



Plant diversity, forest dependency, and alien plant invasions in tropical agricultural landscapes



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ABSTRACT

Land-use change and intensification in tropical rainforest regions is generally linked to a loss in species diversity that especially affects forest-dependent species. Indonesia is currently the country with the highest deforestation rates worldwide with potentially devastating effects on its diverse and highly endemic flora and fauna. Here we present a comprehensive assessment of the varied effects of forest conversion and land-use intensification on vascular plant diversity across the four dominant land-use systems in the lowlands of Sumatra: rainforest, jungle rubber agroforest, rubber plantations, and oil palm plantations. We conducted plot-based species inventories in Jambi Province and assessed a total of 156,006 individuals and 1382 plant species. Forest had the highest levels of alpha, beta, and gamma diversity, followed by jungle rubber. Plant communities in oil palm plantations were characterized by a high density of herbaceous weeds, but low species numbers and low beta diversity. Species numbers were comparable in oil palm and rubber plantations, but the latter showed slightly higher beta diversity. Forest had a clearly distinct floristic composition while the floristic composition of the other systems - and especially the two plantation systems - converged. Alien species were almost completely absent from forest, but the number and relative abundance of alien species increased with increasing land-use intensity and was highest in oil palm plantations where 25% of the species and 62% of the individuals belonged to alien species. Our results represent a first quantitative baseline for how forest conversion in Southeast Asia causes loss in species richness, changes in floristic composition and vegetation structure, as well as a shift from native to alien-dominated plant communities.

1. Introduction

Southeast Asia is globally outstanding for its high diversity and endemism in many plant and animal groups (Kier et al., 2009; Myers et al., 2000). The high levels of regional biodiversity are associated with tropical climates and a diverse and complex geological and biogeographical history (Sodhi et al., 2010a). Tropical forests in Southeast Asia are especially significant carbon storage and biodiversity reservoirs (Margono et al., 2014).

The flora of tropical Asia remains one of the least studied (Webb et al., 2010) and at the same time, it is under enormous pressure from rainforest conversion, habitat conversion, and land-use intensification (Koh and Wilcove, 2008; Miettinen et al., 2011; Stibig et al., 2014). Indonesia, which until recently contained almost half of Southeast Asia's remaining primary forest (Koh, 2007), is currently experiencing the highest deforestation rates worldwide (Margono et al., 2014).

Within Indonesia, the island of Sumatra has the highest deforestation rates (Miettinen et al., 2011), especially in the lowlands (Margono et al., 2014). The main driver for deforestation in the recent past used to be logging, but this has now shifted towards the conversion of remaining natural and logged-over forests and extensively managed agroforestry systems into cash-crop monocultural plantations including oil palm (*Elaeis guineensis*), rubber (*Hevea brasiliensis*), and acacia plantations (*Acacia* spp.) (Abood et al., 2015; Koh and Ghazoul, 2008; Wilcove and Koh, 2010). Rubber and oil palm plantations already cover vast areas in Southeast Asia and continue to expand, and we are just beginning to discover the effects on diversity and ecosystem functioning (Dislich et al., 2016; Koh and Wilcove, 2008; Turner et al., 2008). Recent studies on different taxa (e.g. Böhnert et al., 2016; Gray et al., 2016; Tao et al., 2016) and environmental measures (Hardwick et al., 2015; Luke et al., 2017) indicate that the conversion of rainforest into rubber and oil palm plantations generally leads to a substantial loss of

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taxonomic and functional animal and plant diversity, alters microclimatic and environmental conditions, and reduces above- and below-ground carbon stocks (Drescher et al., 2016). Oil palm plantations have been reported to support even fewer species than other tree plantations (Fitzherbert et al., 2008; Foster et al., 2011; Savilaakso et al., 2014). Unfortunately, areas suitable for oil palm and rubber cultivation overlap with those of highest importance for biodiversity (Fitzherbert et al., 2008).

Species numbers alone are not sufficient to reveal the impact of forest conversion on plant diversity as they cannot inform about more qualitative changes in species composition and the invasion of alien species. For instance, many tropical species are strongly dependent on forests and do not occur in the agricultural matrix (Mendenhall et al., 2016), a phenomenon that is comparatively well studied for animals (e.g. Harvey et al., 2006). If forests are converted, forest-dependent species might be replaced by species from other habitats or areas, often by cosmopolitan and pantropical alien weeds. *Clidemia hirta* for example is native to central and South America, but is nowadays spread worldwide over the tropics including Southeast Asia (e.g. Peters, 2001). By replacing regionally distinct plant communities, alien species may contribute to a loss of native species and lead to biotic homogenization, referring to the process by which the genetic, taxonomic or functional similarities of regional biotas increase over time (Olden, 2006; Olden and Rooney, 2006).

To conserve biodiversity in oil palm and rubber producing countries, more fine-scale data on land-use change are needed to assess the magnitude and extent of the impacts of forest conversion into oil palm or other tree plantations (Koh and Wilcove, 2008). Available studies often focus on changes in alpha diversity (Savilaakso et al., 2014) and/or certain plant groups such as trees (e.g. Kessler et al., 2009; Slik et al., 2002). In contrast, studies of land-use effects in beta- and gamma-diversity that cover all plants or that include also more qualitative aspects like forest dependency or alien plant invasions are rare in tropical systems, limiting our ability to assess and model changes of biodiversity at landscape and regional scales (Mendenhall et al., 2014; Tschamtket et al., 2012).

Here we quantify the effects of rainforest conversion and agricultural intensification on plant diversity by carrying out extensive vegetation surveys in four dominant land-use systems in the lowlands of Sumatra along a land-use intensity gradient (lowest in forest, intermediate in jungle rubber agroforests, highest in monocultural plantations). Our main objectives were to assess (1) how plant diversity varies in the different land-use systems, (2) the degree of forest dependency of species, (3) the change of floristic composition from forest to the agricultural systems including explanatory biophysical parameters, and (4) the degree of alien plant invasions.

2. Methods

2.1. Study area

Field work was conducted from February 2013 to August 2014 in the EFForTS project region in Jambi Province (central Sumatra, Indonesia, Fig. 1, www.uni-goettingen.de/EFForTS). Jambi has a tropical humid climate with a dryer period between July and August. The mean annual temperature is 26.7 °C and annual rainfall amounts 2235 mm per year (Drescher et al., 2016). The natural vegetation of the project area consists of dipterocarp-dominated lowland rainforest (Laumonier, 1997), but the lowlands of Jambi Province experienced rapid large-scale deforestation since the 1970's due to logging concessions and forest conversion into agricultural land (Laumonier et al., 2010; Suyanto et al., 2000). In 2013, only 30% of Jambi Province was covered with forest, most of which is located in mountainous areas (Drescher et al., 2016).

2.2. Field sampling and botanical definitions

We inventoried vascular plant species in a total of 32 core plots (50 m × 50 m) distributed among four land-use systems: lowland rainforest, jungle rubber, rubber plantations (*Hevea brasiliensis*), and oil palm plantations (*Elaeis guineensis*) (eight plots per system). Five subplots (5 m × 5 m) were nested at fixed positions within each core plot (see also Drescher et al., 2016). Lowland rainforest served as reference and presents ‘primary degraded forest’ according to Margono et al. (2014). The selected forest plots did not show any direct sign of disturbance, but both forests in Bukit Duabelas National Park and Harapan Rainforest were affected by selective logging and fragmentation in the past. Jungle rubber represents an extensively managed agroforest system (Gouyon et al., 1993), which is established by planting rubber trees into secondary or disturbed forest. The investigated rubber and oil palm plantations represent tree monocultures aged between 7 and 16 years for rubber and 8–15 years for oil palm in 2012 and are managed by smallholders.

Within each core plot, we measured and identified all trees with a diameter at breast height (DBH) ≥ 10 cm (height, DBH, measured at 1.30 m or for rubber trees at 1.70 m above the tapping zone). All oil palms within our plots still had a ring of leaf petioles attached to their trunks so that the DBH measurements here include the trunk and the ring of petioles. Oil palm leaves are cut during harvest at about 20 cm length and stay attached to the trunk for about 20 years (Corley and Tinker, 2003). Therefore, we additionally measured the DBH of 30 older oil palms outside our plots which already lost the petioles to calculate a mean basal area for an average of 136 oil palms ha⁻¹. All vascular plant individuals growing within the subplots were counted, identified, and measured (height). In case of stolons, the mother plant and its clones were counted as one individual. We collected herbarium specimens of three individuals per species and up to three duplicates per individual and prepared them for identification and later deposition at several Indonesian herbaria, i.e. Herbarium Bogoriense (BO), Herbarium of SEAMEO BIOTROP (BIOT), Herbarium of the University of Jambi, Harapan Rainforest Herbarium. Species and higher-level taxa names follow The Plant List (2013) and The Angiosperm Phylogeny Group (2009).

All plant species were divided into native and alien species after Richardson et al. (2000). See Appendix A for more information about our classification of alien species.

2.3. Statistical analysis

To estimate the total species number per system, we calculated species accumulation curves for each land-use system (Gotelli and Colwell, 2001). To test for the association of species to the four land-use systems, we calculated indicator values for each species using the function “indval” in the R package *labdsv* (Roberts, 2016). At the plot level, we compared the plant communities of all four land-use systems in terms of species richness, density (individuals ha⁻¹ (trees), individuals m⁻² (understorey)), tree basal area (m⁻² ha⁻¹), mean understorey plant height, Shannon effective number of species, Pielou's evenness (Magurran, 2004), and beta diversity (Sørensen dissimilarity based on species incidences) (Appendix C). To test for significant differences between land-use systems, we used analyses of variance (ANOVA) and Tukey's Honest Significant Differences post-hoc test if homoscedasticity was met (Levene-test). In the presence of heteroscedasticity, weighted regressions were used instead. Weighted regressions use the inverse variance of the land-use systems so that observations belonging to a land-use system with higher variance get less weight compared to observations in a land-use system with lower variance (Fahrmeir et al., 2013). Differences in beta diversity were assessed using the test developed by Bacaro et al. (2012) with pairwise combinations of all land-use systems. To account for multiple comparisons, *p*-values were Bonferroni corrected (Sokal and Rohlf, 1995).

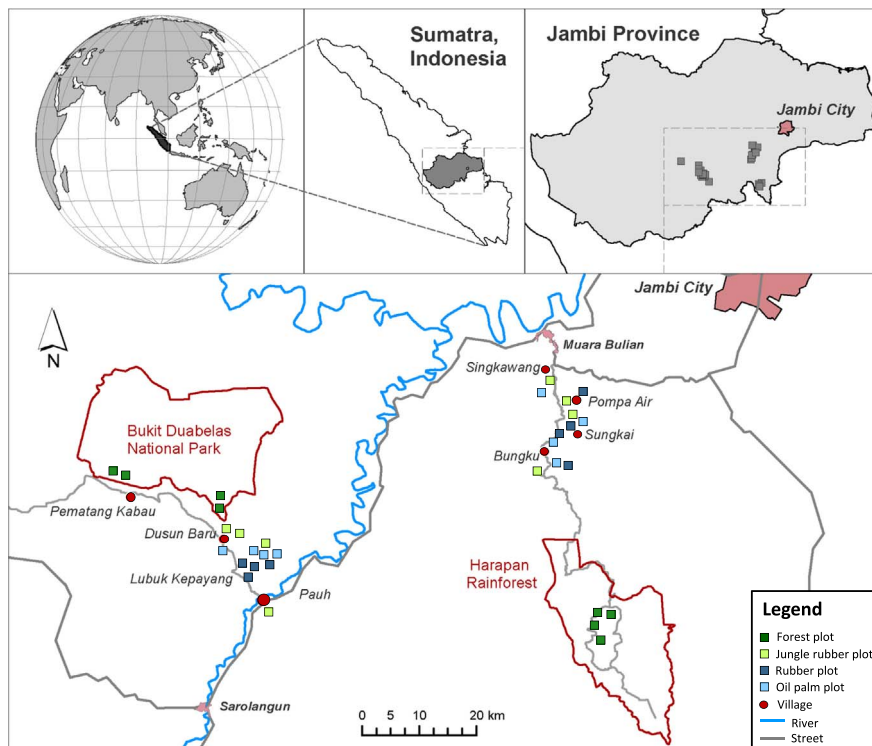


Fig. 1. Location of core plots near Bukit Duabelas National Park and Harapan Rainforest in the EForTS study area in Jambi Province (Sumatra, Indonesia). Map modified after Drescher et al. (2016).

The percentage of alien plant species in the four land-use systems was tested for significant differences by using Kruskal-Wallis rank sum tests and multiple comparison tests after Kruskal-Wallis (function “kruskalmc” in the R package *pgirmess* (Giraudoux, 2016)). To analyze the floristic composition of plots in the four systems, we used non-metric multidimensional scaling (NMDS, 999 permutations) based on Bray-Curtis dissimilarity, a widely used and efficient index of between-sample dissimilarities that accounts for differences in abundance (Clarke et al., 2006). Differences in floristic composition among the land-use systems were tested using permutational multivariate analysis of variance (PERMANOVA, 999 permutations, function “adonis” in R package *vegan* (Oksanen et al., 2013)) (Anderson and Walsh, 2013). To account for multiple comparisons, *p*-values were Bonferroni corrected. In order to explain floristic similarities between the land-use systems, we added floristic (plant families and percentage of native/alien individuals) and environmental parameters as vectors to the NMDS plot and tested for significant correlations between vectors and land-use systems. These parameters were either based on our plant survey or on previous studies carried out on the same core plots: soil parameters (pH, Fe, N, K, Mn, Ca, N, C, P, Al, Mg, Na) (Allen et al., 2015), tree biomass (Kotowska et al., 2015), microclimate (air humidity and air temperature), and canopy openness (both Drescher et al., 2016). We conducted all statistical analyses and prepared figures in the statistic software R version 3.1.3 (R Core Team, 2015) using the packages *vegan* (Oksanen et al., 2013), *pgirmess* (Giraudoux, 2016), *labdsv* (Roberts, 2016), *raster* (Hijmans et al., 2015), *car* (Fox et al., 2016), *ggplot2* (Wickham and Chang, 2016), *vegetarian* (Chorney, 2015), *VennDiagram* (Chen, 2015), and *plyr* (Wickham, 2016).

3. Results

A total of 156,006 individuals and 1382 species and morphospecies from 148 vascular plant families were identified from the 32 core plots (Appendix A). This included 724 tree, 379 shrub, 258 herb species as well as 21 species that were only encountered as seedlings. The most species-rich families were Rubiaceae (96 species), Annonaceae (71 species), Myrtaceae, and Phyllanthaceae (both 60 species). Species

accumulation curves approached saturation for both plantations while the curves for forest and jungle rubber were still increasing (Fig. B.1), indicating that continued sampling in forest and jungle rubber is likely to result in more species, while species richness in the plantations has been nearly fully sampled.

Forest had the highest total species numbers (963), followed by jungle rubber (652), rubber (230), and oil palm plantations (219, Fig. 2a). Most species encountered in forest (85%) and jungle rubber (83%) were woody species (trees and shrubs). Rubber and oil palm plantations in contrast had similar species numbers of all three growth forms (tree, shrub, herbs). In regards of total plant individuals, forest (17,041) and jungle rubber (18,029) reached only about half of the individual numbers in rubber plantations (38,948) and less than a quarter of oil palm plantations (81,986; Fig. 2b). Forest and jungle rubber had similar individual numbers of all three growth forms, but rubber and especially oil palm plantations were clearly herb-dominated.

Both, rubber and oil palm plantations are tree monocultures and were therefore mainly composed of a single tree species. In oil palm, we encountered only two trees (DBH \geq 10 cm) belonging to two non-oil palm tree species and in our rubber plots, four trees (DBH \geq 10 cm) belonging to three non-rubber tree species. Considering also the understorey, however, we found 63 tree species (451 individuals) in oil palm plantations and 77 tree species (685 individuals) in rubber plantations. This is still far less than in forest with 557 total tree species (6499 individuals), but shows that middle-aged first generation rubber and oil palm plantations still have a considerable pool of native tree seedlings in their understorey (110 species). Most of these species were widely distributed, but 11 species were exclusively found in oil palm plantations and nine species only in rubber plantations. The most species rich genera of native tree seedlings in the plantations were pioneer or secondary forest species such as *Macaranga* (6 spp.), *Ficus* (5 spp.), *Artocarpus* (5 spp.), and *Alstonia* (2 spp.). Adult trees of these genera were most common in jungle rubber, but a total of 18 species found in the plantation understorey occurred more often in forest than in any other system and can therefore be considered as true forest species.

Of all 1382 inventoried plant species, 587 species (i.e. 42% of all

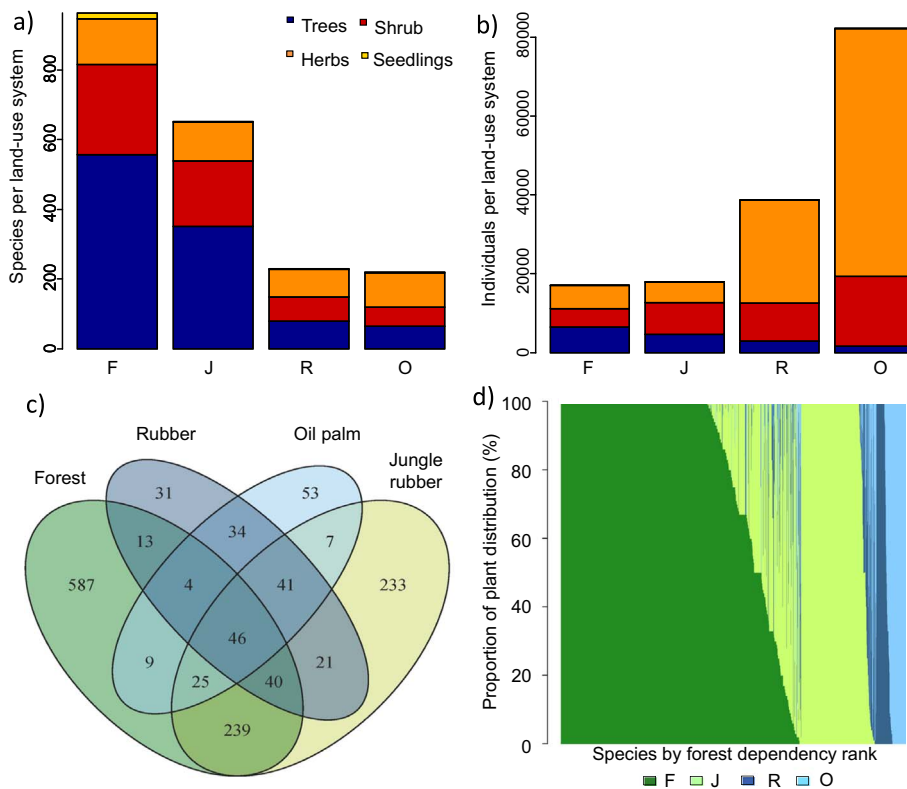


Fig. 2. Total species (a) and individual (b) numbers per land-use system including trees (DBH ≥ 10 cm) and understorey vegetation. The group 'seedlings' combines several currently unidentified non-herbaceous seedlings that might either become a tree or a shrub. Venn diagram (c) showing numbers of shared and unique plant species in the four land-use systems and forest dependency (d) of 1382 plant species and 156,006 individuals across a land-use gradient measured as proportion of each species in each of the four land-use systems: F – forest, J – jungle rubber, R – rubber plantation, O – oil palm plantation.

species and 61% of all species in forest) occurred exclusively in forest (Fig. 2c). In the two plantation systems, in contrast, > 75% of the species also occurred in other land-use systems. Forest and jungle rubber shared 239 species (17%) that did not occur in the plantations. This is more than the total species number found in either of the plantations types. Based on their proportional occurrence in each system, the majority of the species shows a tendency to be forest dependent (Fig. 2d). From our indicator value analysis, 230 species were identified as indicator species for one of the land-use systems. From these indicator species, 160 (70%) species were associated with forest, 31 species with jungle rubber (14%), 33 with oil palm plantations (14%), and 6 with rubber plantations (3%) (Table D.1).

3.1. Land-use effects on plant diversity and vegetation structure

At the plot level, clear differences emerged across the four land-use systems (Fig. 3). Forest and oil palm plantations showed significant differences across all investigated variables (Fig. 3a–i), but the significance of differences between forest and jungle rubber or rubber plantations was more variable. Forest plots had significantly higher species richness than the other land-use systems for both trees and understorey plants (Fig. 3a,d). Both plantation systems had lowest species richness, while jungle rubber had intermediate values. Oil palm plantations had the lowest tree density, but the highest basal area if the ring of leaf petioles around each oil palm trunk is included in the measurements (Fig. 3b–c). The mean basal area calculated from 30 old oil palms without petioles and an average of 136 palms ha^{-1} , ranges between forest and jungle rubber ($25.84 \text{ m}^{-2} \text{ ha}^{-1}$).

Forest, jungle rubber, and rubber plantations had comparable tree densities, but forest had a significantly higher basal area indicating larger trees than in the two rubber systems (Fig. 3b–c). Forest and jungle rubber had a low density of understorey plants compared to plantations (Fig. 3e–f), but plants were significantly taller (Fig. 3f). Shannon effective number of species was significantly higher in forest and jungle rubber (Fig. 3g). Evenness was higher in forest while both plantations had a higher level of dominant species (Fig. 3h). Sørensen

dissimilarity, as a measure of beta diversity, was highest in forest, lowest in oil palm plantations and intermediate in both rubber systems (Fig. 3i).

3.2. Floristic composition

NMDS ordination and PERMANOVA revealed distinct floristic groups for forest and jungle rubber (Fig. 4), but the two plantations did not differ significantly from each other in species composition (Appendix E). We found significant correlations between floristic and environmental parameters and the four land-use systems. Families such as Dipterocarpaceae, Burseraceae, and Lauraceae and the percentage of native plant individuals were strongly correlated with forest while Melastomataceae, Poaceae and the percentage of alien plant individuals were positively correlated with the plantations (Fig. 4a, Table E.2). Among the biophysical plot descriptors, tree biomass and air humidity correlated with forest and air temperature, canopy openness, and soil pH with the plantations (Fig. 4b, Table E.3). Other significant soil parameters (Fe, K, Mn, Ca) did not explain differences in the floristic composition between, but within the land-use systems.

We identified 38 species as alien to our study area (Table A.1), 25 of them were restricted to the plantations. With 82%, the majority of alien species originated from tropical America, others from tropical Africa (8%), tropical America and Africa (5%) or other parts of Asia (5%). The most abundant alien plant species were *Clidemia hirta* (37% of individuals) and *Asystasia gangetica* (19%). Number and density of alien species increased with increasing land-use intensity (Fig. 5). Forest plots were almost entirely composed of native plant species; only 72 (0.4%) individuals belonging to three (0.3%) species were alien (*C. hirta*, *Mikania micrantha*, *Steinchisma laxum*). Jungle rubber had significantly fewer alien species than oil palm plantations but was otherwise statistically indistinguishable from the other systems in terms of alien species and individuals. Both plantations had significantly higher numbers of alien species and individuals than forest with highest numbers in oil palm plantations where 25% of species and 62% of individuals were alien.

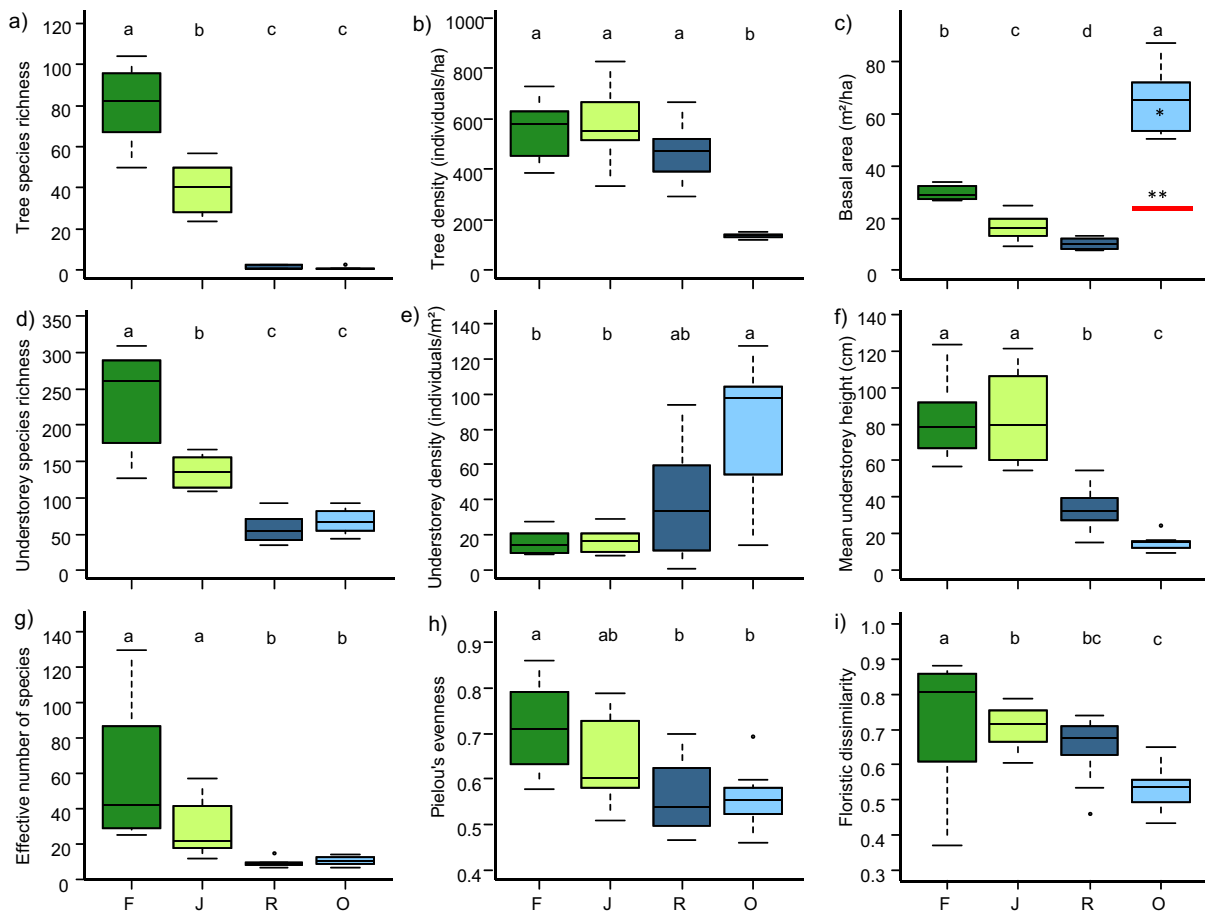


Fig. 3. Plant diversity and vegetation structure in four land-use systems on plot level ($n = 8$) including tree and understorey species richness (a, d), tree and understorey density (b, e), tree basal area (*based on DBH incl. a ring of attached petioles, ** mean basal area based on DBH without petioles) (c), understorey mean height (f), effective number of species (g), evenness (h), and floristic dissimilarity (Sørensen) (i). Letters indicate significant differences between systems (a-g: weighted regression, h: ANOVA/Tukey's Honest Significant Differences, i: Significance test for beta diversity after [Bacaro et al., 2012](#), significance level $p < 0.01$ after Bonferroni correction). Abbreviations: F – forest, J – jungle rubber, R – rubber plantation, O – oil palm plantation.

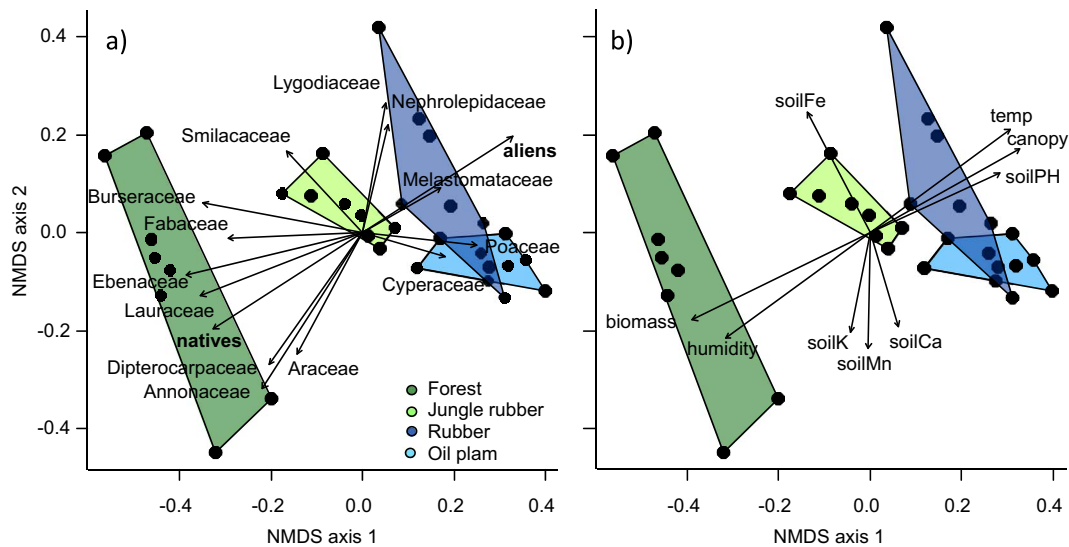


Fig. 4. Floristic composition of the four land-use systems as revealed by non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity ($n = 8$ per system, polygons mark range of each system). PERMANOVA results: $R^2: 0.333, p < 0.001$. Selected significant correlations of floristic (a) and environmental (b) parameters to land-use systems are shown by arrows. Abbreviations: natives - percentage of native plant individuals, aliens - percentage of alien plant individuals, humidity - mean relative air humidity (%), temp - mean canopy air temperature ($^{\circ}\text{C}$), canopy - canopy openness (%), biomass - tree biomass carbon (Mg ha^{-1}). See Appendix E for results of statistical analyzes.

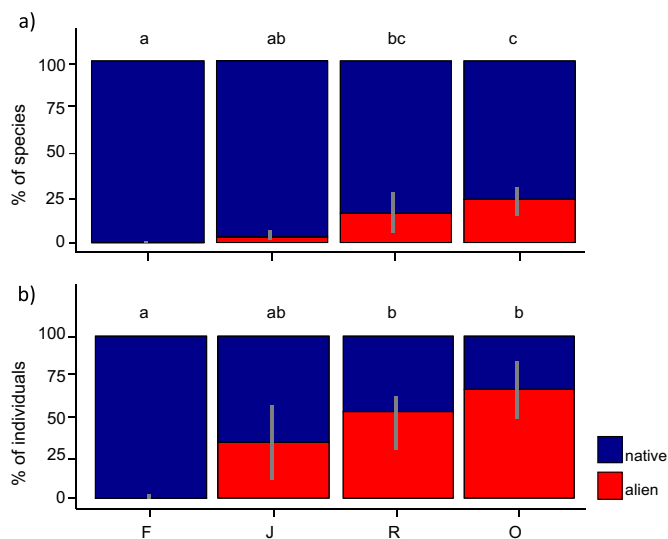


Fig. 5. Percentage of native and alien plant species (a) and individuals (b) in four land-use systems ($n = 32$): F – forest, J – jungle rubber, R – rubber plantation, O – oil palm plantation. Letters indicate significant differences between systems (Kruskal-Wallis and Kruskal-MC test, $p < 0.05$).

4. Discussion

Plants are the first group of organisms directly affected when forest is logged and converted into other land-use systems (Sodhi et al., 2010b). In intensively managed tree plantations such as oil palm and rubber, almost all native tree species are removed during plantation establishment and the understorey is frequently treated with herbicides and manual weeding, often leading to patches with bare soil. Therefore, it is unsurprising that we found a strong decline of plant diversity along the land-use intensity gradient. The development of sustainable management and conservation actions, however, requires a more comprehensive understanding of how much biodiversity can be supported by monoculture plantations and in a landscape context (Fitzherbert et al., 2008). To this end, our results give detailed insights into multiple dimensions of plant diversity loss, forest dependency, changes in floristic compositions, and alien plant invasions.

4.1. Species loss and forest dependency

In our study, both plantations together as the most intensively managed systems had 59% fewer plant species than forest. Plantations and jungle rubber agroforests combined had still 42% fewer plant species than forest. This is consistent with smallholder cacao plantations in Sulawesi where decreasing plant species numbers with increasing land-use intensity have also been observed (Clough et al., 2010; Kessler et al., 2005). Böhnert et al. (2016) found similarly strong declines of species diversity of vascular epiphytes in our study region. For epiphytes, however, this loss of diversity only occurred at the landscape level while at plot level, epiphyte diversity in oil palm plantations was comparable to forest and jungle rubber. In contrast, we find that total plant species richness in our plots was significantly higher in forest than in any other system at both, plot and landscape level. This demonstrates that the influence of land-use change can differ between plant groups.

The majority of species in our study area does not or only rarely occur outside forests and the high amount of forest-dependent species emphasizes the importance of forests as a species reservoir. Given the high deforestation rates in lowland Sumatra and a continuing pressure on the remaining forest patches, this puts many species at risk.

Plant diversity is generally known to positively affect arthropod diversity including arthropod guilds other than herbivores, and plant diversity is even used as a proxy of arthropod species richness (Basset

et al., 2012; Castagneyrol and Jactel, 2012). Consequently, a loss of plant species in general and forest-dependent species in particular might also closely correspond with a loss of animal diversity. In fact, a decline of species richness from forest towards more intensively managed systems has been observed for most animal groups (e.g. Clough et al., 2016; Drescher et al., 2016; Gibson et al., 2011). Plant species loss has further been shown to increase ecosystem vulnerability to alien plant invasions, enhance the spread of plant diseases, and alter animal community structures (Knops et al., 1999).

4.2. Floristic composition and alien species

Our results demonstrate that forest conversion does not only cause species loss, but also leads to altered species composition. Furthermore, the vegetation structure and growth form composition shifts from tall trees and understorey plants in forests towards plantations dominated by a dense layer of small herbaceous or shrubby plants combined with medium sized monoculture trees. This change in plant functional types affects closely related community-ecosystem processes (Diaz and Cabido, 1997).

Despite the low total percentage of alien plant species (2.7%), the increasing abundance of alien plants in the plantations is an important factor. Oil palm plantations have 77% less plant species than forest and most individuals of the remaining species have a South American origin. In other agricultural systems, alien weeds often cause immense economical costs due to a reduction of crop yield and additional costs for herbicides (Pimentel et al., 2005). In tree monocultures, yield reduction caused by alien weeds appears to be of less importance, but as more than half of the plants in both plantations are alien weeds, they increase costs for weeding and herbicides. From the ecological point of view it is more concerning that most of the observed alien plants are pantropical weeds such as *Clidemia hirta* (e.g. Wester and Wood, 1977). *C. hirta* was the most dominant alien plant in our study and has even been found in forest gaps. It has been shown in Malaysia that the spread of *C. hirta* to intact forests was facilitated by wild boars from nearby oil palm plantations (Peters, 2001). Thus, even the few remaining forests are affected by land-use change in their surroundings as agricultural lands and disturbed forests present a source for invasive species introduction into native forests.

Factors driving the altered plant communities in the plantations are management (weeding, fertilization, and herbicide application) and stand characteristics such as high canopy openness and dry and hot microclimate which create unfavourable conditions for most forest species. Forest has a denser canopy and a cooler and more humid microclimate while the canopy in jungle rubber and especially in the plantations is more open, corresponding with a hotter and dryer climate (Drescher et al., 2016; Hardwick et al., 2015). Changes in light and climate conditions exert strong influences on plant composition as many species are adapted to high or low light conditions (Chazdon, 1988; Wang et al., 2009) and especially invasive plants are not adapted to low-light conditions (Fine, 2002). Together with the lower propagule pressure, this might explain why invasive species are rarely found in intact forests. Intact lowland rainforests are nowadays rare in Sumatra and with increasing human population growth and extreme forest fire events, it is likely that forest degradation/conversion and alien plant invasions will both continue to spread.

4.3. Conservation implications

Lowland rainforests are outstanding in terms of plant diversity, composition, and structure and cannot be replaced by any of the agricultural systems. From a conservation point of view, it is therefore imperative to protect the remaining forests including the strengthening of the governance of protected areas, which are currently under enormous pressure and poorly managed (Curran et al., 2004; Gaveau et al., 2009; Joppa et al., 2008). In areas where forest has already

disappeared or people depend on income from their land, agroforestry systems could represent a solution for sustainable agriculture in tropical landscapes (Beukema and van Noordwijk, 2004). Jungle rubber used to be a major agricultural land-use system in the Sumatran lowlands since the beginning of the 20th century (Beukema et al., 2007) and like other agroforestry systems, jungle rubber combines economic income with conserving a considerable amount of biodiversity and ecosystem services (Beukema et al., 2007; Clough et al., 2016; Gouyon et al., 1993). Even if jungle rubber could not replace natural forests in terms of species richness, tree basal area, and beta diversity, it is comparable to forest in terms of tree and understorey density, understorey plant height, effective number of species, and evenness. Further, jungle rubber supports a considerable subset of forest species (36% in our study). Unfortunately, also jungle rubber is currently converted into rubber or oil palm plantations at immense speed due to the higher profitability of monocultural plantations (Drescher et al., 2016; Gouyon et al., 1993). Therefore, jungle rubber could be a viable option for sustainable agriculture, but as it yields lower profits, its wider implementation currently seems unrealistic.

Monoculture tree plantations are composed of few and often alien species with a different structural composition compared to forest systems, what affects various animal communities, environmental parameters, and ecosystem functions (e.g. Barnes et al., 2014; Bunker et al., 2005; Guillaume et al., 2016; Prabowo et al., 2016). Conventional plantations are therefore of very limited conservation value, but the high number of native tree seedlings in the understorey might provide a basis for ecosystem restoration (Chazdon, 2003) as it shows potential to recover into a species rich secondary forest.

We are confident that our results can serve as an important basis for landscape scale modeling and predictions on biodiversity impacts of different land-use scenarios.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.07.020>.

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