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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 aliendominated 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 belowground 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; Tscharntke 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 $(50 \text{ m} \times 50 \text{ m})$ 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 \times 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 Part 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) \geq 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 pant 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 devided 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).

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