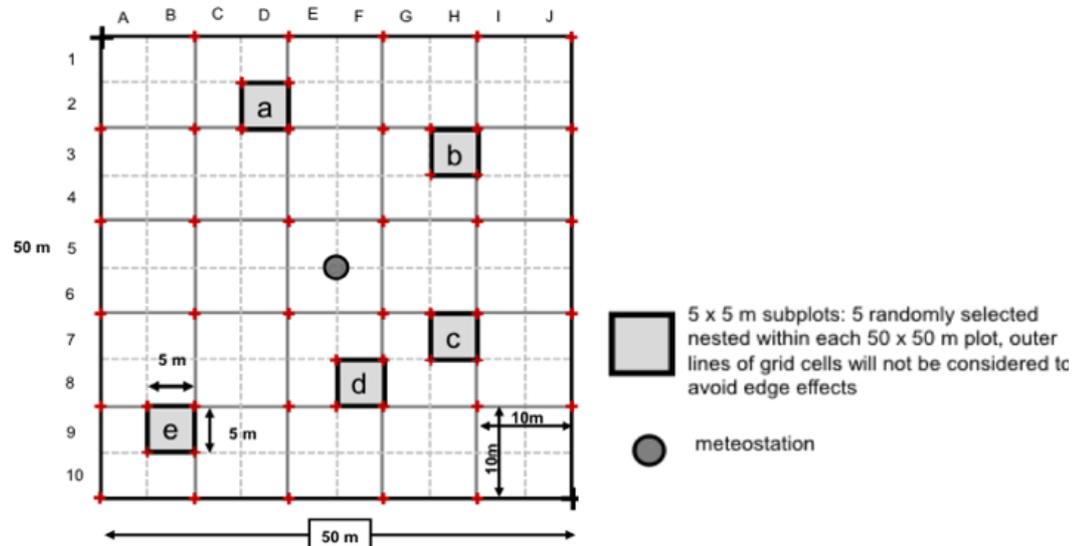


Figure 3. Detailed plot design of one 50 x 50 m² core plot and five 5 x 5 m² subplots. (Source: Efforts, 2015).

2.4. Data preparation

All plant species from the 32 core plots that have been identified to species level (including morpho-species) were included in this study. All names were checked following The Plant List (<http://www.theplantlist.org>) and classified according to APG III system (Angiosperm Phylogeny Group III system) (Boyle et al., 2013; The Plant List, 2013). The status of native or alien was determined by using several references (see appendix 1 for details). For the purposes of this study, a species was considered alien if it had a native distribution range outside of Sumatra. The final list consisted of standardized name with proper APG III classification for genus and family, with alien or native status.

2.5. Phylogenetic tree reconstruction

The final plant species list was then used to construct a phylogenetic tree of Sumatran understorey plant communities in four different land-use systems. Online web-service phylomatic provided with megatree R20120829 was used to create the phylogenetic tree (Webb and Donoghue, 2005). The final tree afterwards was dated using the

BLADJ algorithm in Phylocom software (Webb et al., 2008), which is based on the fossil dating proposed by Wikström (2001). Since the backbone tree was based on a family level phylogeny (APG III), there were many polytomy clades below family level. To resolve these polytomies, all species were assigned randomly within each clade using multi2di function in R (Roquet et al., 2013). The result was an ultrametric (all the tips are equidistant from the root) and rooted tree (ancestor-descendant relationship is provided) with its appropriate evolutionary date, which was then ready for further analyses.

2.6. Metric calculations and statistical analyses

Taxonomic diversity (TD) of the four different land-use systems was calculated. TD (species accumulation curve with rarefaction method) were calculated using vegan package (Oksanen et al., 2013), while rank abundance curves highlighting alien species in the different transformation systems were computed using BiodiversityR package (Kindt and Coe, 2005).

Five common phylogenetic metrics were used to determine phylogenetic diversity and structure of each land-use systems. These metrics are:

- i. Faith's PD (Phylogenetic Diversity), the sum of all branch lengths connecting all species in a community.

$$PD = \sum_i^n l_i$$

Where, n is the number of the branches which having a length of l for each species I (Faith, 1992; Swenson, 2014; Winter et al., 2013).

- ii. Weighted-Faith's PD, incorporating relative abundance of individual species in a community.

$$\text{Weighted PD} = n \times \frac{\sum_i^n l_i \bar{A}_i}{\sum_i^n \bar{A}_i}$$

Where, \bar{A} is the average abundance of all species subtended by its particular branch (Swenson, 2014).

- iii. MPD (Mean Pairwise Distance), the average evolutionary distance between all pairwise species.

$$MPD = \frac{\sum_i^n \cdot \sum_j^n \delta_{i,j}}{n}, \text{ where } i \neq j$$

Where, n is the number of species in the community, δ is the phylogenetic distance matrix, and $\delta_{i,j}$ is the phylogenetic distance between species I and j (Swenson, 2014; Webb, 2000).

- iv. MNTD (Mean Nearest Taxon Distance), the mean of the branch lengths connecting each species to its closest relative.

$$MNTD = \frac{\sum_i^n \min \delta_{i,j}}{n}, \text{ where } i \neq j$$

Where, n is the number of species in the community, $\delta_{i,j}$ is the phylogenetic distance between species i and species j, and $\min \delta_{i,j}$ is the minimum phylogenetic distance between species i and all other species in the community (Swenson, 2014; Webb, 2000).

- v. NRI (Net Relatedness Index) and NTI (Nearest Taxon Index), the effects of species richness via repeated random resampling from a source pool based on a null model. In this study, 999 permutations were used for the computation.

$$SES_{metric} = \frac{Metric_{observed} - Mean(Metric_{null})}{sd(Metric_{null})}$$

Where, metric is the value of MPD for SES_{NRI} , and MNTD for SES_{NTI} , $NRI = -1 * SES_{NRI}$ and $NTI = -1 * SES_{NTI}$ (Swenson, 2014; Webb, 2000).

Phylogenetic diversity was estimated with four metrics (Faith's PD, weighted Faith's PD, MPD, and MNTD), while phylogenetic structure were assessed with NRI and NTI. All calculations for these metrics were computed using Picante package (Kembel et al., 2010).

Statistical comparisons of each metric for different land-use systems were carried out in order to test hypothesis 1a by using a one-way ANOVA and Tukey's HSD post hoc analyses (Zuur et al., 2007). For hypothesis 1b, linear regression fitting will be applied to compare and correlate PD with TD. To test the hypothesis 2, similar analyses in hypothesis 1b were implemented. Additionally, to investigate the role alien plant species, the alien plant species occurring in each land-use system were excluded from the dataset. Then, the phylogenetic metrics that assess the community structure (NRI and NTI) were calculated again for each treatment (include and exclude alien plant species) for each land-use system.

NRI and NTI reflects the phylogenetic structure (clustered or overdispersed) of taxa from the community phylogeny which is observed based on randomization on the source pool (Webb, 2000). While NRI assess more to the overall phylogeny (similar with MPD), NTI is focusing on the terminal taxa of the phylogeny (similar with MNTD). Both metrics estimate the deviation of the current communities from the expected communities based on null model. The value of both metrics will range from positive to negative, positive value with low quantiles ($\text{mpd.obs.p} < 0.5$) indicates significantly phylogenetic clustered while negative value with high quantiles ($\text{mpd.obs.p} > 0.95$) indicates significantly phylogenetic overdispersion or even. Non significantly positive or negative value indicates that species were structured randomly (Kembel et al., 2010; Swenson et al., 2006; Vamosi et al., 2009; Webb, 2000; Winter et al., 2013). Weighted metrics that incorporate abundance in the calculation were also computed for both metrics. This abundance-based metrics will change the interpretation from the phylogenetic distance among species to among individuals (Kembel, 2010). To test the different between these treatments (include and exclude alien), paired t-test was applied.

The applied statistical analyses were computed by using stat in R Environment (R Core Team, 2013). Data visualization for graphs and phylogenetic tree figures were generated using ggplot2 package (Wickham, 2009), and FigTree v.1.4.2 software (<http://tree.bio.ed.ac.uk/software/figtree/>).

3. Results

A total of 151,728 individuals comprised of 1,533 morphologically identified species and 135 families were incorporated in the analysis (Table 1). The data covered more than 95% of total abundance, 91% of total species and 95% of total families of the understorey communities in the core plots. Forest had the highest number of species and families followed by jungle rubber, rubber and oil palm plantations. Conversely, the total abundance (number of individuals) was the opposite in sequence, oil palm plantations harboured the highest number of individuals followed by rubber plantations, jungle rubber and forest (Table 1, Appendix 6.1).

Table 1. Number of families, species and individuals of understorey plants in each land-use system that was used in the analyses.

Land-use System	Families	Species	Individuals
Forest	111	1,041	14,660
Jungle rubber	100	604	16,716
Rubber plantations	74	250	38,586
Oil palm plantations	67	244	81,766
Total	135	1,533	151,728

Most families occurred in more than one land-use system, while 31 families only occurred in one specific land-use system. The highest amount of specialized families only occurring in one land-use system was found in forest (18% of total families in the forest), while other systems had less than 7% (Figure 4, Appendix 6.2). There were four families that were shared by rubber and oil palm plantations, two of which represented species that were considered as alien and invasive species. Those species were *Solanum jamaicense* and *S. quitoense* (Solanaceae), and *Lantana camara* (Verbenaceae).

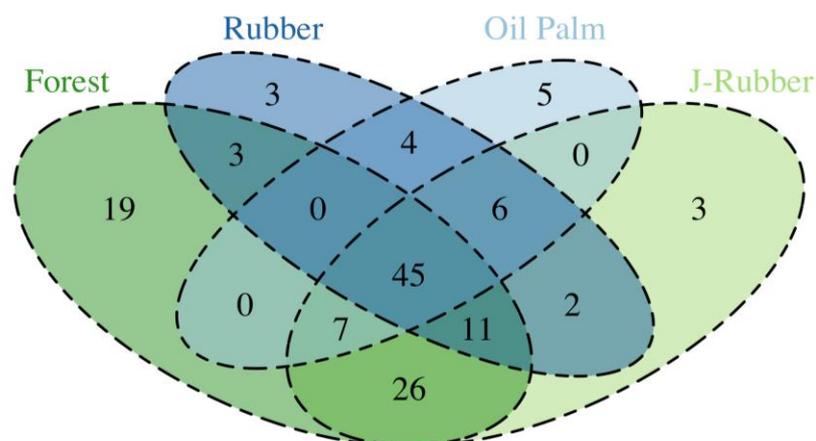


Figure 4. Venn diagram of all families in the four land-use systems.

Rubiaceae was the most species rich family in all four land-use systems while for all other families there was a variation of species richness between the systems (Table 2). Euphorbiaceae was also among the 10 most species rich families in jungle rubber, rubber and oil palm plantations, but not in forest. Meanwhile, Poaceae was important in both monocultures (rubber and oil palm plantations) but not in forest and jungle rubber; this family was also among the 10 most individual rich families.

Table 2. The 10 most species-rich families in each land-use system and in total. (Number of species is shown in bracket).

No.	Forest	Jungle rubber	Rubber	Oil Palm	Total
1.	Rubiaceae (84)	Rubiaceae (40)	Rubiaceae (27)	Rubiaceae (31)	Rubiaceae (138)
2.	Annonaceae (81)	Annonaceae (40)	Phyllanthaceae (19)	Euphorbiaceae (17)	Annonaceae (97)
3.	Arecaceae (53)	Fabaceae (39)	Euphorbiaceae (16)	Fabaceae (17)	Phyllanthaceae (73)
4.	Lauraceae (50)	Phyllanthaceae (35)	Poaceae (15)	Phyllanthaceae (17)	Myrtaceae (70)
5.	Myrtaceae (50)	Myrtaceae (24)	Fabaceae (12)	Poaceae (17)	Fabaceae (67)
6.	Fabaceae (48)	Euphorbiaceae (23)	Asteraceae (9)	Melastomataceae (10)	Arecaceae (66)
7.	Phyllanthaceae (46)	Moraceae (23)	Melastomataceae (9)	Asteraceae (9)	Lauraceae (62)
8.	Araceae (35)	Lauraceae (20)	Moraceae (9)	Cyperaceae (9)	Euphorbiaceae (50)
9.	Meliaceae (33)	Arecaceae (18)	Myrtaceae (8)	Moraceae (7)	Apocynaceae (40)
10.	Apocynaceae (29)	Zingiberaceae (17)	Cyperaceae (7)	Annonaceae (6)	Araceae (40)

In the abundance-wise list, Melastomataceae was the most abundant family in total and also in jungle rubber and oil palm plantations, while in rubber and forest the most abundance family was Poaceae and Fabaceae, respectively (Table 3). Moreover, Poaceae and Melastomataceae were not even listed in the 10 most abundant families in the forest.

Table 3. The 10 most abundant families in each land-use system and in total.
(Number of individuals (abundance) is shown in bracket).

No.	Forest	Jungle rubber	Rubber	Oil Palm	Total
1	Fabaceae (2,476)	Melastomataceae (5,724)	Poaceae (11,975)	Melastomataceae (18,791)	Melastomataceae (34,048)
2	Myrtaceae (753)	Poaceae (1,296)	Melastomataceae (9,264)	Rubiaceae (15,900)	Poaceae (28,962)
3	Phyllanthaceae (711)	Fabaceae (871)	Acanthaceae (4,592)	Poaceae (15,617)	Rubiaceae (18,608)
4	Burseraceae (680)	Euphorbiaceae (836)	Cyperaceae (3,185)	Acanthaceae (10,731)	Acanthaceae (15,356)
5	Sapindaceae (663)	Phyllanthaceae (713)	Linderniaceae (2,192)	Asteraceae (8,465)	Asteraceae (9,338)
6	Euphorbiaceae (581)	Gleicheniaceae (646)	Rubiaceae (1,766)	Linderniaceae (3,709)	Linderniaceae (5,909)
7	Annonaceae (512)	Apocynaceae (632)	Euphorbiaceae (1,644)	Thelypteridaceae (1,134)	Cyperaceae (4,582)
8	Malvaceae (505)	Moraceae (614)	Gleicheniaceae (811)	Pteridaceae (1,059)	Fabaceae (3,567)
9	Connaraceae (468)	Zingiberaceae (574)	Asteraceae (723)	Cyperaceae (1,027)	Euphorbiaceae (3,196)
10	Arecaceae (461)	Malvaceae (558)	Phyllanthaceae (570)	Arecaceae (854)	Phyllanthaceae (2,713)

3.1. Phylogenetic trees of understorey plant communities across land-use systems in Sumatra

Family based phylogenetic trees illustrated the evolutionary relationship among all species that were found in the understorey communities. The phylogenetic tree consisted of three main groups, namely Angiosperms with 119 families (97.46% of total species), Ferns with 14 families (2.28% of total species) and Gymnosperms with 2 families (0.26% of total species). Angiosperms were then divided into four main clades, i.e. the ANITA Grade (0.13% of total species, e.g. Chloranthaceae and Schisandraceae), Magnolids (11.39% of total species, e.g. Annonaceae and Lauraceae), Monocots (12.52 % of total species, e.g. Araceae and Arecaceae), and the largest group was Eudicots (73.96% of total species) such as Rubiaceae and Phyllanthaceae (Figure 5).

The Figure 6 showed the presence and absence of the total families found in all four land-use systems. The absent families were approximately spread over the entire phylogenetic tree, however in rubber and oil palm plantations some absent families were clustered which contributed to a small absent clade.

The highest number of absent families was found in oil palm plantations (68 families), followed by rubber plantations (61 families), jungle rubber (35 families) and forest (24 families). Thus, the number of absent families was two times lower in forest and jungle rubber than in rubber and oil palm plantations. Linderniaceae and Thelypteridaceae for instance were absent in forest (Figure 6a), while Capparaceae and Monimiaceae for example did not occur in jungle rubber (Figure 6b). Two

examples of families that were absent in rubber (Figure 6c) and oil palm plantations (Figure 6d) were Meliaceae and Myrysticaceae, and Burseraceae and Sapotaceae, respectively. The total list of families in each land-use system is shown in appendix 6.2.

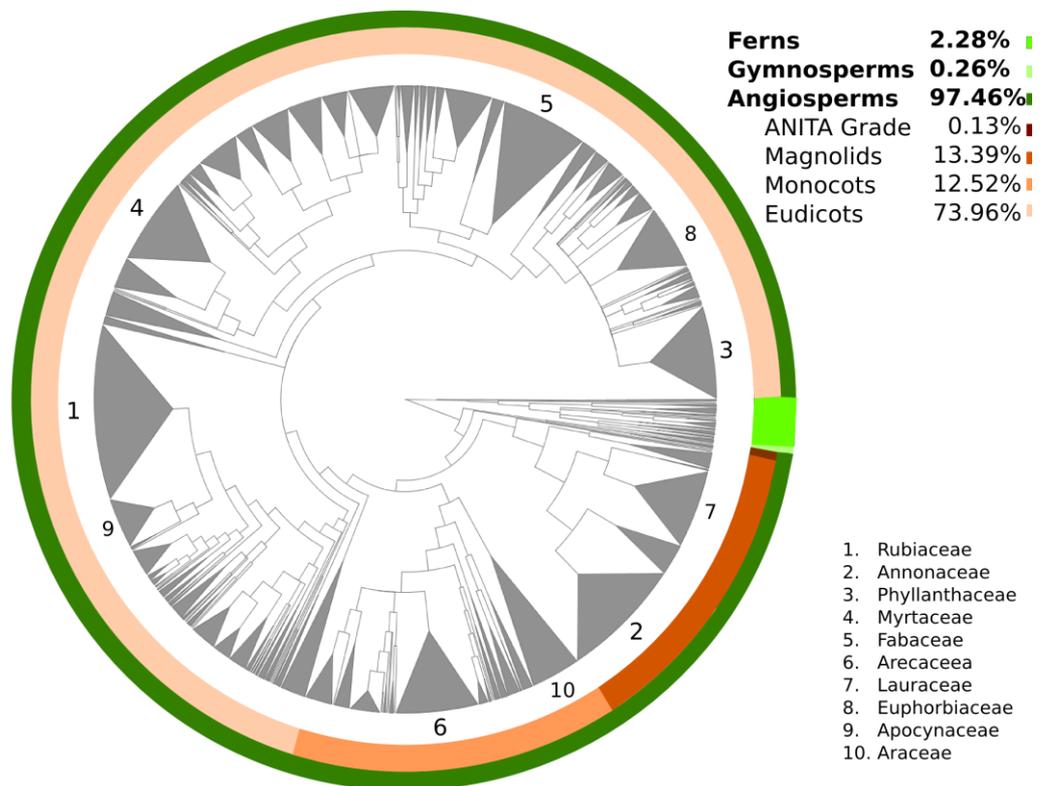


Figure 5. Phylogenetic tree of all species found in the understory communities of four land-use systems (forest, jungle rubber, rubber and oil palm plantations). Legend shows proportion based on species (above) and the top 10 species rich families (below).

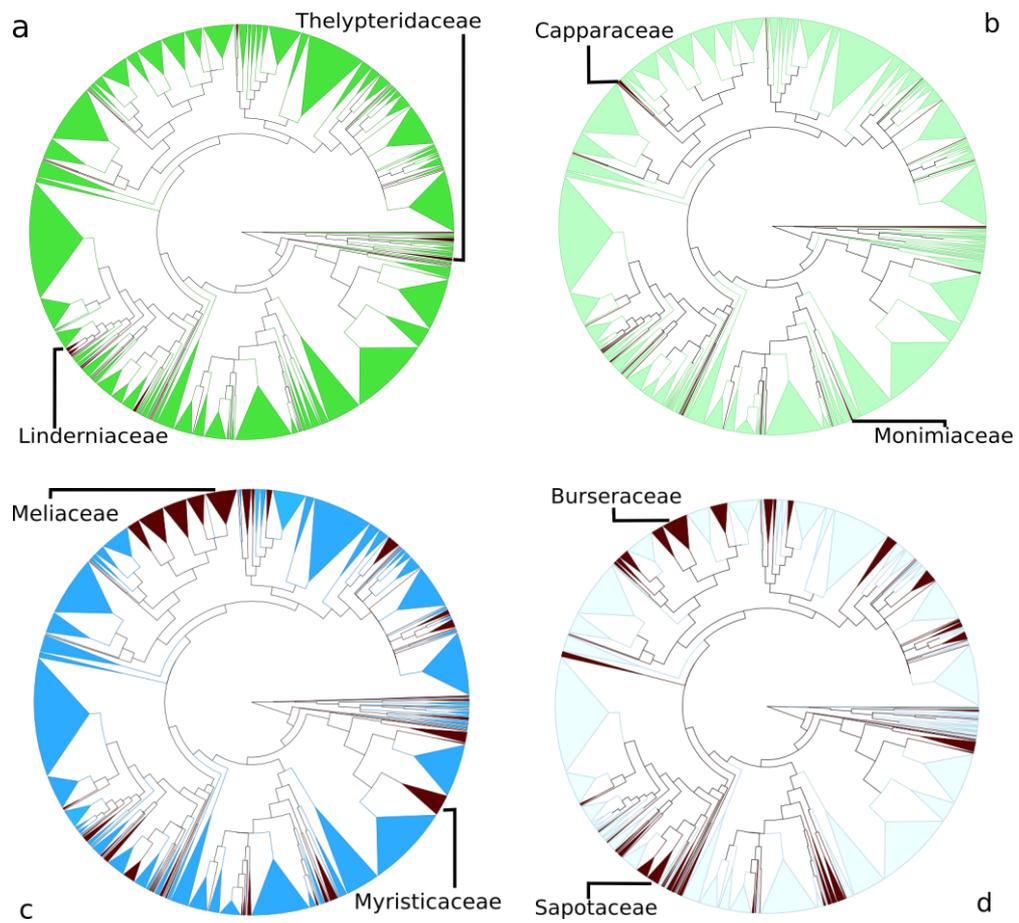


Figure 6. Phylogenetic trees for each land-use system. Dark-brown color indicates families that were absent in the system (a. forest, b. jungle rubber, c. rubber plantations, d. oil palm plantations).

3.1.A. The impact of forest conversion on phylogenetic diversity (PD) compared to taxonomic diversity (TD)

Analysis in the plot level on Faith's Phylogenetic Diversity (Faith's PD) using one-way ANOVA showed that all land-use systems had significant differences in Faith's PD ($F = 41.39$, $df = 3$, $p < 0.001$). Further statistical tests revealed that forest had by far the highest Faith's PD ($22,820.70 \pm 5,231$ million years) among other land-use systems. Meanwhile, Faith's PD in jungle rubber ($15,400.39 \pm 1,839$ million years) was significantly lower than in forest but higher than in rubber and oil palm plantations. However, rubber and oil palm plantations had similar Faith's PD, with $8,377.54 \pm 1,817$ and $7,548.66 \pm 2,271$ million years, respectively (Figure 7a).

The species richness (SR) likewise varied among the land-use systems ($F = 35.73$, $df = 3$, $p < 0.001$). Post hoc test (Tukey's HSD) then indicated that forest (238.50 ± 71 species per plot) had significantly higher SR than jungle rubber and other land-use systems. The SR in jungle rubber (134.38 ± 21 species per plot) was significantly lower than forest but higher than rubber and oil palm plantations. However, rubber (58.65 ± 21 species per plot) and oil palm plantations (65.5 ± 18 species per plot) had a closely similar SR (Figure 7b).

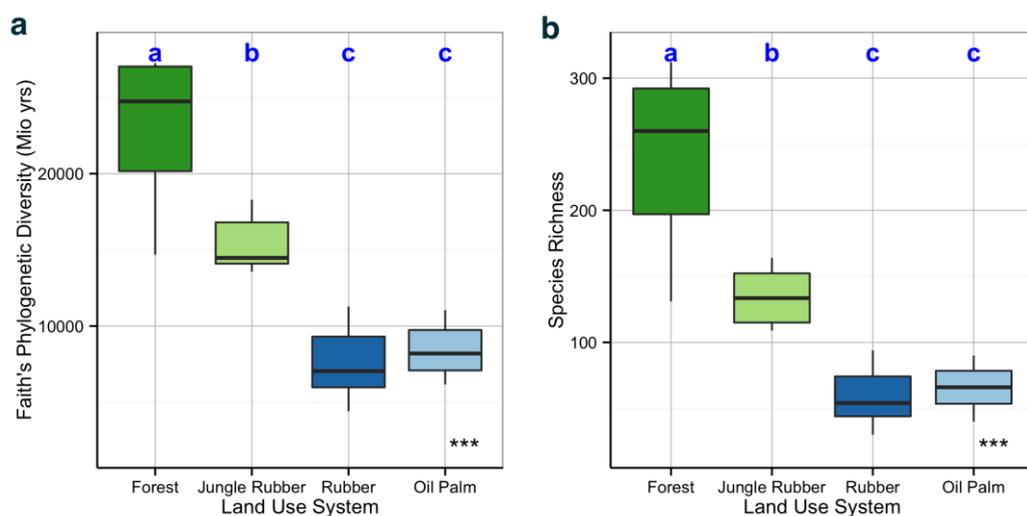


Figure 7. Faith's phylogenetic diversity (a) and species richness (b) across the four land-use systems ($n = 32$). One-way ANOVA and Tukey's HSD test were used for multi comparison analysis (different letters indicate significant differences). Significant code: $p < 0.001$ '***'.

The weighted-Faith's PD (Faith's PD which incorporated abundance) similarly showed significant differences across the land-use systems ($F = 26.3$, $df = 3$, $p < 0.001$). The weighted-Faith's PD in the forest ($22,451.70 \pm 7,048$) was the highest among other land-use systems. Jungle rubber ($15,524.59 \pm 2,612$) had significantly lower weighted-Faith's PD than forest but higher than rubber ($7,006.40 \pm 3,091$) and oil palm plantations ($6,803.49 \pm 1,699$) (Figure 8a). Both rubber and oil palm plantations had equally weighted-Faith's PD.

Taxonomic diversity measured by Simpson index showed that the diversity index was significantly ($F = 26.63$, $df = 3$, $p < 0.001$) higher in forest (0.95 ± 0.04) than in jungle rubber (0.86 ± 0.08), rubber (0.82 ± 0.06) and oil palm plantations (0.82 ± 0.07). The diversity index of jungle rubber did not differ significantly from rubber or oil palm plantations (Figure 8b).

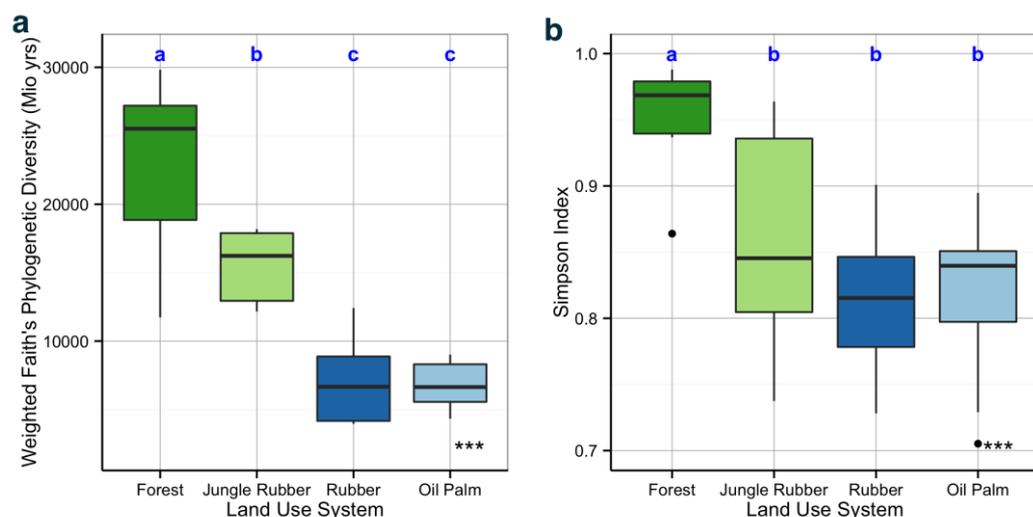


Figure 8. Weighted Faith's phylogenetic diversity (incorporate number of individuals in the calculation) (a) and Simpson index (b) across land-use systems ($n = 32$). One-way ANOVA and Tukey's HSD test were used for group comparison analysis (different letters indicate significant differences). Significance codes: $p < 0.001$ '***'.

MPD and MNTD showed significant differences among the land-use systems ($F = 15.89$, $df = 3$, $p < 0.001$ and $F = 14.96$, $df = 3$, $p < 0.001$, respectively) (Figure 9). The MPD of forest (498.41 ± 8 million years) was similar to jungle rubber and rubber plantations (512.51 ± 12 and 518.07 ± 12 million years, respectively), while oil palm plantations had significantly higher MPD with 551.08 ± 20 million years (Figure 9a).

MNTD of forest (150.74 ± 11 million years) was the lowest among other land-use systems. Meanwhile, jungle rubber (174.87 ± 12 million years) was not significantly different from rubber and oil palm plantations with 193.88 ± 13 and 192.61 ± 19 million years, respectively (Figure 9b).

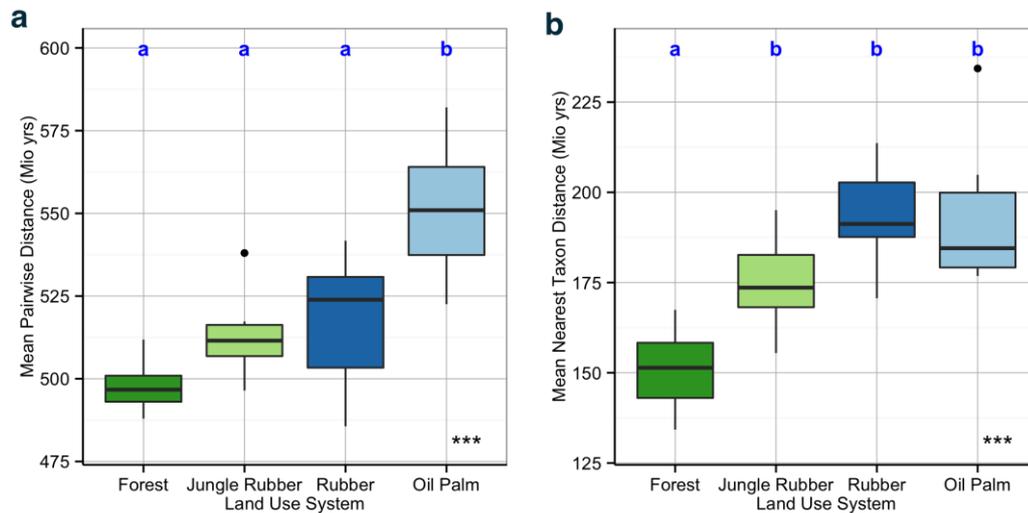


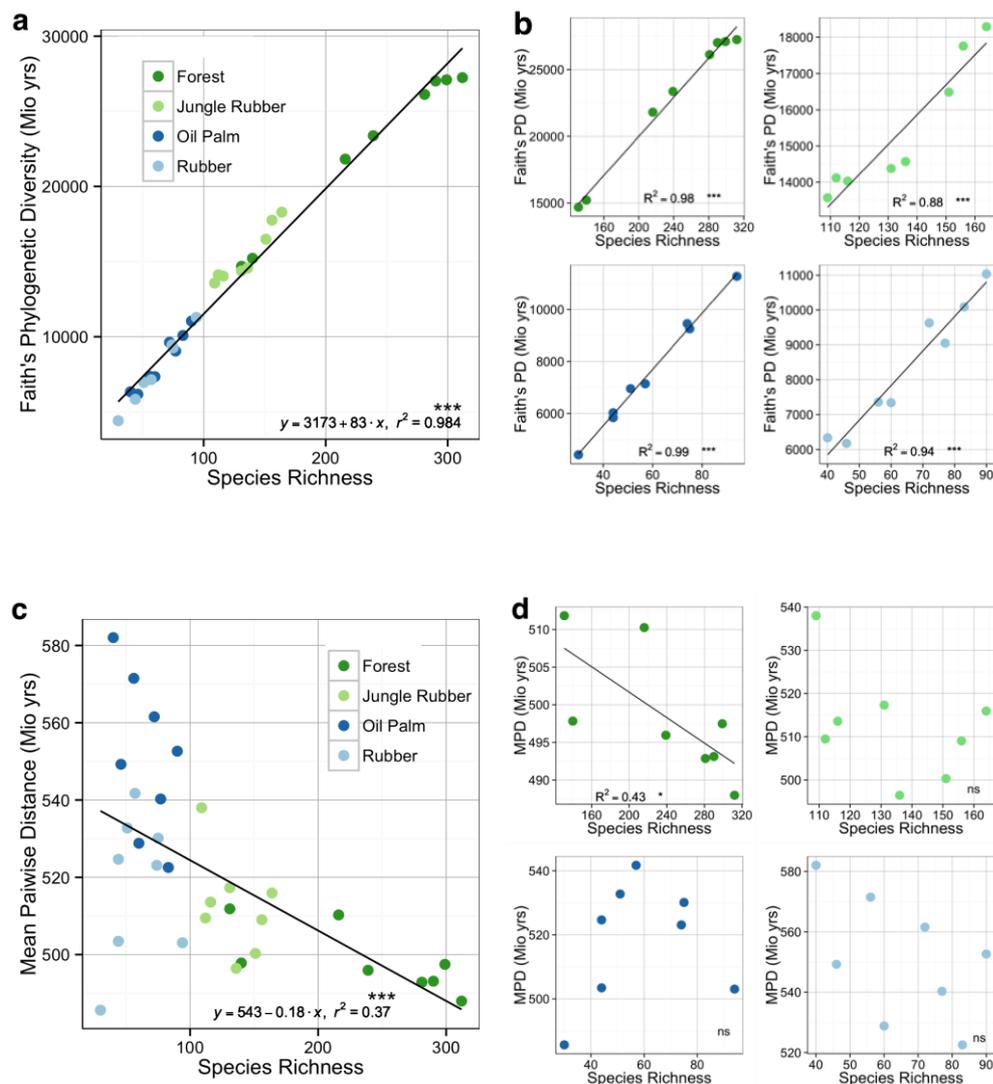
Figure 9. Mean pairwise distance (a) and mean nearest taxon distance (b) across land-use systems ($n = 32$). On-way ANOVA and Tukey's HSD test were used for multi comparison analysis (different letters indicate significant differences). Significant code: $p < 0.001$ '***'.

Generally, Faith's PD and SR showed a similar pattern. The mean value of both metrics reached the highest in the forest and gradually decreased to the more intensively managed systems. Similarly both the Weighted-Faith's PD and the Simpson index, which included abundance in its calculation illustrated similar pattern and trends in regard to the impact of forest conversion. The mean value of both metrics was highest in the forest and declined towards the more intensively managed systems.

In contrast, MPD and MNTD illustrated the opposite pattern from the other four metrics. The mean value of MPD and MNTD reached the lowest in the forest and gradually increased to the more intensively managed system. It indicated that phylogenetic distance in basal and terminal phylogeny, as represented by MPD and MNTD respectively, increased toward the more intensively managed systems.

3.1.B. Correlation of phylogenetic diversity and taxonomic diversity

The phylogenetic diversity metrics that were used in this analysis (Faith's PD, MPD, and MNTD) had a linear correlation with species richness (SR) (Figure 10a, c, d). SR demonstrated as stronger predictor for Faith's PD ($R^2 = 0.98$, $df = 30$, $P < 0.001$) than for MPD ($R^2 = 0.34$, $df = 30$, $P < 0.001$) and MNTD ($R^2 = 0.72$, $df = 30$, $P < 0.001$). While the correlation of SR and Faith's PD was positive, the correlation of MPD and MNTD was negative. On land-use level only Faith's PD had a significant correlation with SR in all land-use systems ($R^2 > 0.85$, $df = 8$, $P < 0.001$ for all land-use systems) (Figure 10b), while MPD and MNTD were only significantly correlated with SR in forest ($R^2 = 0.43$, $df = 8$, $P < 0.04$ and $R^2 = 0.84$, $df = 8$, $P < 0.001$, respectively) (Figure 10d, f). In the other land-use systems the pattern was not linear.



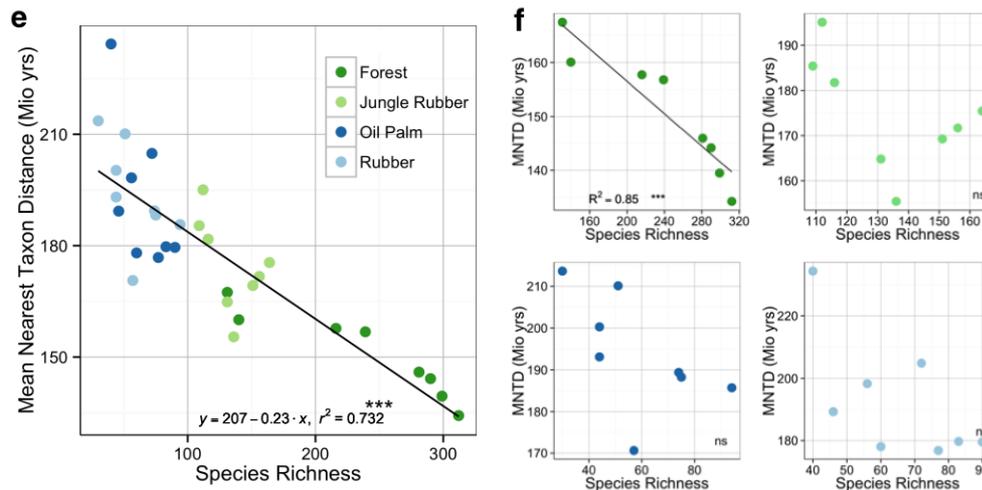


Figure 10. Linear correlation of SR and Faith's PD (a), MPD (c) and MNTD (d) in all plots ($n = 32$) and each land-use system (b, e, f, $n = 8$). On-way ANOVA and Tukey's HSD test was used for multi comparison analysis (different letters indicate significant differences). Significant codes: $p < 0.001$ '***', $p < 0.05$ '*', $p > 0.05$ 'ns'.

3.2. Phylogenetic structure of understorey plant communities across land-use systems

NRI and NTI showed significant differences among land-use systems ($F = 14.3$, $df = 3$, $p < 0.001$ and $F = 3.05$, $df = 3$, $p < 0.01$). Forest had the highest NRI (0.63 ± 1), while oil palm plantations had the lowest NRI (-3.17 ± 1) (Figure 11a). However, jungle rubber and rubber plantations similarly had a NRI averaged at -0.98 ± 1 and -1.03 ± 1 , respectively). In more detailed observations, most plots ($>50\%$) in forest, jungle rubber and rubber plantations similarly had NRI values that were not significantly different from expected by null model. This means that all three land-use systems had randomly distributed phylogenetic structure on the basal phylogenetic tree (overall phylogeny). In contrast, most plots (87.5%) in oil palm plantations had more overdispersed phylogenetic structure (NRI was significantly greater than expected by null model).

These results were slightly different for NTI. In jungle rubber, the NTI (0.15 ± 1) was the lowest among other land-use systems. Meanwhile, forest, rubber and oil palm plantations had similar NTI (1.7 ± 1 , 1 ± 0.9 and 1 ± 0.8 , respectively). Nonetheless, NTI value in each plot in all land-use systems showed comparable phylogenetic structure except for plots in the forest. Equally half of total plots in the forest had

clustered phylogenetic structures in the terminal phylogeny (NTI was significantly lower from expected by null model). Conversely, more than 50% of plots in jungle rubber, rubber and oil palm plantations had randomly distributed phylogenetic structure in overall phylogeny (NTI does not differ significantly from expected by null model (Figure 11b)).

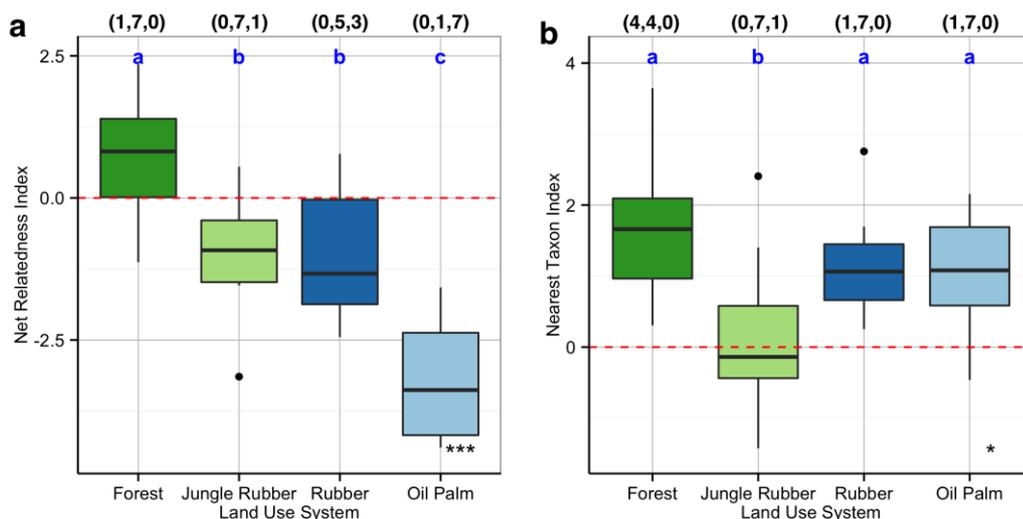


Figure 11. Net relatedness index (a) and nearest taxon index (b) among all land-use systems ($n = 8$). On-way ANOVA and Tukey's HSD test were used for multi comparison analysis (different letters indicate significant differences). Values on top of each graph give the number of plots that were significantly clustered (left), were random (middle) or were significantly overdispersed (right). Significant codes: $p < 0.001$ '***', $p < 0.05$ '*'.

3.3. The role of alien species on the phylogenetic structure of understorey plant communities

The total species list from all four land-use systems included 44 alien species from 22 families (see Appendix 6.3 for detailed list). Those species were introduced from Africa (11.5%), America (75%), both Africa and America (4.5%) and other countries in Asia (9%). Alien species were found in all land-use systems, but both mean species richness and abundance were much lower in forest compared to the agricultural areas (0.5 ± 0.7 species, 9 ± 21 individuals). The highest mean species richness (SR) and abundance were found in oil palm plantations with 17.6 ± 5 species and $7,386.1 \pm 3,683$ individuals. Hence, the proportion of SR of alien species increased gradually towards the more intensively managed systems (from $0.21\% \pm 0.3$ in forest, increased to $3.81\% \pm 2$ in jungle rubber, $17.25\% \pm 6$ in rubber and $27.61\% \pm 7$ in oil palm plantations) (Figure 12a). Meanwhile, the abundance of alien species, however, was

increased more severely towards the more intensively managed systems (from 0.53% \pm 1 in forest, to 34.35% \pm 16 in jungle rubber, 48.07% \pm 14 in rubber) and even outnumbered the native plant species in oil palm plantations (69.36% \pm 10) (Figure 12b).

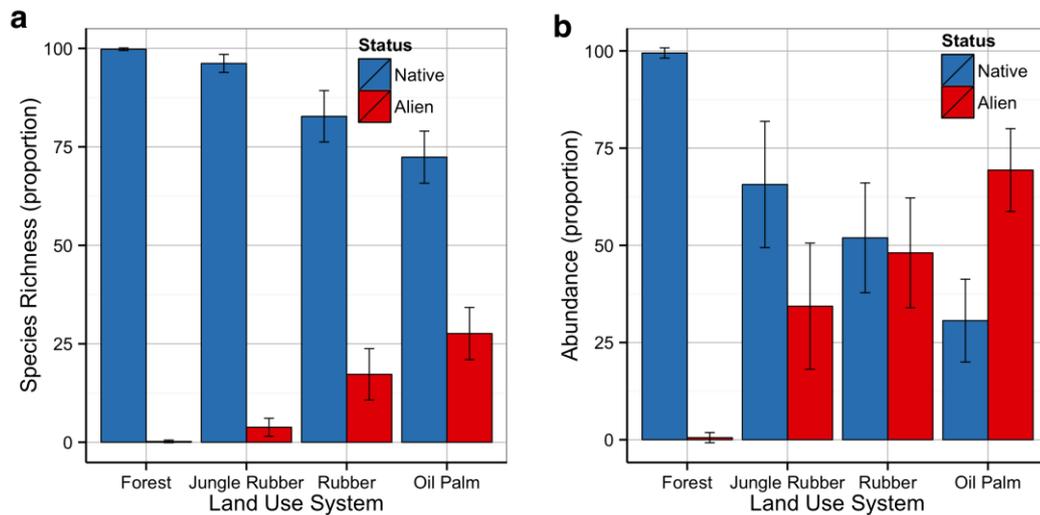


Figure 12. Proportion of species richness (a) and abundance of alien species (b) compared to native species in plot level ($n = 32$) in all land-use systems (n total = 1,533 species, 152,728 individuals). Error bars show standard deviation.

The invasive alien species *Clidemia hirta* (Melastomataceae) was the most abundant species in all agricultural areas. In forest the native species *Kunstleria ridleyi* (Fabaceae) was found to be the most abundant. However, *C. hirta* was also found in the forest with relatively high abundance (67 individuals in two plots). This said, in forest *C. hirta* was still only ranked 46th based on its abundance and was only found in two plots. In oil palm plantations and jungle rubber *C. hirta* occurred in all plots, and was only absent in one plot in rubber plantations. There were two other alien plant species that were found in the forest, i.e. *Mikania micrantha* Kunth (Asteraceae) and *Panicum laxum* Sw. (Poaceae) (Figure 13), but both of them were only found each in one single plot in the forest.

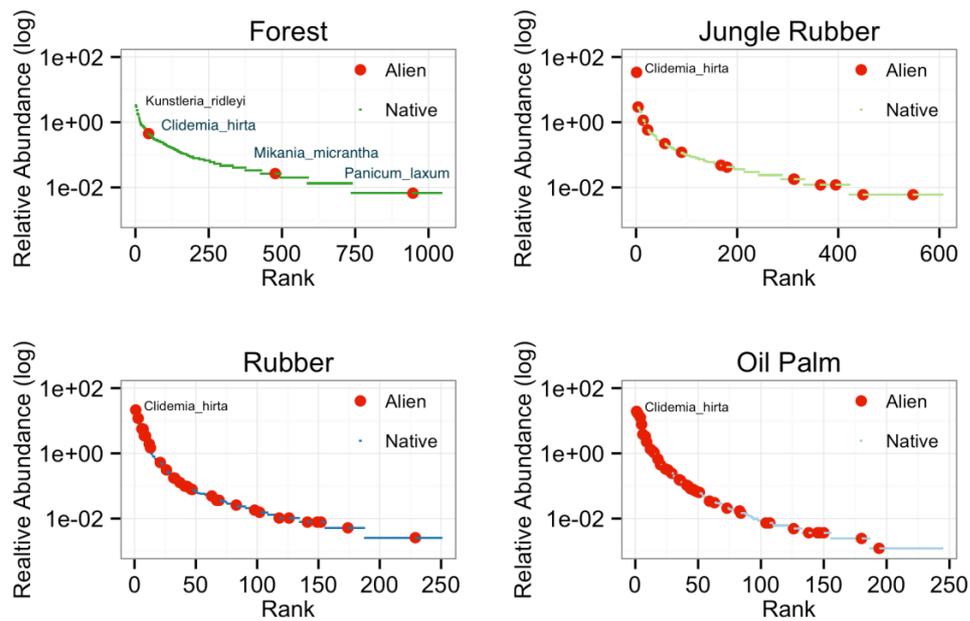


Figure 13. Rank abundance curves for understory plant species in each land-use system. Alien species are highlighted in red.

The existence of alien plant species in each land-use system had some influences in phylogenetic structure (NRI and NTI) of most understory communities. Excluding the alien species from the community significantly reduced the mean NRI in jungle rubber, rubber and oil palm plantations ($t = -2.96$, $df = 7$, $p < 0.05$, $t = -2.68$, $df = 7$, $p < 0.01$ and $t = -4.32$, $df = 7$, $p < 0.01$, respectively), but not in forest (Figure 14a). In more detailed observations, the exclusion of alien plant species increased the number of plots (12.5-25%) with an over-dispersed phylogenetic structure on the overall phylogeny (NRI was significantly greater from expected by null model).

Conversely with NRI, excluding the alien plant species in the communities influenced the terminal phylogeny (NTI) only in agricultural systems, namely rubber ($t = -2.9$, $df = 7$, $p < 0.05$) and oil palm plantations ($t = -4.64$, $df = 7$, $p < 0.01$). However, most plots (>50%) in both land-use systems were still randomly distributed phylogenetic structure in overall phylogeny (NRI does not significantly different from expected by null model). Moreover, the exclusion also led to a randomly distributed phylogenetic structure (NTI) in all oil palm plantations plots (Figure 14b).

In the individual-based (weighted metrics) (Figure 14c, d), the exclusion of alien plant species only reduced the weighted NRI, particularly in jungle rubber ($t = -8.42$, $df = 7$, $p < 0.001$) and oil palm plantations ($t = 3.74$, $df = 7$, $p = 0.007$), while in the other land-use systems the exclusion apparently had no influence. Furthermore, this exclusion increased the number of plots (25 - 37.5%) with overdispersed phylogenetic structure in jungle rubber and oil palm plantations (weighted NRI was significantly greater from expected by null model). But, it had no effect on the terminal phylogeny (weighted NTI).

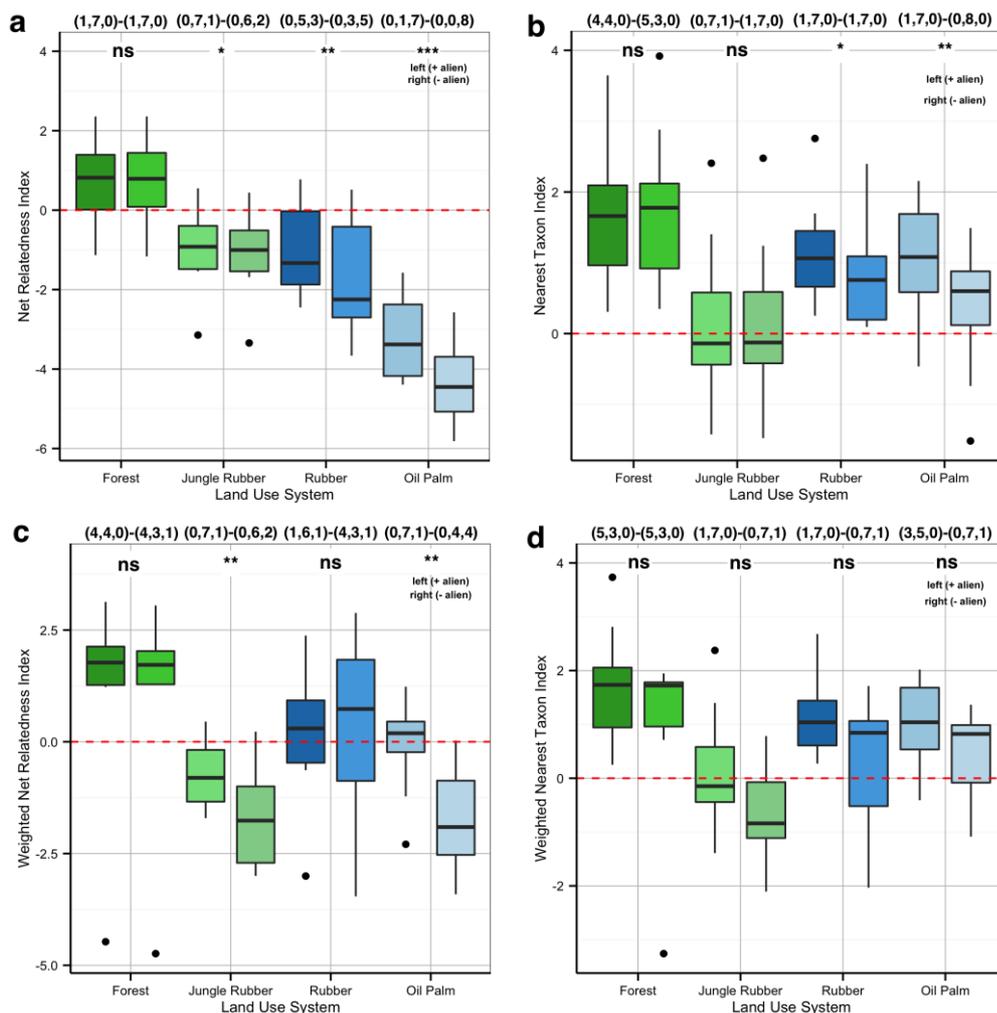


Figure 14. Phylogenetic structure of total (including alien; dark colors) with native (excluding alien; light colors) plant communities in the four land-use systems. Paired t-test was used for comparison analysis ($n = 16$). The value above the graph is the number of plots that was significantly clustering (left), random (middle) and overdispersed (right). Significant codes: $p < 0.001$ ‘***’, $p < 0.01$ ‘**’, $p < 0.05$ ‘*’, $p > 0.05$ ‘ns’.

4. Discussion

Plant diversity in the Malesian region has been known for its high number of species richness. As reported in Silk et al. (2015), the Indo-pacific region including Malesia had an equivalent amount of tree species richness to that which can be found in tropical American forests. The understorey plant communities in tropical forest often consisted of tree seedlings, herbs, shrubs, lianas and epiphytes (Cicuzza et al., 2013). However within these understorey communities herbs and treelets often represent almost 45% of the vascular plant diversity in tropical forests (Cicuzza et al., 2013; Duivenvoorden, 1994; Linares-Palomino and Kessler, 2009). Therefore, it was not surprising that in the study there was a relatively high number of understorey species richness (more than 1,000 morpho-species in 2 ha) in forest areas (Table 1).

Moreover, I also found that Rubiaceae was the most species rich family in the forest and other land-use systems. This result was similar to what Lü et al. (2011) found in the tropical forest in Southern China. Nevertheless, for the number of individuals per family, instead of Rubiaceae I found Fabaceae as the most individual rich family in the forest plots. In Borneo, Poulsen (1996) found that Zingiberaceae accounted as the most species and individual rich family in the understorey communities, while in Sulawesi Willinghöfer et al. (2012) reported that Polypodiaceae was the most species rich family. However, those studies only account for herbaceous plants and exclude other vascular plants.

When I looked into details in the human modified land-use systems (jungle rubber, rubber and oil palm plantations) my results showed that the total species that was found in those systems was relatively higher than in other areas. Bhagwat et al. (2008) reported that in agroforestry system the upper range number of understorey plant communities (herbaceous and woody plants) in most tropical region across continents was approximately 244 species. Meanwhile, in this study area the total species in jungle rubber, rubber and oil palm plantations were approximately 604, 250 and 244 species, respectively. However, all of these were a conservative estimate based on morpho-species identification.

Furthermore, I also discovered that each land-use system in this study area had specialized plant families (Figure 4). The specialized families in the forest mostly composed of families that are commonly found in the forest for instance Monimiaceae and Escalloniaceae. However, there were also several specialized families that were found in plantations (rubber and oil palm plantations) for example Musaceae and Cleomaceae. Musaceae only occurred in rubber plantations and represented by one species of *Musa* sp. It is likely that this species was a common cultivated *Musa acuminata* which were planted by the plantation's owner or dispersed by birds from the orchard nearby. Meanwhile, Cleomaceae, which was only found in oil palm plantations, was also only represented by one species *Cleome rutidosperma*. This species was considered as alien species and natively distributed in tropical Africa (Soerjani et al., 1987). Therefore, it explained why Cleomaceae was only found in oil palm plantations because *C. rutidosperma* is a common weeds in agricultural areas (Moody, 1989).

4.1. Phylogenetic trees of understorey plant communities across land-use systems in Sumatra

The family and species distribution within the communities was visualized in the phylogenetic trees. This way of visualization provides better overview and incorporates more comprehensive information of the origin and evolution of the species in the communities. It also contributed to more understanding on the evolutionary relationship among the species. For example, the top 10 most diverse families that were found have various evolutionary distances. Annonaceae and Rubiaceae as two of the most diverse families belong to different clades and were located further to each (Figure 5). It means that both families had a very distant evolutionary relationship. Furthermore, absent families in each land-use systems can also be clearly observed by using this visualization. The distribution of absent families within the phylogenetic tree also was also well detected. For example, in forest and jungle rubber, the absent families were distributed more scattered within the phylogenetic tree (Figure 6a, b). In contrast, in rubber and oil palm plantations, the absent families were more clustered in several clades (Figure 6c, d).

4.1.A. The impact of forest conversion on phylogenetic diversity (PD) and the correlation of PD with taxonomic diversity (TD)

In this study, forest conversion into intensively managed land-use systems was proven to have a significant impact on phylogenetic and taxonomic diversity. Faith's PD and weighted-Faith's PD were decreased towards the more intensively managed land-use systems or agricultural areas (from forest to jungle rubber to rubber and oil palm plantations). This pattern was exactly the same with species richness, but faintly changes in the diversity index, where diversity species in jungle rubber was similar to rubber and oil palm plantations.

These results were consistent with a previous study in temperate areas, where Faith's PD was lower in agricultural areas with a high land-use intensity (van Meerbeek et al., 2014). Another study in grassland areas showed similarly that average weighted-Faith's PD was significantly reduced with increasing land-use intensity (Egorov et al., 2014). Moreover, a study in subtropical region in Africa even reported that not only land-use intensity but forest disturbance was likely to alter Faith's PD across all plant life stages not only understorey plant communities (Grass et al., 2015).

I also detected that land-use system with less intensive management (in this case jungle rubber) harbored relatively higher Faith's PD (and weighted-Faith's PD) as well as TD compared to more intensively managed systems (e.g. rubber and oil palm plantations). This matches with the study of Mo et al. (2013) showing that young secondary forest (15-50 years after slash and burn) had similar Faith's PD in understorey communities compared to old growth forest. Thus, land-use systems with an intermediate intensity could accommodate higher taxonomic and phylogenetic diversity than intensively managed systems.

According to Faith (2002, 1992), Faith's PD was expected to be more sensitive to community changes than TD because it takes into account the evolutionary history of each species. My results are in accordance with this idea. The pattern of Faith's PD and weighted-Faith's PD were almost exactly the same with species richness, but compared to Simpson's index both metrics provides more information. Faith's PD

was able to detect the changes from forest to jungle rubber in which was not distinguished by Simpson's.

In contrast to Faith's PD and weighted Faith's PD, the analysis on MPD and MNTD showed that forest conversion to more intensively managed land-use system significantly increased the average phylogenetic distance. This result was different from the study that was conducted by Meerbeek et al. (2014) in the temperate areas, where lower MPD were more likely to be found in the more intensive managed system. However, in the same study Meerbeek et al. (2014) also reported land-use intensification significantly increase the value of MNTD in the communities. This result was similar to what I found in this study.

Overall, in the case of Faith's PD and weighted-Faith's PD my results confirm the hypothesis (Hypothesis 1a) that forest conversion into agricultural areas has a negative impact on PD and PD would be highest in forest and lowest in the more intensively managed systems. However, forest conversion into agricultural areas also tended to increase phylogenetic distance (MPD and MNTD) in the communities.

Conversely to what I found, some other studies reported that the impact of forest disturbance, forest conversion or even land-use intensification on phylogenetic metrics were not prominent (Arroyo-Rodríguez et al., 2012; Dinnage, 2009; Egorov et al., 2014). This situation was likely due to the tendency of those metrics, especially Faith's PD to correlate with species richness (SR).

4.1.B. Correlation of phylogenetic diversity and taxonomic diversity

My analysis on the correlation of SR and some phylogenetic metrics clearly illustrated that species richness correlated significantly with Faith's PD, MPD and MNTD. It means that my hypothesis (Hypothesis 1b) is confirmed. The increases of SR, Faith's PD will necessarily increase (Vamosi et al., 2009). This pattern was observed in all land-use system in my study. Similarly to what Mo et al. (2013) had observed in young secondary forest and in understorey planted forest in southern China. This correlation was also detected in the Mediterranean climate shrublands of Australia, California, Chile and South-Africa by Morlon et al. (2011) and also along

urbanization gradient in Germany by Knapp et al (2008). However, both studies reported a strong but different relationship between species richness and PD.

Moreover, I also found that the relationship of MPD and MNTD values by SR was nicely explained with linear regression in forest, but not in other land-use systems. The increase of SR is likely to lead to the decline of MPD and MNTD. This pattern was also observed in different regions worldwide (Cadotte et al., 2010, 2008; Mo et al., 2013). However, according to Vamosi et al (2009) the response of MPD to the increasing of SR depends upon the balance of the tree and not the addition of species. In contrast to that, the response of MNTD is the more direct, and with increase of SR, MNTD will decrease because as more species are included in the community, the additional species will tend to be a close relative of the already-sampled species (Vamosi et al., 2009).

The collinearity (refers to the non independence of predictor variables (Dormann et al., 2013)) of phylogenetic metrics and SR is important to take into account when modeling the impact of forest conversion on taxonomic and phylogenetic diversity. Therefore, in this study I treat these metrics separately as predictor variables.

4.2. Phylogenetic structure of understorey plant communities across land-use systems

Turning to the phylogenetic structure (PS) that assesses the phylogenetic dispersion (NRI and NTI), I found that both metrics were significantly different among land-use systems. It means that forest conversion into more intensively managed systems significantly affected both NRI and NTI in the study area. Moreover, detailed analysis showed that most plots in the forest had clustered structures, especially in terminal phylogeny (NTI) and shifted to random in jungle rubber and rubber plantations (NRI and NTI), and eventually became over-dispersed in oil palm plantations (NRI). However, in the basal phylogeny (NRI) most plots in the forest tended to show more random structure.

The fact that clustered pattern was prominent in the forest indicates that the communities were composed of closely related species (confamilial or cogenetic species). Environmental filtering on shared physiological tolerances (trait

conservatism) has been suggested to be the strong influence of this pattern (Baraloto et al., 2012; Cavender-Bares et al., 2009; Erickson et al., 2014; Webb et al., 2002). As species are able to retain ecological traits and environmental distribution ('niche conservatism') (Crisp et al., 2009), then closely related species are expected to have similar ecological requirements (Cavender-Bares et al., 2009). Therefore, as a result communities will consist of closely related species. The underlying assumption is niche assembly theory where plant species tends to segregate along various environmental niche (Silvertown, 2004).

Furthermore, clustered pattern was also observed in various type of forests such as tropical forest in Borneo and Barro Colorado Island, subtropical forest in Florida, and dry forest in Mexico (Cavender-Bares et al., 2006; Kembel et al., 2006; Webb, 2000). Additionally, a study in African rain forest reported that phylogenetic clustering of tree communities were also found at multiple scales (Parmentier et al., 2014). At a global scale, Weigelt et al. (2015) also reported that plant communities (angiosperm and palm) in islands tended to have phylogenetic clustered structures.

Another important result from this study is the over-dispersed phylogenetic structures that were detected in oil palm plantations. In this situation the plausible explanation is there was an intensive competition among closely related species which resulting a species expulsion with similar ecological traits (Cavender-Bares et al., 2009; Webb et al., 2002). Furthermore, environmental filtering on ecologically important convergent traits may also cause the over-dispersed patterns (Cavender-Bares et al., 2004; Vamosi et al., 2009; Webb et al., 2002).

Hence, these results confirm my second hypothesis (Hypothesis 2a and 2b), that forest has clustered phylogenetic structure and forest conversion lead to more random or over-dispersed structures. Nevertheless, there were also some studies that demonstrated that forest disturbance led to clustered phylogenetic structure (Ding et al., 2012; Dinnage, 2009; Feng et al., 2014; Helmus et al., 2010; Mo et al., 2013). This contradiction lead to another possible hypothesis (Hypothesis 3), that is the existence of alien plant species in intensively managed land systems might contribute to create random or over-dispersed phylogenetic structure.

4.3. Influence of alien species on the phylogenetic structure of understorey plant communities

Species richness and abundance of alien plant species increased towards the more intensively managed systems; even they became dominant in all agricultural areas. For example *Clidemia hirta* (introduced from tropical America (Peters, 2001)) was the most abundant species in jungle rubber, rubber and oil palm plantations. Moreover, most of these alien plant species came from tropical America (Tjitrosoedirdjo, 2007a, 2005). However, recent study reported that the sources of naturalized alien plant species across the globe were temperate Asia and Europe (van Kleunen et al., 2015).

Some records on the initial introduction of these alien species was mostly related to the economic activities, which caused the intentionally or accidentally introduction of these weeds (Tjitrosoedirdjo, 2007b). One of the intentional examples is *Mikania micrantha*, which was introduced as a non-legume ground cover in rubber plantations due to the scarcity of legume seeds. *C. hirta* was likely to be the result of accidental introduction, similarly to what happened in other regions (DeWalt et al., 2004).

The existence of alien species in the local plant communities often reduces the native species diversity and abundance (Murphy and Romanuk, 2014). Additionally, disturbances for instance conversion of forest into other land-use systems enhance the diversity and abundance of alien species, and leads to the decline of native plant species (Jauni et al., 2015).

My results demonstrate that the existence of alien species in the communities changed the phylogenetic structure of understory plant communities in all land-use systems. When alien species were excluded from the communities, the phylogenetic structure in basal and terminal phylogeny became more overdispersed. This means that alien species contributed to more random phylogenetic structures in the communities.

Correspondingly, from the individual perspective the existence of alien plant individuals shifted the phylogenetic structures in rubber and oil palm plantations became more randomly distributed instead of overdispersed. Even in rubber plantations, the exclusion of alien species created more clustering phylogenetic structures, although based on t-test analysis the difference was not significant, but in

the phylogenetic structure analysis the significant of deviation from null model is the correct parameterization. Therefore hypothesis that alien plant species contributes to create more overdispersed phylogenetic structures is not confirmed.

These results indicated that alien species in this area had short evolutionary distances or were closely related to native species in the communities. In accordance to this, Carvallo et al. (2014) reported that alien plant species in Australia had a phylogenetically clustered structure caused by the con-familiar co-occurrence of common native and alien species in the communities (native/alien pairs such as *Sonerilla* / *Clidemia*, *Psychotria* / *Spermacocce*, *Synedrella* / *Ageratum*, *Centotheca* / *Axonopus*, and *Clerodendrum* / *Hyptis*). This implies that traits similarity is likely to support the survivability of alien species in the communities.

Ricotta et al. (2010) also found similar patterns in European urban areas where the most noxious alien species are those with high taxonomic similarity to natives. By using global datasets of native and alien species Ordonez (2014) also confirmed this pattern that alien species are most likely to have phylogenetic similarity with natives. The similar response of alien to native species regarding their environmental conditions (e.g. climatic and edaphic conditions) was explained by a shared evolutionary history. Hence, alien species had higher chance to successfully established or even outnumbered the native due to its ability to adapt with the local conditions (Ordonez, 2014). The successful establishment of alien species with phylogenetic similarities, besides extirpating the native species, also leads to taxonomic and phylogenetic homogenization of plant communities (Winter et al., 2009).

In conclusion, forest conversion into more intensively managed systems negatively affects understorey plant diversity both at taxonomic and phylogenetic level (Hypothesis 1a is confirmed). PD has strong correlation with TD (Hypothesis 1b is confirmed). Furthermore, forest conversion generates random and overdispersed PS along an intensification gradient (Hypothesis 2a and 2b are confirmed). Invasion of alien plant species evidently plays a strong role in changing the phylogenetic structure of the plant communities. Instead of creating more overdispersed community structures, the existence of alien plant species upon the phylogenetic structure lead to less overdispersed and a more randomly structure (Hypothesis 3 is rejected).

Therefore, I recommend that future studies should give more attention to the invasion of alien plant species in the local plant communities, and investigate not only the impact upon species loss, but also the change in overall community composition due to forest conversion.

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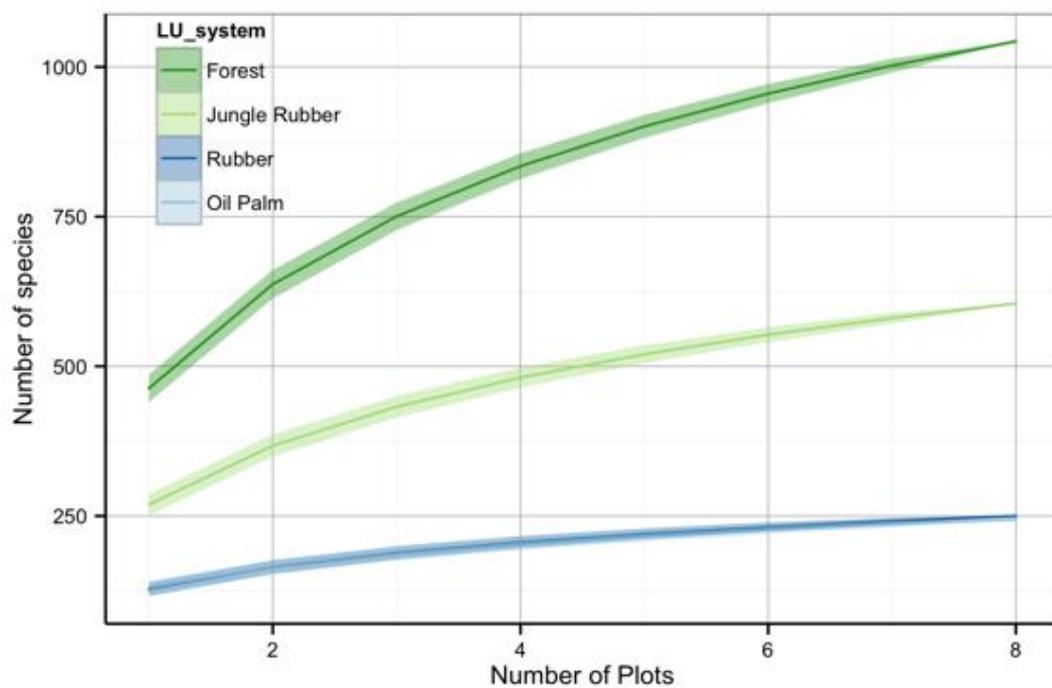
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6. Appendices

6.1. Sample Representativeness

The sample representativeness in this study was considered sufficient in particular for rubber and oil palm as shown in the species accumulation curve. Although in jungle rubber and forest the curve still demonstrated an increasing trend. Yet, there was tendency of saturating with an addition of more samples.

Table 4. Species accumulation curve of understorey plant community in four land-use systems (n = 8 plots/system).



6.2. List of all families in each land-use system

The value represents the numbers of species, the number inside the bracket indicates the total abundance.

No.	Family	Forest	Jungle rubber	Rubber	Oil Palm
1	Acanthaceae	-	4 (33)	2 (4,592)	2 (10,731)
2	Achariaceae	5 (23)	1 (1)	-	-
3	Actinidiaceae	1 (1)	1 (1)	-	-
4	Amaryllidaceae	3 (29)	-	-	-
5	Anacardiaceae	10 (25)	7 (17)	-	-
6	Ancistrocladaceae	1 (15)	-	-	-
7	Anisophylleaceae	1 (7)	1 (6)	1 (4)	1 (8)
8	Annonaceae	81 (512)	40 (184)	3 (4)	6 (6)
9	Apocynaceae	29 (155)	13 (632)	6 (201)	4 (63)
10	Aquifoliaceae	1 (3)	-	-	-
11	Araceae	35 (409)	8 (136)	1 (2)	1 (1)
12	Araliaceae	2 (16)	1 (2)	-	-
13	Arecaceae	53 (461)	18 (143)	1 (14)	1 (854)
14	Aristolochiaceae	-	1 (22)	-	-
15	Asparagaceae	4 (43)	4 (32)	2 (21)	1 (5)
16	Aspleniaceae	3 (20)	1 (16)	-	2 (34)
17	Asteraceae	2 (7)	4 (143)	9 (723)	9 (8,465)
18	Begoniaceae	1 (4)	-	-	-
19	Blechnaceae	1 (1)	2 (97)	2 (197)	2 (27)
20	Burseraceae	29 (680)	8 (44)	-	-
21	Calophyllaceae	7 (232)	1 (1)	2 (2)	1 (3)
22	Cannabaceae	4 (122)	3 (17)	3 (13)	2 (19)
23	Capparaceae	2 (14)	-	1 (1)	-
24	Caprifoliaceae	-	-	1 (9)	-
25	Cardiopteridaceae	1 (61)	1 (5)	-	-
26	Celastraceae	7 (136)	5 (40)	3 (31)	-
27	Chloranthaceae	1 (4)	-	-	-
28	Cleomaceae	-	-	-	1 (53)
29	Clusiaceae	11 (68)	7 (197)	1 (1)	-
30	Combretaceae	2 (49)	2 (16)	-	-
31	Commelinaceae	2 (25)	1 (1)	-	1 (12)
32	Connaraceae	12 (468)	10 (99)	-	1 (1)
33	Convolvulaceae	2 (39)	3 (24)	1 (3)	3 (3)
34	Cornaceae	5 (19)	2 (10)	-	-
35	Costaceae	1 (13)	1 (1)	-	-
36	Ctenolophonaceae	1 (2)	-	-	-
37	Cucurbitaceae	-	1 (1)	2 (3)	1 (2)
38	Cyperaceae	2 (13)	2 (357)	7 (3,185)	9 (1,027)
39	Davalliaceae	1 (1)	1 (4)	1 (14)	2 (197)
40	Dennstaedtiaceae	1 (4)	1 (78)	1 (368)	2 (747)
41	Dichapetalaceae	1 (1)	3 (7)	2 (2)	2 (6)
42	Dilleniaceae	6 (192)	5 (108)	1 (1)	-
43	Dioscoreaceae	4 (25)	7 (82)	5 (17)	3 (6)

44	Dipterocarpaceae	12 (294)	1 (1)	1 (1)	-
45	Dryopteridaceae	1 (2)	-	-	-
46	Ebenaceae	14 (44)	4 (10)	-	-
47	Elaeocarpaceae	8 (20)	7 (50)	2 (30)	3 (23)
48	Escalloniaceae	1 (1)	-	-	-
49	Euphorbiaceae	19 (581)	24 (836)	17 (1,644)	17 (135)
50	Fabaceae	49 (2,476)	39 (871)	12 (119)	17 (101)
51	Fagaceae	9 (35)	3 (5)	-	-
52	Flagellariaceae	-	-	-	1 (2)
53	Gentianaceae	1 (2)	-	-	-
54	Gesneriaceae	2 (7)	-	-	-
55	Gleicheniaceae	1 (1)	1 (646)	1 (811)	1 (360)
56	Gnetaceae	3 (101)	1 (38)	1 (10)	1 (4)
57	Hanguanaceae	1 (34)	-	-	-
58	Hypericaceae	4 (4)	2 (26)	2 (5)	2 (5)
59	Hypoxidaceae	1 (4)	1 (74)	1 (48)	1 (105)
60	Icacinaceae	-	2 (3)	1 (1)	-
61	Irvingiaceae	1 (4)	-	-	-
62	Ixonanthaceae	-	1 (3)	1 (2)	-
63	Lamiaceae	9 (53)	12 (70)	7 (55)	4 (218)
64	Lauraceae	50 (339)	20 (75)	3 (8)	2 (4)
65	Lecythidaceae	4 (20)	4 (7)	1 (8)	-
66	Linaceae	1 (11)	1 (5)	-	-
67	Linderniaceae	1 (1)	1 (8)	3 (2,192)	5 (3,709)
68	Loganiaceae	1 (1)	2 (13)	-	-
69	Loranthaceae	1 (6)	-	-	-
70	Lowiaceae	1 (1)	-	-	-
71	Lygodiaceae	-	4 (21)	4 (42)	4 (285)
72	Lythraceae	-	-	1 (3)	-
73	Malpighiaceae	-	-	-	-
74	Malvaceae	29 (505)	15 (558)	3 (70)	3 (32)
75	Marantaceae	2 (40)	1 (2)	-	-
76	Marattiaceae	1 (211)	-	-	-
77	Melastomataceae	13 (269)	9 (5,724)	9 (9,264)	10 (18,791)
78	Meliaceae	33 (158)	8 (16)	-	-
79	Menispermaceae	15 (65)	8 (99)	6 (26)	4 (10)
80	Monimiaceae	2 (2)	-	-	-
81	Moraceae	18 (83)	23 (614)	9 (113)	7 (130)
82	Musaceae	-	-	1 (8)	-
83	Myristicaceae	24 (124)	4 (6)	-	1 (4)
84	Myrtaceae	50 (753)	24 (152)	8 (34)	5 (20)
85	Ochnaceae	-	1 (2)	-	-
86	Olacaceae	2 (53)	-	-	-
87	Oleaceae	5 (60)	1 (2)	-	1 (1)
88	Onagraceae	-	-	1 (1)	1 (2)
89	Ophioglossaceae	-	-	-	2 (10)
90	Opiliaceae	1 (10)	1 (42)	1 (24)	1 (1)
91	Orchidaceae	3 (4)	2 (3)	1 (2)	-

92	Oxalidaceae	-	1 (3)	1 (3)	1 (127)
93	Pandaceae	3 (16)	3 (26)	2 (3)	-
94	Pandanaceae	7 (38)	3 (13)	-	-
95	Passifloraceae	3 (3)	2 (10)	1 (9)	1 (3)
96	Pentaphragaceae	1 (1)	1 (2)	1 (2)	1 (4)
97	Phyllanthaceae	46 (711)	35 (713)	19 (570)	17 (719)
98	Piperaceae	9 (35)	6 (46)	-	-
99	Poaceae	4 (74)	15 (1,296)	15 (11,975)	17 (15,617)
100	Podocarpaceae	1 (4)	-	-	-
101	Polygalaceae	7 (52)	5 (8)	2 (2)	2 (68)
102	Polypodiaceae	2 (6)	4 (7)	2 (5)	1 (241)
103	Primulaceae	16 (164)	7 (27)	1 (13)	1 (23)
104	Proteaceae	4 (146)	4 (19)	1 (5)	-
105	Pteridaceae	2 (137)	1 (357)	1 (179)	1 (1,059)
106	Putranjivaceae	1 (4)	-	-	-
107	Rhamnaceae	6 (268)	2 (7)	1 (1)	1 (3)
108	Rhizophoraceae	3 (9)	3 (30)	1 (4)	4 (14)
109	Rosaceae	4 (71)	2 (21)	-	-
110	Rubiaceae	84 (455)	40 (487)	27 (1,766)	31 (15,900)
111	Rutaceae	17 (45)	8 (67)	-	2 (2)
112	Salicaceae	8 (19)	3 (36)	-	-
113	Sapindaceae	23 (663)	10 (25)	-	-
114	Sapotaceae	14 (211)	4 (36)	3 (8)	-
115	Schisandraceae	-	1 (1)	-	-
116	Schizaeaceae	2 (51)	3 (7)	-	-
117	Scrophulariaceae	-	-	-	1 (2)
118	Simaroubaceae	1 (27)	1 (5)	1 (1)	-
119	Smilacaceae	2 (45)	6 (20)	-	-
120	Solanaceae	-	-	1 (10)	2 (28)
121	Staphyleaceae	-	-	-	1 (6)
122	Stemonaceae	1 (2)	-	1 (4)	-
123	Stemonuraceae	2 (9)	2 (6)	-	-
124	Symplocaceae	-	2 (13)	2 (3)	2 (12)
125	Tectariaceae	1 (115)	-	1 (2)	-
126	Theaceae	2 (11)	1 (4)	-	-
127	Thelypteridaceae	-	2 (4)	2 (20)	2 (1,134)
128	Thymelaeaceae	4 (12)	3 (21)	1 (1)	-
129	Trigoniaceae	1 (3)	1 (192)	-	-
130	Urticaceae	6 (765)	1 (1)	-	-
131	Verbenaceae	-	-	2 (56)	2 (548)
132	Violaceae	2 (128)	1 (10)	-	1 (4)
133	Vitaceae	19 (97)	8 (83)	1 (3)	1 (3)
134	Xanthorrhoeaceae	-	-	1 (1)	1 (26)
135	Zingiberaceae	7 (332)	17 (574)	4 (11)	1 (1)
	Total	1,043 (15,007)	605 (16,716)	250 (38,586)	244 (81,766)

6.3. List of alien species found in the four land-use systems

No.	Species	Family	Origin	Sources
1	<i>Acmella paniculata</i>	Asteraceae	Trop. America	2
2	<i>Ageratum conyzoides</i>	Asteraceae	Trop. America, Central & South America	3
3	<i>Andrographis paniculata</i>	Acanthaceae	India and Sri Lanka	8
4	<i>Asystasia gangetica</i>	Acanthaceae	Africa	2
5	<i>Axonopus compressus</i>	Poaceae	Trop. America	2
6	<i>Bellucia pentamera</i>	Melastomataceae	Trop. America	7
7	<i>Calopogonium mucunoides</i>	Fabaceae	Trop. America, from Mexico to Argentina	3
8	<i>Centrosema pubescens</i>	Fabaceae	Central and South America	8
9	<i>Chromolaena odorata</i>	Asteraceae	Central and South America	2
10	<i>Citrus nobilis</i>	Rutaceae	Trop. America	8
11	<i>Cleome ruidosperma</i>	Cleomaceae	West Trop. Africa	2
12	<i>Clibadium surinamense</i>	Asteraceae	Trop. America	2
13	<i>Clidemia hirta</i>	Melastomataceae	South America	2
14	<i>Crassocephalum crepidioides</i>	Asteraceae	Trop. Africa	2
15	<i>Croton hirtus</i>	Euphorbiaceae	Trop. America	8
16	<i>Diodella sarmentosa</i>	Rubiaceae	South Mexico to Trop. America, Trop. Africa	10
17	<i>Elaeis guineensis</i>	Arecaceae	West Africa	3
18	<i>Ficus auriculata</i>	Moraceae	Nepal and India to Southern China, Hainan and Indochina	7
19	<i>Hevea brasiliensis</i>	Euphorbiaceae	South America	11
20	<i>Hyptis capitata</i>	Lamiaceae	Trop. America	8
22	<i>Kohautia cynanchica</i>	Rubiaceae	Africa	4
22	<i>Lagerstroemia speciosa</i>	Lythraceae	India	3
23	<i>Lantana camara</i>	Verbenaceae	Trop. America	3
24	<i>Lindernia diffusa</i>	Linderniaceae	Trop. America, Trop. Africa	8
25	<i>Mikania micrantha</i>	Asteraceae	Trop. America	3
26	<i>Mimosa pudica</i>	Fabaceae	Trop. America	6
27	<i>Morinda villosa</i>	Rubiaceae	North India to China (South Yunnan)	10
28	<i>Oxalis barrelieri</i>	Oxalidaceae	Trop. South America	10
29	<i>Panicum laxum</i>	Poaceae	Trop. South America	10
30	<i>Paspalum conjugatum</i>	Poaceae	Trop. America	2
31	<i>Paspalum dilatatum</i>	Poaceae	Trop. America	10
32	<i>Piriqueta racemosa</i>	Passifloraceae	South America	9
33	<i>Polygala paniculata</i>	Polygalaceae	Trop. America	2
34	<i>Psidium guajava</i>	Myrtaceae	Trop. & S. Trop. America	10

35	<i>Rhynchospora colorata</i>	Cyperaceae	S.E. U.S.A. to N. S. America	10
36	<i>Rolandra fructiosa</i>	Asteraceae	South America	9
37	<i>Scoparia dulcis</i>	Scrophulariaceae	Trop. America	1
38	<i>Solanum jamaicense</i>	Solanaceae	America	9
39	<i>Solanum quitoense</i>	Solanaceae	Trop. America	5
40	<i>Spermacoce exilis</i>	Rubiaceae	S. Mexico to Trop. America	10
41	<i>Spermacoce laevis</i>	Rubiaceae	Mexico, Caribbean to S. Trop. America	10
42	<i>Spermacoce latifolia</i>	Rubiaceae	S. Mexico to Trop. America	10
43	<i>Spermacoce ocymifolia</i>	Rubiaceae	S. Mexico to Trop. America	10
44	<i>Stachytarpheta indica</i>	Verbenaceae	Mexico to Trop. America	10

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Statement of Originality

I hereby assure that this thesis was exclusively made by myself and that I have used no other sources and aids than the ones enlisted.

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