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Source: Tropical Conservation Science, 11(1)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/1940082918813908

Research Article

Tropical Conservation Science
Volume 11: 1–14
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DOI: 10.1177/1940082918813908
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Genetic Diversity of Dominant Plant Species in Tropical Land-Use Systems in Sumatra, Indonesia

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Abstract

Biodiversity hotspots like tropical lowland rainforests in Sumatra are threatened by the agricultural expansion, which increases the deforestation rate in Indonesia, which is highest worldwide. Main land-use change drivers in Indonesia include the production of rubber and palm oil, both of which lead to a high forest conversion rate. In the remaining and degraded forest patches, species diversity has declined and species composition has been altered. Effects of habitat fragmentation and land-use change on genetic structure were frequently investigated at the species level and compared across plant species, but not for plant communities. In addition, the effect of land-use change on the genetic structure of plants has not yet been investigated. Using Amplified Fragment Length Polymorphism marker, the genetic diversity of 112 dominant plant species was assessed in four different land-use systems in Sumatra: old growth tropical lowland rainforest, jungle rubber, rubber plantation, and oil palm plantation. The four systems were investigated in two regions with four replicates, respectively. Because of different species compositions, characterized by different life history traits, forest and jungle rubber plots showed the highest diversity level, while oil palm and rubber plantations showed the lower diversity levels. The two intensively managed plantation systems showed similar genetic diversity levels as the tree dominated systems but are dominated by mainly alien species. This indicates that oil palm and rubber plantations could not be identified as habitats of conservational value. The newly introduced collection and analysis approach presents a universally applicable method to investigate different ecosystems in their plant genetic diversity to support the identification of habitats with high conservational value.

Keywords

plant genetic diversity, land-use change, AFLP, oil palm, rubber, *Hevea brasiliensis*, *Elaeis guineensis*

Introduction

Threats to Biodiversity

Globally, tropical forests harbor two thirds of terrestrial species, while covering only approximately 5% of the global surface (Gardner et al., 2009). Most tropical regions are, on one side, categorized as biodiversity hotspots and on the other side, have above-average human population growth rate (Cincotta, Wisnewski, & Engelman, 2000). Biodiversity hotspots are characterized by a high number of endemic species, high species richness, and increased habitat loss (Myers, 1988). Causes of deforestation are the expansion of agricultural land-use, logging, and mining activities at high rates for the last three decades (Abood, Lee, Burivalova, Garcia-Ulloa, & Koh, 2015; Food and Agriculture Organization

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Received 2 August 2018; Revised 30 September 2018; Accepted 28 October 2018

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[FAO], 2010; Lambin, Geist, & Lepers, 2003). Consequently, the most diverse ecosystems are under increasing danger of biodiversity degradation and species extinction, because of human expansion (Brooks et al., 2006; Cincotta et al., 2000; Sloan, Jenkins, Joppa, Gaveau, & Laurance, 2014).

Sumatra belongs to the Indonesian biodiversity hotspot Sunda-land (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). In Indonesia, the area of annual forest cover loss increased in 11 years from approximately 0.22 Mha in 2001 to 0.84 Mha in 2012 (Margono, Potapov, Turubanova, Stolle, & Hansen, 2014). Since the 1970s, the two nonnative crop species oil palm (*Elaeis guineensis* Jacq.) and rubber, *Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg., became the major crop species planted in monoculture (both species) and agroforest systems (rubber) in Sumatra (Noordwijk, Suyamto, Lusiana, Ekadinata, & Hairiah, 2008; Villamor, Pontius, & Noordwijk, 2013). *E. guineensis* is currently considered as the biggest and main threat to biodiversity in Southeast Asia (Wilcove & Koh, 2010). In 25 years, the oil palm production area in Indonesia reached approximately 12 million hectares in 2017 (Hendaryati et al., 2017) and since 2008, the country became the largest producer of palm oil worldwide (FAO, 2014). *H. brasiliensis* was introduced in Indonesia around 1900. Rubber was primarily produced in an agroforestry system, called "jungle rubber," which is an integrated complex agricultural system within secondary forest vegetation and can be seen as more sustainable rubber production (Gouyon, Foresta, & Levang, 1993; Michon & Foresta, 1995). Between 1993 and 2005, rubber production was shifted from agroforest to monoculture (Villamor et al., 2013). The rubber producing area increased from 1.9 Mha in 1990 to 3.6 Mha in 2013 and has remained at this level until 2017 (FAO, 2014; Hendaryati et al., 2017).

Consequences of Land-Use Change

Land-use change and the agricultural intensification in Indonesia have a global effect on biodiversity and human welfare with an impact which can only be estimated (Foley, De Fries, Asner, Barford, & Bonan, 2005; Laurance, Sayer, & Cassman, 2014; Newbold et al., 2015). In general, the most severe consequences, habitat loss and fragmentation, result in the decline of species diversity and change of plant species composition (Rodríguez-Echeverry, Echeverría, Oyarzún, & Morales, 2018; Savilaakso et al., 2014; Sodhi et al., 2010), in an alteration of ecosystem processes (Laliberté & Tylianakis, 2012), and an increased proportion of invasive species (Rembold, Mangopo, Tjitrosoedirdjo, & Kreft, 2017). Further, for many species, an alteration of genetic structures was observed (Honnay & Jacquemyn, 2007; Mona, Ray, Arenas, & Excoffier, 2014; Vranckx, Jacquemyn, Muys, & Honnay, 2011).

In theory, consequences of habitat loss at the intraspecific diversity level are the loss of genetic diversity and increased differentiation of populations, caused by genetic drift, inbreeding and isolation by distance, and increased differentiation of populations, but not all empirical studies confirm this (A. T. Kramer, Ison, Ashley, & Howe, 2008; Lesser, Parchman, & Jackson, 2013; Sampson et al., 2014). The different consequences of population fragmentation for species are caused by different life history traits such as, gene flow, dispersal strategy, mating system, degree of isolation, and tree density of populations (Bacles & Jump, 2011; Breed et al., 2015; Ganzhorn, Perez-Sweeney, Thomas, Gaiotto, & Lewis, 2015; Jacquemyn, De Meester, Jongejans, & Honnay, 2012; Kashimshetty, Pelikan, & Rogstad, 2015; Kettle, 2014; Sebbenn et al., 2008). Thus, it is not advisable to develop conservation strategies of genetic resources for a plant community based on results of one or few species only. A universal approach is needed, which is able to compare entire plant communities concerning their genetic variability.

Genetics in Conservation Management

The conservation of natural ecosystems depends on human intervention and management (Sloan et al., 2014). Different definitions and goals of tropical forest management techniques can lead to contradictory results (Lynam, De Jong, Sheil, Kusumanto, & Evans, 2007). Furthermore, economic and social factors, such as high human population growth, corruption, agricultural expansion, and the lack of experience in nature conservation strategies, increase the difficulty to manage tropical ecosystems in a sustainable manner and to assess their conservation value (Kettle, 2014; Sodhi, Koh, Brook, & Ng, 2004; Wilcove, Giam, Edwards, Fisher, & Koh, 2013). The growing area of secondary forests and the efforts to maintain connectivity among remaining natural habitats enhance challenges for predicting parameters to assess habitats of conservational value (HCV; Roundtable on Sustainable Palm Oil [RSPO], 2013).

Genetic information of a species can support the evaluation of survival probabilities and conservation requirements of the target species (Leimu, Vergeer, Angeloni, & Ouborg, 2010; Sthultz, Gehring, & Whitham, 2009) and help to maintain or even increase its viability in the context of landscape management (Bozzano et al., 2014; Li & Jin, 2007; Thomas et al., 2014). Genetic diversity of plants is not only important for the survival of the plant species itself, but also influences other levels of organization and dynamics within the ecosystem (Bailey et al., 2009; Whitham et al., 2006), especially when genetic resources of dominant or keystone species are concerned (Crawford & Rudgers, 2013; Hughes, Inouye, Johnson, Underwood, & Vellend, 2008; Whitham et al., 2003). Suggestions for sustainable management and monitoring programs of particular forest areas are mainly based on data about species richness, particular indicator species, and ecosystem processes (Bustamante et al., 2016; Corona, Chirici, McRoberts, Winter, & Barbati, 2011; Rametsteiner & Simula, 2003; Thompson et al., 2013), and have not always been sufficient and adequate to maintain important ecosystem structures and services (Porter-Bolland et al., 2012; Stoll-Kleemann, 2010). Various studies (Lande, 1988; Laurance et al., 2012; Symes, Rao, Mascia, & Carrasco, 2015) have emphasized the importance of investigating aspects concerning population genetics in a conservation context but do not include genetic diversity as a parameter to identify habitats or landscapes to be conserved. Hawthorne and Abu-Juam (1995) developed a Genetic Heat Index based on the abundance of rare or common species in a particular area to assess conservation priorities. This index is not based on genetic data, and hence, it cannot consider the far reaching consequences of habitat loss for each species.

The lack of information on genetic diversity, combined with different consequences of population fragmentation for various species (Kashimshetty et al., 2015) can result in inefficient management strategies to conserve plant communities. In an era of fast and vast land-use change in the tropics, an applicable and effective method for identifying biodiversity hotspots and determining protected areas is necessary (Ferraro et al., 2015; Lee, Garcia-Ulloa, & Koh, 2011; Reed, Sarasan, Kane, Bunn, & Pence, 2011). At the genetic diversity level, methods for the determination of hotspots in plant communities are not established yet (Souto et al., 2015). We introduce a universally applicable method to investigate genetic diversity of a high number of plant species. The objective is to compare the genetic diversity of the dominant plant species community in different land-use systems because of different species compositions. These results can enrich biodiversity baseline data to support the identification of habitats of high conservational value (HCV; RSPO, 2013) and conservation management of threatened landscapes.

Methods

Study Sites and Sample Collection

As a part of the interdisciplinary collaboration project "EFForTS" in Sumatra, Indonesia (Drescher et al., 2016), three land-use systems in Jambi Province, with different agricultural intensity are compared with old-growth tropical lowland rainforest: jungle rubber < rubber plantation < oil palm plantation, totaling in four land-use systems (Figure 1). Each of these investigated land-use systems had four replicates in two regions, one named after the national park "Bukit Dua Belas" and one after the forest restoration concession "Harapan." The distance between the two regions was approximately 55 km. In each of the 32 (4 replicates × 4 land-use systems × 2 regions) 50 m × 50 m plots, 10 vascular plant species, dominant by biomass, were selected using the "Bitterlich-Method" (H. Kramer & Akca, 2008). The total sample size was 10 (plants/species) × 10 (species/plot) × 32 (plots) = 3,200 plants, including 112 different species. The "Bitterlich-Method" was applied at 16 predefined positions in each of the plots (online Appendix 1). In the plantation systems, the dominant nonwoody, noncrop species were identified by the shortest distance to the same 16 positions used in the tree-dominated systems. If necessary, individuals were also sampled in the area surrounding the plots (up to 300 m). For the noncrop species, collected individuals had a minimum distance of 10 m to each other to minimize the risk of clone sampling in the plantation systems. The two crop species *H. brasiliensis* and *E. guineensis* occurred in high numbers in the transformed systems, and hence, the sampled individuals were chosen randomly. Species identification was carried out with the support of the EFForTS-subproject B06, the staff of Kebun Raya, Bogor, and Harapan. From each selected individual of each species, leaf material was sampled and dried in sealed plastic bags filled with silica gel. Herbarium specimen were collected from all individuals, excluding crop species, and stored at Jambi University.

DNA Extraction and AFLP Analysis

DNA extraction was carried out using the Dneasy 96 Plant kit and its manufactory's protocol (Qiagen, Hilden, Germany). The total genomic DNA was extracted out of approximately 1 cm^2 dried leaf material. The DNA was stored at −20°C.

Amplified Fragment Length Polymorphisms (AFLPs) were investigated according to the protocol of Vos et al. (1995) with minor modifications. All samples were analyzed with the one single enzyme/primer combination. The restriction was carried out simultaneously with the *Eco*RI/*Mse*I primer combination and incubated overnight.

For the preselective polymerase chain reaction (PCR), the E01/M03 primer combination was used and as selective E35/M63 (Keygene N.V. nomenclature). The PTC 200, Pelmer thermal cycler (MJ Research, Hampton, USA) was used for the PCR, and the applied preselective

Figure 1. The investigated old-growth forest (a) and the land-use systems jungle rubber (b), rubber plantation (c), and oil palm plantation (d) in Jambi Province, Sumatra, Indonesia.

and selective PCR-program protocols were according to Kuchma (2010).

The in-water-diluted selective PCR product was separated using the ABI genetic analyzer (3130, ABI PRISM, Waltham, USA), and the size standard GENSCAN 500 ROX was added to the solution. Fragment determination was carried out with the program GeneMapper 4.1. (Applied Biosystems, Waltham, USA).

The reproducibility of the AFLP profiles was assessed with two samples of each species, which were repeated from DNA extraction onward. Species with only 10 individuals, a second repetition for all samples was conducted from the restriction step onward and only fragments occurring in both repetitions were considered. Only unambiguous and reproducible fragments were used for the analysis. The results were transformed into a fragment present–absence (1–0) matrix.

Data Analysis

All analyses were based on the 1–0 matrices for each of the 104 successfully genotyped species. For the following analyses, two aspects were considered: the high variation in number of individuals per species collected in the study (minimum 10, maximum 160) and the high variation in number of AFLP-loci between species (minimum 37, maximum 212). These differences restrict the use of common genetic diversity indices (Bonin, Ehrich, & Manel, 2007). For example, the Shannon Index (Shannon & Weaver, 1949) can be biased because of the different number of samples (Goodmann, 1975). In this study, however, the Shannon Index was applied to the varying number of AFLP fragments per species. For that reason, genetic diversity was calculated using two different approaches. For the first approach to calculate genetic diversity, the Shannon's information Index (I; Shannon & Weaver, 1949) was used because of its commonness and comparability with other studies. Genetic diversity (I) was calculated based on 10 individuals per species in each plot respectively with the program PopGen1.32 (Yeh & Boyle, 1997). Considering the limitations of the Shannon Index, a second approach was carried out. For this second approach, each fragment of all sampled species is considered as a unit of genetic diversity. As in phylogenetic analyses (Robinson & Harris, 1999), each locus was assumed to be an independent unit. All scored loci of all 104 species in all 32 plots are presenting a pool of fragments in which a single AFLP fragment of a species can be present. The 100 individuals per plot were combined into 10 fragment pools per plot. Every plot was presented by 10 rows with each successively 10 individuals with their individual 1–0 order. The first row contained successively the first individuals, each with the respective 1–0 AFLP score, of every species collected in this plot (online Appendix 2). Each fragment was placed in one column. The second row contained all second individuals, each with the respective 1–0 AFLP score, of every species collected in this plot. Hence, the 1–0 AFLP fingerprint of the second individual of the same species was in the same columns as the first individual. This was continued for all 10 individuals and 10 species for all plots. In the following, these rows are called fragment pools. If the species occurred again in a different plot, the 1–0 matrix for these individuals was accordingly placed into the same columns. This concept was followed for all species and plots. Online Appendix 2 illustrates an example of the fragment pool approach with seven species and four plots.

The pairwise Morisita–Horn dissimilarity index (Horn, 1966) based on the fragment pool approach allows to compare plots and land-use systems genetically while simultaneously considering differences in species composition. To compare dissimilarities among plots and land-use systems only because of the genetic structure of the species, the species effect was accounted for by the following procedure. A second input file was built where all individuals were considered to be clones, that is, all fragments of the occurring species in each plot were present (online Appendix 2a). Based on these clone fragment pools, the Morisita–Horn pairwise distance matrix was calculated. Herewith, the resulting distances between the clone fragment pools are only because of the species differences and the genetic diversity is zero. The difference between the two pairwise distance matrices, the fragment pool matrix and the clone fragment pool matrix, corresponds to the pairwise genetic fragment pool distance matrix. This pairwise *genetic* fragment distance matrix was used for the calculations among fragment pools. For this calculation, the Morisita–Horn dissimilarity index was used, which calculates the number of shared fragments to the overall number of fragments in the two compared samples (Bonin et al., 2007). The calculation was carried out using the "vegdist" function of the R-package vegan (Oksanen, Blanchet, & Kindt, 2015).

Heterogeneity of the Analyzed Plots and Land-Use Systems

The heterogeneity of the land-use systems was visualized using the mean value of dispersion of each plot in a Principal Component Analysis (Gower, 1966) based on the fragment pool distance matrix. The calculation was conducted by using the function "betadisper" in the R-package "vegan" (Oksanen et al., 2015). The graph was built with the R-package "ggplot2" (Wickham, 2009).

Genetic Diversity and Differentiation Levels Within and Among Land-Use Systems

To assess genetic diversity with increasing population size of the dominant species and to test the genetic diversity dependency on the land-use system, different spatial scales were established. The different spatial scales are presented by the three levels: the lowest, α-level, corresponds to the diversity within each plot; the β-level to diversity within each land-use system; and the highest, γ-level, to the diversity within each region, that is, the diversity within the 16 plots in each region (online Appendix 1).

For the fragment pool approach, the α-level differentiation was calculated by taking the mean of the 10 pairwise *genetic* fragment pool distance values within each plot. The β-diversity level was calculated by taking the mean values of the 40 pairwise *genetic* fragment pools within each land-use system, for example, of the pairwise *genetic* distance values from all 40 forest fragment pools in the region Harapan. The γ-diversity level was based on the mean values of the 160 pairwise *genetic* fragment pool values within each region. The results were 10 mean values per plot for the fragment pool for all three diversity levels, respectively. The genetic diversity is represented by the Shannon Index (Lewontin, 1972; Shannon & Weaver, 1949) among individuals of each species in one plot, α-level; among individuals within each land-use system, β-level; and within each region, γ-level. The α-level calculation is based on 10 individuals, β-level on 10 to maximum 40 individuals, and γ-level on 10 to maximum 160 individuals depending on the number of plots the species was dominant.

The data sets, α-, β-, and γ-diversity levels for genetic diversity and differentiation were checked for normal distribution using the Kolmogorov–Smirnov test (Stephens, 1979) for continuous data in STATISTICA version 12 (StatSoft Inc., Tulsa, USA). Results were graphed using R-package "reshape2" (Wickham, 2007). Differences among the land-use systems in genetic diversity and differentiation at the α-, β-, and γ-diversity levels were assessed using a generalized mixed fixed effect model in the R-package nlme (Pinheiro, Bates, Debrov, Sarkar, & R Core Team, 2015). The model of the best fit was chosen based on the Akaike Information Criterion: the land-use system as the fixed variable and the plots nested in a region as the random effects. The results of the mixed effect models were generalized for multivariate comparisons with the function "glht" of the R-package "multcomp" (Hothorn, Bretz, & Westfall, 2008).

Results

Heterogeneity of the Analyzed Plots and Land-Use Systems

Based on the genetic and species distance matrix of the genotyped 104 species (online Appendix 3), using the fragment pool approach, two groups could be identified: the tree-dominated systems that consist of forest or jungle rubber and the plantation systems that consist of oil palm or rubber. Each land-use system within the respective plot replicates grouped together but showed no differences between the two regions (Figure 2 and online Appendix 5a). Results indicate the partly overlapping species compositions among the different land-use systems. Of the two plantation systems, oil palm and rubber showed higher similarity in species composition than jungle rubber and forest. The jungle rubber system shares with the rubber plantation at least one species and also shares species with the forest.

Genetic Diversity and Differentiation Levels Within and Among Land-Use System

Both approaches showed for all land-use systems moderate but different differentiation and diversity results. In general, the tree dominating systems of forest and jungle rubber showed higher diversity levels of the two groups. But with increasing spatial scales (within plot to within region), the mean diversity and differentiation of each land-use system depend on the respective species occurring in each plot. Results at α-level (within plot) indicate highest values for jungle rubber, lowest for oil palm plantation, and intermediate levels for forest and jungle rubber (Figure 3). Significance could only be detected between jungle rubber (highest) and oil palm plantation (lowest). The β-level (within land-use system) showed the highest genetic differentiation for jungle rubber and the lowest for forest. At γ- level (within region), the differentiation among all fragment pools was lower than that of the α- and β-levels. Significant differences within the regions were only between forest (lowest) and oil palm plantation (highest). Differentiation at γ-level was highest for oil palm followed by jungle rubber and rubber plantation. The comparison of all three levels of differentiation with the fragment pool approach showed that from α-, β- and γ-levels, there is a decline for forest species, with jungle rubber to a lesser extent. The two plantation systems showed a decrease in differentiation at the three diversity levels but in a lesser extent than the tree-dominated plots.

The α-level genetic diversity calculations based on the Shannon Index were moderate and differ little among all

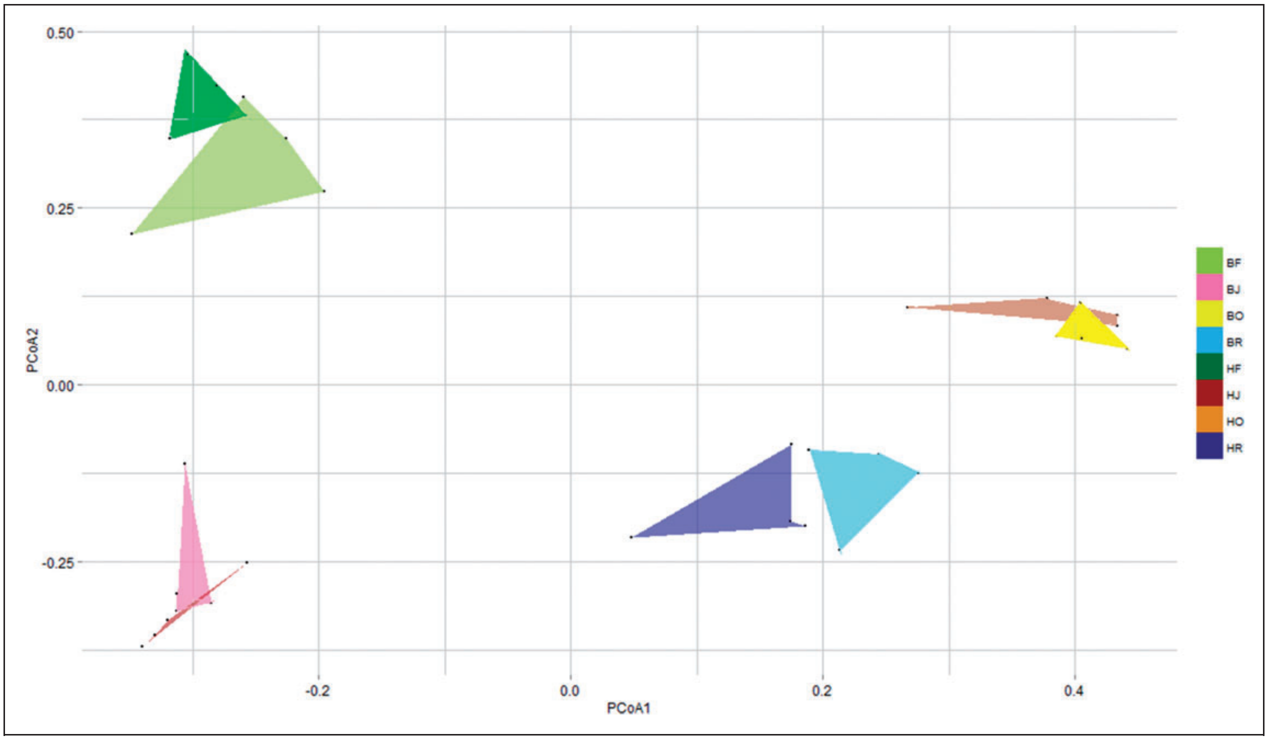

Figure 2. PCoA based on genetic and species dissimilarity of all 32 plots. BF = Bukit Duabelas forest, BJ = Bukit Dua Belas jungle rubber; BO = Bukit Dua Belas oil palm plantation; BR = Bukit Dua Belas rubber plantation; HF = Harapan forest; HJ = Harapan jungle rubber; HO = Harapan oil palm plantation; HR = Harapan rubber plantation; PCoA = Principal Component Analysis.

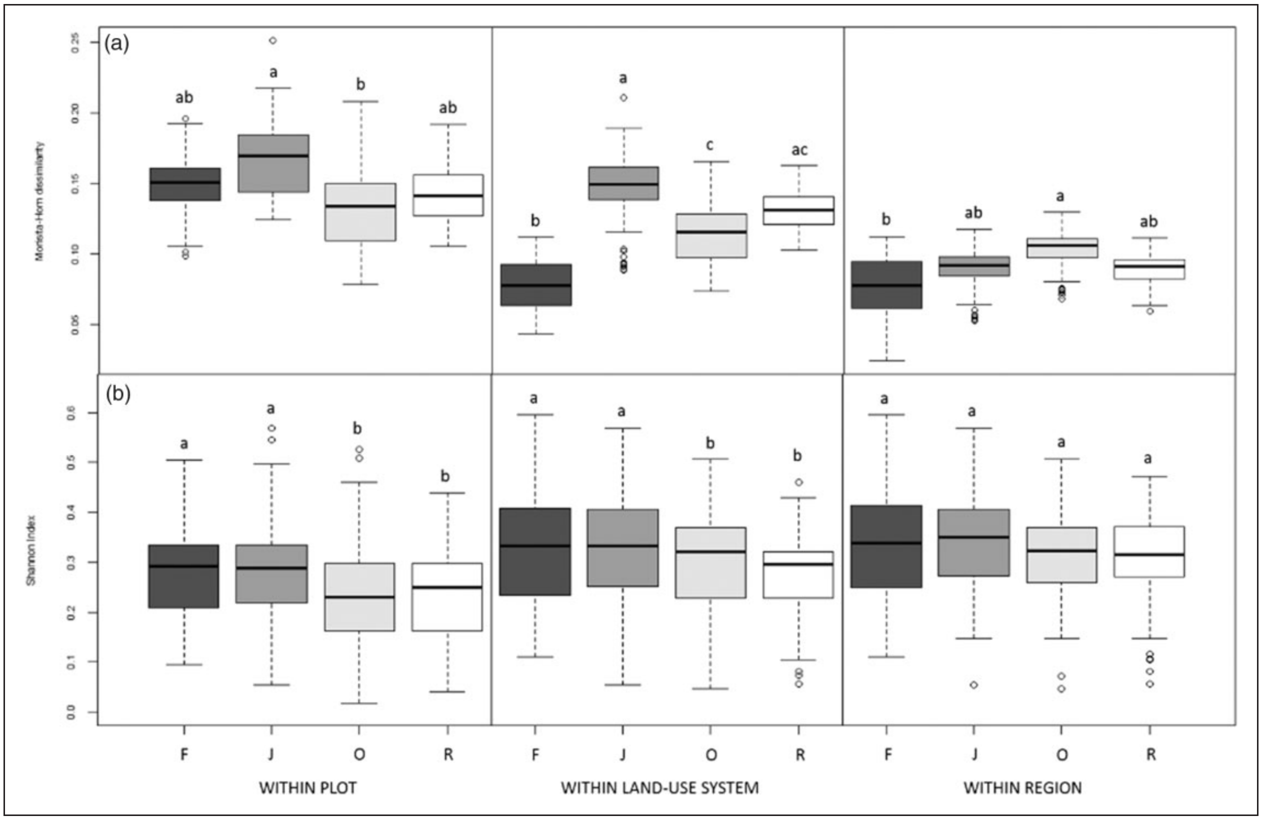

Figure 3. Mean genetic differentiation (a) and diversity (b) per land-use system F (forest), J (jungle rubber), O (oil palm plantation), and R (rubber plantation) for the three spatial levels α (within plot), β (within land-use system), and γ (within region). Significant differences indicated by letters ($p < .01$). Values for each species and fragment pool are shown in online Appendices 4 and 5.

four land-use systems (Figure 3). The results at the α-diversity and β- diversity levels revealed two groups with significant difference: forest and jungle rubber with high mean genetic diversity and oil palm and rubber plantations with low mean genetic diversity. Species of rubber plantations showed slightly higher mean diversities than oil palm plantation species. Genetic diversity differences among the four land-use systems at γ-diversity level were low and no significant differences could be detected. Mean value for jungle rubber is slightly higher than the forest mean values. As for genetic differentiation, the mean genetic diversity for the forest species did not change from β- to γ-levels. Variance within each land-use systems was high and increased with increasing spatial scale.

Discussion

The four investigated land-use systems reflect different agricultural intensities with specific dominant plant species composition. On the level of genetic diversity, observations concerning the consequences of land-use change were not as clear as previously observed species diversity studies conducted on the same research sites (Drescher et al., 2016; Rembold et al., 2017). Current results indicate that land-use change per se does not have an effect on genetic diversity of the analyzed dominant plant species, but has an impact on the particular species composition with their respective genetic characteristics.

Heterogeneity of the Analyzed Plots and Land-Use Systems

The uniqueness of the dominant species composition in each plot and land-use system was only partly confirmed. The two plantation systems were very similar concerning dominant species composition and showed low genetic differentiation between plots and regions. As expected, jungle rubber plots present an intermediate system between forest and rubber plantations, having trees as the dominant life form and sharing with the rubber plantation at least one species, *H. brasiliensis*. Dominant species of the plantations systems possibly occur in jungle rubber and forest but do not dominate the system in biomass. Differences and variability between plots of each plantation system and jungle rubber occurred mainly because of different management strategies (Drescher et al., 2016; Rembold et al., 2017). In general, the structure and species composition depend among others on the degree of disturbance in jungle rubber (Laumonier, 1997; Schroth, Harvey, & Vincent, 2004) and as well in forest (Burivalova, Şekercioğlu, & Koh, 2014). Compared with the forest with a closed canopy, the higher temperature in the more open jungle rubber and plantation systems alters the microclimatic conditions, which increases the effect of land-use change concerning biodiversity and ecosystem processes (Hardwick et al., 2015; Drescher et al., 2016). Further, landscape dynamics, ecosystem heterogeneity, and the niche size is influencing the community similarity regarding their phylogenetic and intraspecific variance (Gascuel, Ferrière, Aguilée, & Lambert, 2015; Parks & Beiko, 2012; Violle et al., 2012).

Genetic Diversity and Differentiation Levels Within and Among Land-Use Systems

Three spatial scales (within plot, within land-use system, within region) were investigated to assess the mean genetic differentiation and diversity of the dominant plant species with different potential population sizes and the dependency on the land-use systems. The tree-dominated systems were expected to have high local (α-level) genetic diversity and lower differentiation on a larger scale (γ-level), while the plantation systems dominated by vegetative growing species may show the opposite pattern. Analyses of genetic diversity and genetic differentiation show results that vary from the aforementioned hypothesis. For the fragment pool approach, the observed decreasing level of differentiation with increasing spatial size was not expected. The mean genetic diversity values for all land-use systems, calculated using the Shannon Index, increased only little from α- to γ-diversity levels.

The unexpected variation in results of mean genetic differentiation and diversity are because of the dependency on the dominant species composition with their abundance within and among land-use systems and on the nature of the two indices (White, 1986). The influence of the species composition is mainly because of the very different abundance of each species. Differences between α- and β-levels are based on the species which occurred in more than one plot within each land-use system and region. For the forest, 38% (13 species of 34) of the tree species were dominant in more than one plot, in jungle rubber 24% (8 species of 33), and in the two plantation systems it is 45% (19 species of 42). Eight of the 13 forest species showed a decreased genetic differentiation within the land-use system in comparison with the mean differentiation within plots, which results in a decrease in of pairwise distance among each fragment pool within the forest system. Three of these species (*Porterandia anisophylla*, *Gironniera nervosa*, and *Baccaurea sp.* III; online Appendix 4) showed decreased genetic diversity using the Shannon Index as well, but because of the high variance within each land-use system, the effect of these results was not visible. Differences between β- and γ-levels were based on an even more reduced number of species. The land-use systems of oil palm and rubber plantation share seven species. Forest and jungle rubber share three species, *Macaranga bancana* (Miq.) Müll.Arg., *Endospermum malayanum* (Pax & K.Hoffm) Chatterjee, and *Parkia speciosa* Hassk., with each other. *M. bancana* was also dominant in two rubber plantations in the Harapan region, *P. speciosa* in one rubber plantation in Harapan. *E. malayanum* only occurred in the Bukit Dua Belas region. Together, a maximum of two plots of different land-use systems per species were shared. Hence, for most tree species, the differentiation or diversity results did not change from the β-level to the γ-level (online Appendices 4 and 5). In contrast, the seven species shared by the plantations occurred in the most of the 16 plots. Hence, more populations were considered in the analyses and the changes in results were higher. Greater changes from α- to β-/γ-level, using both approaches, in the plantation systems compared with the tree-dominated systems can be explained by the higher similarity in the species composition and the differences in gene flow between nonwoody and woody species (Austerlitz, Mariette, Machon, Gouyon, & Godelle, 2000; J. Hamrick, Godt, & Sherman-Broyles, 1992).

The influence of each index is intensified by the unique number of AFLP loci, abundance, and particular genetic differentiation of each species. Using the fragment pool approach, the total number of loci of all species occurring in the respective plot/land-use system/region was included in every distance calculation. Hence, with increasing spatial scale, the number of loci is increased while the weight of the genetic differentiation among individuals of the species, dominant only in one plot, decreased. Shannon Index values were calculated for each species separately and only changed for the species occurring in more than one plot/land-use system/region, which increased the variance within each land-use system with increasing spatial scale. The main disadvantage when comparing mean values per species is the high variance within the land-use system and the disadvantage of the fragment pool is the high effect of extreme values, which increases the high effect of potential outliers and the decreasing influence of each locus with increasing scale. Because of the increased number of loci considered and increasing variance with increasing spatial scale, the three diversity levels are only comparable in each level but are less comparable among levels.

Further, results may be influenced by the sampling method, the chosen genetic marker and the calculation methods for the estimated diversity parameters. Dominant species are expected to have highest influence on the ecosystem and may represent them most (Avolio, Chang, & Smith, 2011; Grime, 2001). Using the "Bitterlich Method" to choose the dominant tree species in every plot assures the randomization and objectivity of the selection. Selecting species with only 10 individuals in or close to the 50×50 m plot means neglecting large trees with low densities. Outcrossing species which recently declined in their population size, for example, because of deforestation, are assumed to be most threatened by genetic consequences of forest fragmentation (Aguilar, Quesada, Ashworth, Herrerias-Diego, & Lobo, 2008). Albeit, a larger investigation area could not be defined because of the small jungle rubber patches and is still remaining in the area.

As expected, the mean genetic diversity depends on the species dominating the respective land-use system but not on the land-use system itself. The comparatively low values for forest and jungle rubber and their small differences to plantation systems may indicate that the analyzed species in forest and jungle rubber might have experienced limitations in gene flow and genetic drift, as a consequence of population fragmentation (Bacles & Jump, 2011; Vranckx et al., 2011; Young, Boyle, & Brown, 1996). Differences in mean genetic diversity and differentiation between single plots and the regions could be detected, although not significantly (data not shown). Jambi Province experienced high forest transformation rates since the 1970s, resulting in a land cover of more than 50% of crop producing land-use systems. Accessible forest plots for this study were classified as "primary, degraded" (Drescher et al., 2016). The fragment pool approach suggests for the forest land-use system differences between particular plots and regions. The forest plots in the region Harapan seem more homogeneous (Figure 1). Despite low genetic differentiation, these four forest plots might be of higher conservational value than the forest plots in Bukit Dua Belas, because the individuals of the four plots seem to be one, more continuous and larger, population. Laumonier et al. (2010) identified Harapan as a forest with high priority for conservation because of its size and comparable low disturbance. The forest in Bukit Dua Belas region seems more fragmented, individuals in BF1 and BF2 showed higher differentiation to all other individuals of shared species than all other plots (online Appendix 5). The increased differentiation might indicate that the two plots were experiencing limitations in gene flow (Hahn, Kettle, Ghazoul, Hennig, & Pluess, 2013; Wang & Bradburd, 2014). In the plantations, dominant species from the three life forms herb, grass, and fern are mainly alien or colonizing species and hence are adapted to disturbance (DeWalt & Hamrick, 2004; Ootsuki, Sato, Nakato, & Murakami, 2012; Rembold et al., 2017) and do not show any signs of genetic diversity loss. All invasive species have already been introduced in Indonesia decades before this study and because of their rapid growth and possible multiple introductions, which makes the possible genetic consequences of a bottleneck undetectable. But a comparison with native populations would be necessary (DeWalt & Hamrick, 2004; Dlugosch & Parker, 2008). Further, the differentiation may be as high as the tree dominated systems because of the size of the population/plots. For herbaceous species, one plot can be considered as one population, that is, at β-level, the differentiation among plots are higher than for tree species which can have a larger geographic population size, that is, several plots in one region. Despite the similar genetic diversity levels in tree dominated and plantation systems, the dominance of herbaceous species, accompanying the crop species, and the high abundance of nonnative colonizing species in the latter, exclude the plantations from preserving forest genetic diversity and its resources. Therefore, the plantation systems are not considered as habitats of conservational value.

Molecular Marker and Statistical Analyses

AFLP markers were preferred to other molecular markers for the following reasons: In this study, a high number of species was expected and prior knowledge about the species' DNA sequence is for the anonymous AFLP method not necessary. Fragments of the same size can originate from different regions of the DNA, which is a major advantage of the method, especially for polyploid species (Després, Gielly, Redoutet, & Taberlet, 2003; Goldman et al., 2004) and tropical species for which taxonomic identification are often ambiguous (Kremer et al., 2005; Mace, Gebhardt, & Lester, 1999).

The dominant nature of the AFLP marker limited the availability of analytical methods that could be used in this study. Three further aspects needed to be considered for the analysis, which led to the use of AFLPs as a molecular marker and the Morisita–Horn and the Shannon Indices as the diversity measures. First, AFLP fragments of different species could not be compared as the origins of fragments of the same size are unknown. Second, the different weight per species within the analysis because of the varying number of collected individuals (Mba & Tohme, 2005; Meudt & Clarke, 2007). Third, every species has its unique number of fragments, which varied highly among the sampled species (Linton, Davies, & Wrona, 1981; Wolda, 1981). Recent studies about plant genetic structure have not used the Morisita–Horn dissimilarity to analyze genetic diversity. Hence, for a better comparison with previous studies, the Shannon Index (Shannon & Weaver, 1949) was also used as a common genetic diversity measure.

In this project, several species with a high variation in fragment number were compared, which can lead to a bias using the Shannon Information Index. Further, the Morisita–Horn index is widely used as a β-diversity index and the Shannon Index as an α-diversity index in ecology. Both were compared at the three different scales during this study. In ecology, "differentiation" and "diversity" are used as synonyms when calculating β-diversity (Koleff, Gaston, & Lennon, 2003).

Implications for Conservation

Despite differences in mean genetic differentiation that were detected using the fragment pool approach, a generalization about each land-use system is not possible. This may be because of very different genetic diversity results within each plot and land-use system in this project, which confirm the high dependency of genetic diversity and structure on very different life forms, reproduction systems, dispersal strategies, dispersal ranges and population densities, among species (Ewers & Didham, 2006; J. Hamrick et al., 1992; J. L. Hamrick, Linhart, & Mitton, 1979; Sebbenn et al., 2008). For conservation purposes, it would be best to investigate each species in detail, to be able to consider their characteristics. That being impossible, the combination of sampling dominant species and the analysis with the fragment pool approach presents a method which is suitable to calculate genetic differentiation of a plant community of different compositions with a very simple and universally applicable method. Even with a low number of individuals the fragment pool approach is suitable to detect differences among plots and land-use systems regarding their genetic constitution.

Results of this study suggest that aside from forest, the investigated agroforest system jungle rubber also can be an HCV. Jungle rubber cannot replace forests (Rembold et al., 2017) but can present buffer zones and increase connectivity between HCV habitats and facilitate gene flow (Orrock, 2005). The theoretical design of Koh, Levang, and Ghazoul (2009) studies options for a compromise between conservational and economic interests in a tropical landscape. The planned mosaic landscape contains forest fragments, continuous forest, monocultures, and agroforestry parts. In the overall landscape, biodiversity, ecosystem functions, and human welfare are assured. Rules and indicators for HCV habitats would give the possibility to design landscapes with effective palm oil (or other crops) productivity, buffer zones, and areas of natural forest. Jungle rubber with high conservational value could be included in such a designed landscape, but also agroforests ecosystems are vulnerable. Agroforest systems depend on the economic advantages for the owner, and, hence, older agroforests with higher conservational value but decreased crop productions have an increased probability to be converted to monocultures or rejuvenated (Rembold et al., 2017; Schroth et al., 2004). Furthermore, the presence of agroforestry in a region does not necessarily protect natural stands from exploitation (Dawson et al., 2013). Schemes like Payment for Ecosystem Services, which are considered to increase the protection of forests (Lee et al., 2011), could also be a possibility to protect agroforest systems of high conservational value.

However, it is necessary to have a universal applicable method to identify HCV habitats, especially in the highly heterogeneous and fast changing tropical ecosystems. Considerations of genetic diversity of plants in conservation management plans increases the capability to conserve global biodiversity of similar natural ecosystems, not only in Indonesia, particularly with regard to future challenges caused by forest loss and climate change.

Acknowledgments

The authors thank the landowners of the plots and the staff of Taman Nasional Bukit Dua belas and Harapan Rainforest. The authors thank the herbarium staff of Harapan Rainforest and Katja Rembold for their support in the plant identification. The authors thank Alexandra Dolynska and Christine Radler for their help during lab work. The authors express their appreciation to Tamar Weinberg and Ludger Leinemann for their suggestions on the manuscript. The authors thank the Ministry of Research, Technology, and Higher Education for research permission in Indonesia. This study was conducted using samples based on the Collection Permit No. 2697/IPH.1/KS.02/XI/2012 and 493/IPH.1/KS.02.04/II/2015 recommended by the Indonesian Institute of Science and issued by the Ministry of Forestry.

Declaration of Conflicting Interest

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: The study was funded by the Deutsche Forschungsgemeinschaft (DFG), as part of EFForTS, CRC (Collaborative Research Centre) 990 (https://www.uni-goettingen.de/de/310995). We acknowledge the support by the Open Access Publication Funds of the Georg-August Universität of Göttingen.

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Supplemental Material

Supplemental material for this article is available online.

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