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Effects of rainforest transformation to monoculture cash crops on soil living ants (Formicidae) in Jambi Province, Sumatra, Indonesia

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Abstract. Ants (Formicidae) are fundamental components of almost every terrestrial ecosystem, especially in the tropics. While epigeic ants are extensively studied, hypogaeic, soil living ants are still neglected to a large extent. To remedy this, in this paper we explore the effects of rainforest transformation cash crop monocultures on abundance, richness and community composition of soil living ants (Formicidae). Ants in this study were procured as a by-product of extensive sampling of soil meso- and macrofauna along a land-use gradient from lowland rainforest via jungle rubber to monocultures of rubber and oil palm in Jambi Province, Sumatra, Indonesia. Sampled in 32 plots of 50 * 50 m each, with three 16 cm * 16 cm * 5 cm soil cores each, we collected 2.079 worker ant individuals, belonging to 90 morphospecies from 37 genera and six subfamilies. Land use had a significant effect on abundance and richness, while distance-based community composition was not affected. Cumulatively, lowland rainforest had the highest number of ant species exclusively living in it, and the highest average ant abundance, although multiple comparison tests did not detect significant differences. We also found highest species richness in the lowland rainforest in one of the two investigated landscapes, while not significantly different from the agricultural systems in the other. High abundance variances among the sample sites suggest inadequacy of the sampling method, however. Despite that, our study provides a first glimpse into hypogaeic ant community responses to rainforest conversion to cash crop monocultures in Sumatra, Indonesia.

1. Introduction

The conversion of natural ecosystems into production or agricultural land is a major cause of ecosystem function losses [1]. Even so, the mechanism governing the relationship between biodiversity and ecosystem function is still little known, especially in tropical rainforest ecosystems that often experience land conversion and intensive land use [2]. Tropical rain forests in Southeast Asia have experienced large-scale logging since the mid-20th century, followed by land transformation into monoculture plantations, such as acacia, rubber, and palm oil. In Indonesia, this process has accelerated over the past few decades, where the annual loss of tropical rain forests increased to around 0.84 million hectares in 2012, the then largest figure



in the world [3]. Among the many islands in Indonesia, Sumatra is among the most affected by rainforest conversion to agriculture [3–5]. Thus, an effort is needed to understand the relationship patterns of biodiversity and ecosystem functions in the transformation mechanism of tropical rain forests through ecological evaluation [6]. The mechanism of the relationship between biodiversity and ecosystem function can be assessed through patterns of changes in the composition of the fauna contained in the ecosystem landscape [7]. Ants (Hymenoptera: Formicidae), are one of the most dominant groups of insects in the tropics [8]. Ants occupy various trophic levels [9], acting as predators, herbivores, carnivores or decomposers [10–14]. Ants thus have a unique role in their interactions with other organisms such as the ability to modify soil by enriching organic substances, nutrient cycles, and soil biophysical structures that can provide living space for other soil organisms [15,16]. Ants can act as a counterweight to ecosystems: As the level of ant diversity becomes higher, the food chain and ecological processes with other biotic components are more balanced [17]. Several studies have also shown that ants are very sensitive to microclimate changes. Several factors can affect changes in microclimate, such as changes in the structure of vegetation, changes in food availability, and changes in natural resources. All of these factors can influence the presence of ant nests [18].

In this study, we use soil living ants as biotic indicators for environmental degradation along a transformation gradient from secondary lowland rainforest via jungle rubber to rubber and oil palm monoculture plantations. All of the above agricultural systems have dramatically expanded in Sumatra in general, and in Jambi Province in particular, over the last decades [19–21]. We compare soil ant abundance, richness, beta diversity, and community composition among these four land-use systems. Based on the results of previous studies on a range of taxa in the same research plots [22–26], we expected (1) higher abundance and (2) higher species richness of soil ants in lowland rainforest than in monoculture plantations, with jungle rubber in an intermediate position. We also expected (3) the soil ant community of lowland rainforest and jungle rubber to be similar, but significantly different from rubber and oil palm monocultures.

2. Materials and methods

2.1. Study sites

Soil ants were collected in dry season 2013 in the lowlands of Jambi Province, Sumatra, Indonesia, as part of a general sampling campaign of soil fauna by Klärner et al. within the EFForTS project [23,27,28]. Four land use types were investigated: (1) Lowland rainforest, (2) jungle rubber and monoculture plantations of (3) rubber and (4) oil palm. For each land-use type, eight 50m * 50m research plots were established, with four replicates located in the “Bukit Duabelas” landscape and the other four in the “Harapan” landscape, resulting in 32 research plots in total. The landscapes were named after two reference forest reserves, i.e. the Bukit Duabelas National Park and the Harapan Rainforest. All plots were placed on Acrisol soils. However, soils in the Harapan landscape were characterized by rather even fractions of sand, silt, and clay (loam Acrisol), while soils in the Bukit Duabelas landscape contained a higher proportion of clay (Clay Acrisols) [29,30]. Rainforest sites used in the two reserves were secondary forests in a near-natural condition which were subjected to selective logging ca. 30 years ago. Jungle rubber agroforestry is an extensive form of rubber production, in which rubber trees are planted in rainforest patches from which timber is regularly extracted; jungle rubber thus represents a low-intensity agricultural system, in which usually no fertilizer or herbicide is used, and which still contains remnants of the original rainforests vegetation [31]. Monocultures of rubber and oil palm on the other hand represent high-intensity agriculture with frequent fertilizer and herbicide application and were on average 12.5 and 13.5 years old, respectively. All research plots were located in the lowlands between 41m – 91m a.s.l. For further details including regional maps and plot, setup details see Drescher et al. [23].

2.2. Sample collection

Soil samples were taken between October and November 2013 from three subplots in each of the 32 research plots, resulting in a total of 96 samples. Samples were taken by Klarner et al [27] at random from the subplot at least 2 m distant to the next tree or accumulation of deadwood using a spade. Each sample measured 16 x 16 cm and included the full litter layer and underlying topsoil to a depth of 5 cm. Soil arthropods were extracted by heat using the method established by Kempson et al. [32]. Ants were separated from the other soil arthropods and stored in 70% ethanol for further processing. From October 2019 until April 2020, worker ants were identified to genera using the keys by Shattuck [33], Bolton [34], and Fayle [35]. Wherever possible, worker ants were then further determined to species using keys available on AntWiki [36] and compared to images on AntWeb [37]. If no Linnéan species could be assigned, morphospecies series was established by comparing various morphological features within the collection as well as collections of litter ants and canopy ants from the same plots, documented in “A guide to the ants of Jambi (Sumatra, Indonesia)” [38] and on Ecotaxonomy.org. [39]. Both Linnéan species and morphospecies will henceforth be referred to as “species”.

2.3. Statistical analysis

Statistical analysis was performed using R v 3.6.3 [41] and visualized using ggplot2 [42]. Exploratory data analysis was performed to ensure the data met the underlying assumptions of the statistical tests [43]. Accordingly, response variables total abundance N/m², species richness, and inverse Simpson Index (calculated using `vegan::diversity`) [44] were analyzed separately using `lm` (richness only) or `glm` family Gaussian with the log link function. Initial models all included land use (4 levels: forest, jungle rubber, rubber, oil palm), landscape (2 levels: Bukit Duabelas and Harapan), and their interaction as fixed factors. Step-wise simplification based on AIC was used to arrive at the minimal adequate model for each response variable. Model fit was checked, then multiple comparisons using pairwise t-tests with Holm corrections (`multcomp::glht`) [45] were made as appropriate for each final model. Rank abundances were compared (`vegan::radrit`) and visualized (`RankAbund`) [46].

Beta diversity was partitioned into turnover, nestedness, and overall beta diversity using Sørensen pairwise dissimilarities (`betapart::beta.pair`) [47]. For each partition, multivariate dispersions were tested by the factors land use and landscape, then differences in community composition compared using permutational manova (`vegan::adonis`) and pairwise multilevel comparisons (`pairwiseAdonis::pairwise.adonis`) [48]. Non-metric multidimensional scaling (NMDS, `vegan::metaMDS`) was applied to each partition separately. Multivariate anova (`manova`, Wilk's lambda) was used to test the extent to which land use and landscape predicted the variability in nmDS scores, followed by FDR-adjusted pair-wise contrasts (FDR = False Discovery Rate) [49].

3. Results and Discussion

Overall, 2,079 worker ants were collected, which were sorted into 90 species from 37 genera and six subfamilies. The most abundant genus was *Pheidole* WESTWOOD 1839 but was only represented by the highly numerous *Pheidole parvicorpus* EGUCHI 2001 (N = 525) and a rare, unidentified *Pheidole* sp. (N = 4). The four subsequently abundant genera were *Tetramorium* MAYR 1855 (N = 359), *Carebara* WESTWOOD 1840 (N = 314), *Lophomyrmex* EMERY 1892 (N = 246), and *Hypoponera* SANTSCHE 1938 (N = 103). These five genera combined comprised almost 75% of all worked ants in our collection and almost 40% of all species (N = 35 spp.). Among the five most abundant genera were also the four most species rich, i.e. *Hypoponera* with 11 species, *Tetramorium* with 9 species, *Carebara* with 7 species, and *Lophomyrmex* with 6 species. The only other low abundance genus with many species was *Ponera*, with 7 species but only 55 individuals. All other genera had less than 5 species.

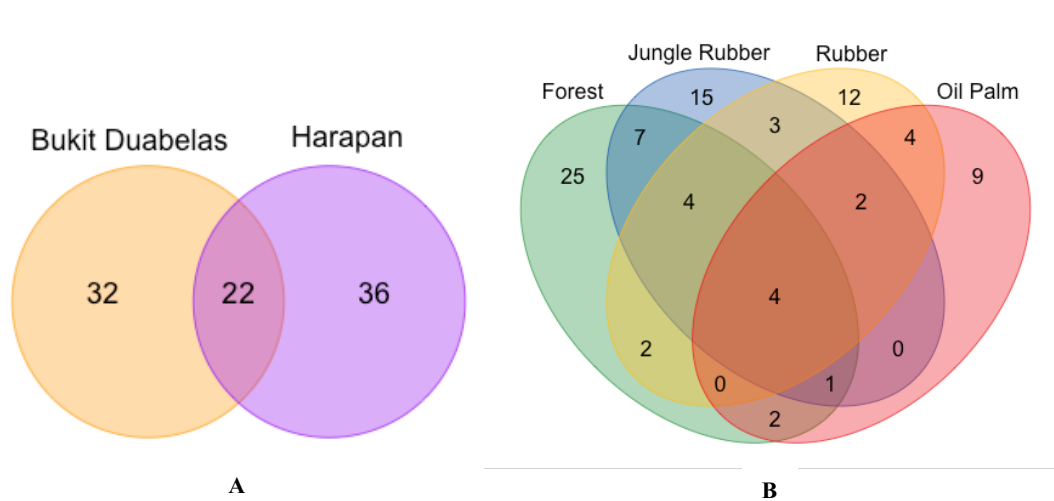


Figure 1. Venn diagram of cumulative soil ant species overlap between the two landscapes Bukit Duabelas and Harapan (A), and overlap among four land-use systems (B) in Jambi, Sumatra, Indonesia.

We observed marked differentiation of species between the two landscapes: 32 species were exclusively found in the Bukit Duabelas landscape, and 36 species in the Harapan landscape. Only 22 species were found in both landscapes (Fig. 1A). Cumulatively, more than half of all species were found exclusively in the low-intensity land-use systems forest and jungle rubber (47 spp.), and more than a fourth of all species exclusively in the forest (Fig. 1B). Conversely, rubber and oil palm together had less exclusive species than forest, and only four species occurred in all four land-use systems.

Ranked abundances indicated that higher numbers and more species were found in the forest than in the other three land-use systems, with the underlying model of forest being significantly different from those of jungle rubber, rubber, and oil palm (Tukey's HSD, all $t < -7.19$, all $p < 0.001$, Fig. 2). Total soil ants abundance per plot (three subplots combined) ranged from 1 to 460, showing the high variance of abundance in our data set. Extrapolated from our sampling to soil ant abundance per m^2 , 2216.7 ± 1819.8 ants were found per m^2 in the forest, 400.4 ± 307.6 in jungle rubber, 449.2 ± 532.3 in rubber, and 317.4 ± 537.1 in oil palm (means \pm S.D., Fig. 3). Land use had a significant effect on soil ant abundance per m^2 (glm, $F_{3,28} = 6.74$, $p = 0.0015$), but no significant differences in soil ant abundance per m^2 between the land-use systems were found in pairwise t-tests with Holm's correction.

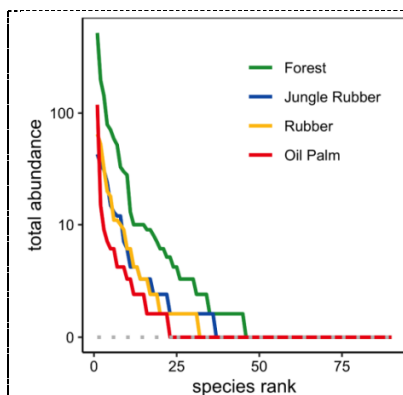


Figure 2. Ranked abundances of soil ant communities in four land-use systems in Jambi, Sumatra, Indonesia.

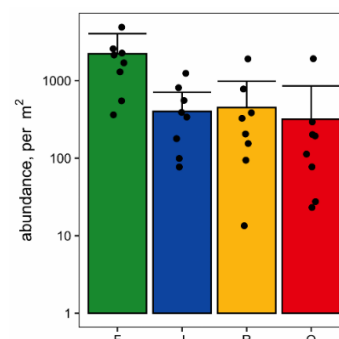


Figure 3. Log abundance of soil ant communities in four land-use systems (F = Forest, J = Jungle Rubber, R = Rubber, O = Oil Palm).

High variance in soil ant abundances likely had a large effect on species accumulation curves, average abundances and estimated species numbers, and possibly on other downstream analyses. The species accumulation curve SAC over the entire soil ant collection was well below saturation, suggesting that our data is suffering from considerable undersampling (Fig. 4A). Splitting SAC between the land-use systems revealed that slopes were nearer to saturation in oil palm than in forest (Fig. 4B), suggesting there may be many more soil ant species to be found in the forest than in oil palm (jungle rubber and rubber intermediate). This is partially supported by species pool extrapolations using Chao, first and second order jackknife and bootstrap estimations, which on average suggest 89.5 ± 23.2 species in the forest (45 observed), 114.5 ± 65.9 in jungle rubber (36 observed), 68.7 ± 24.6 in rubber plantations (31 observed) and 44.2 ± 14.3 in oil palm (22 observed). However, all estimates likely suffered from high abundance variance, thus species number extrapolations have to be treated with caution.

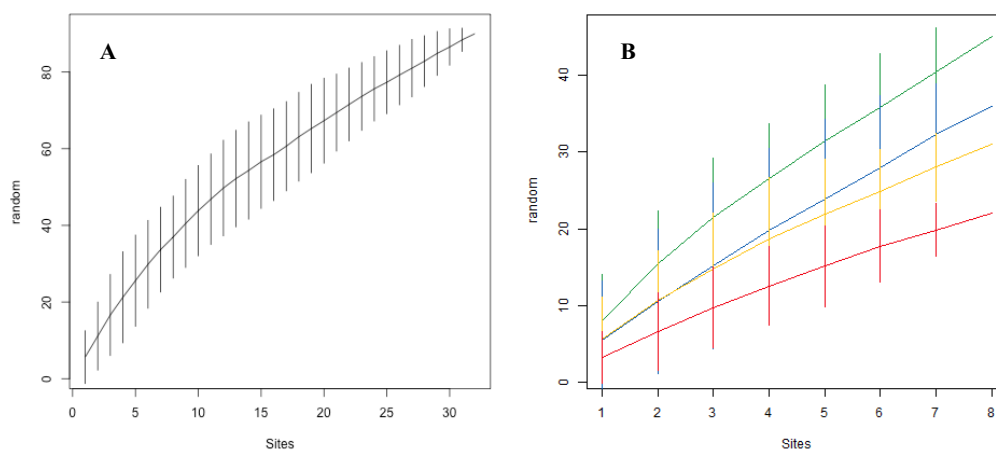


Figure 4. Species accumulation curves of (A) the entire sampled soil ant community, and (B) for the sampled soil ant community each of the four land uses separately (from top to bottom: forest/green, jungle rubber/blue, rubber/yellow, oil palm/red).

Average species richness, which is independent of abundance, was highest in the forest ($S = 8.5 \pm 3.2$), intermediate in jungle rubber ($S = 5.5 \pm 2.5$) and rubber plantations ($S = 5.8 \pm 3.0$), and lowest in oil palm plantations (3.8 ± 2.1) (Fig. 5). We detected a significant effect of land use on species richness (lm , $F_{3,24} = 3.8$, $p = 0.024$), no effect of landscape, and a significant interaction between the factors (lm , $F_{3,24} = 3.1$, $p = 0.044$). Pairwise comparisons (t tests, Holm's correction) detected significant differences between forest and the three other land-use systems in the Bukit Duabelas landscape, but not the Harapan landscape.

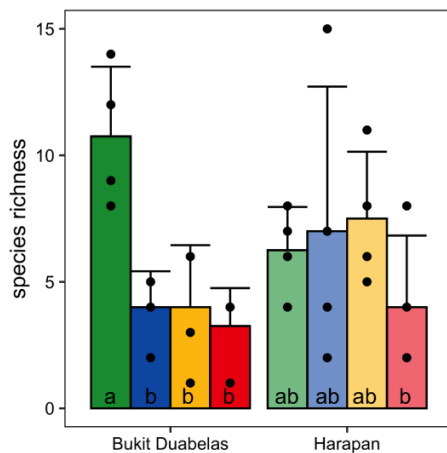


Figure 5. Species richness of soil ants in four land-use systems in Jambi, Sumatra, Indonesia, separated by landscape (in each cohort, from left to right: green = forest, blue = jungle rubber, yellow = rubber, red = oil palm). Different letters indicate significant differences after pairwise t-tests after Holm's correction.

Community composition or overall beta diversity, visualized by NMDS and analyzed by pairwise ADONIS between the land-use systems, revealed no influence of land use or landscape (Fig. 6). Average Sørensen dissimilarities for beta diversity partitions turnover and nestedness were not different among the land-use systems or landscapes in terms of turnover (Fig. 7A), but were significantly influenced by landscape in nestedness, and the interaction between land use and the landscape was also significant (Fig. 7B).

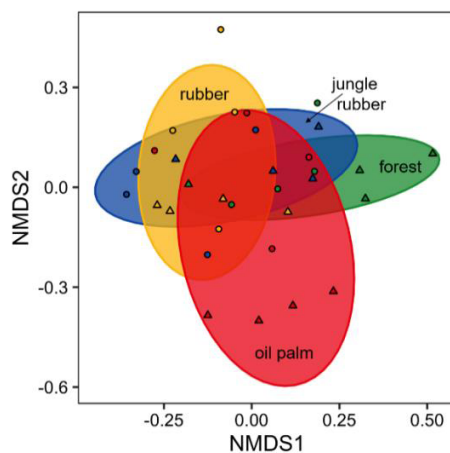


Figure 6. NMDS of soil ants community composition in four land-use systems, combined over two landscapes, based on Sørensen dissimilarities (green = lowland rainforest, blue = jungle rubber, yellow = rubber, red = oil palm). Relative positions of individual plots are shown by triangles (Bukit Duabelas landscape) and circles (Harapan landscape), colored by land-use affiliation.

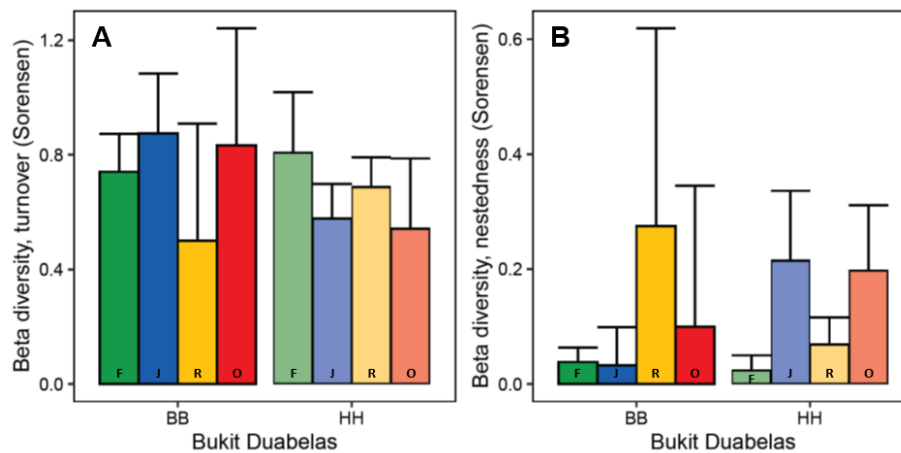


Figure 7. Average Sorensen dissimilarities for the beta diversity partitions turnover (A) and nestedness (B) in relation to four land-use systems (F = forest, J = jungle rubber, R = rubber, O = oil palm), separated by landscape (BB = Bukit Duabelas, HH = Harapan).

Despite a clear trend towards higher soil ant abundance in lowland rainforest than in the monoculture plantations of rubber and oil palm, we found no significant differences in per square meter abundance among the land-use systems, thus rejecting hypothesis (1). Our expectation was based on aboveground surveys of ants and other arthropods in this research setting in Jambi Province, especially from the canopy [22,24]. As has been shown, however, abundance and richness patterns of aboveground ants may differ substantially from those belowground [50,51]. The observed patterns of soil ants per square meter may thus be a realistic representation of actual soil ant abundance patterns across the investigated land-use systems. On the other hand, we observed considerable variance in collected ant individuals among plots, ranging from a single ant to 460 in a plot, thus very likely significantly impacting statistical downstream statistical analyses.

Ranked abundances and species accumulation curves suggested that, cumulatively, lowland rainforest sites had highest ant abundances and species richness, thus suggesting that hypothesis (2) may be verified. We indeed found significantly higher species richness of soil living ants in lowland rainforest sites of Bukit Duabelas National Park compared to all agricultural systems in the Bukit Duabelas landscape. However, somewhat contrasting patterns were found in the Harapan landscape where soil ant species richness in all four land use systems (including forest) were intermediate between Bukit Duabelas forest on the one hand, and the Bukit Duabelas agricultural systems on the other. Again, this observation may possibly be representative of the actual distribution of the soil living ant community, while at the same time possibly being an artefact of an improper sampling method. Similar reservations have to be applied when interpreting the community composition metrics in the ordinations of Fig 6-7, leaving the verification/falsification of hypothesis (3) impossible to answer.

Most available literature on how to sample ground living ants, including soil living ants, does not recommend soil cores, but a range of other methods[50–53]. We thus have to assume that our methods, which are not in line with the methods most commonly used to sample soil ants, have a systemic bias which leads to unreliable patterns in many diversity metrics, including abundance and richness. It is here important to note, however, that the sampling was not done to deliberately sample ants, but was part of a larger sampling campaign of soil living animals, which has repeatedly yielded important and reliable results [27,28]. Hence, the present study and its results have to be interpreted with appropriate caution.

4. Conclusion

With the present study, we were able to demonstrate that lowland rainforest soils, and soils of derivate agricultural land-use systems in Indonesia cumulatively are home to an immense number of morphological ant species (morphospecies). We also found trends of declining abundance and species richness among the land-use systems, indicating that an ecologically relevant shift of ant communities is indeed occurring, similar to published observations of ant communities in the aboveground realm of the same research area. The lack of statistically significant differences in some metrics is quite likely due to the employed sampling method (soil cores), which seems inadequate for ants specifically. However, if sampled as a mere byproduct of an otherwise highly relevant and reliable campaign targeting soil meso and microfauna, analyzing ants from soil cores can offer an interesting and relevant aspect to our understanding of the ecological consequences of lowland rainforest transformation to agricultural monocultures in the Asian tropics.

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