



Rainforest conversion to smallholder plantations of rubber or oil palm leads to species loss and community shifts in canopy ants (Hymenoptera: Formicidae)

Rizky NAZARRETA*, Tamara R. HARTKE*, Purnama HIDAYAT, Stefan SCHEU, Damayanti BUCHORI & Jochen DRESCHER

Abstract

Currently, our understanding of the responses of ant communities under rainforest conversion to cash crops in SE Asia is based on comparisons of primary rainforests to large company-owned oil palm estates in Malaysian Borneo and a few comparisons of natural forests to rubber plantations in Thailand and China. In Indonesia, second largest rubber producer and largest oil palm producer worldwide, the vast majority of its rubber economy and almost half its oil palm acreage relies on smallholder farmers. This study compares canopy ant communities among four land-use systems in Jambi Province, Sumatra, Indonesia: 1) lowland rainforest, 2) jungle rubber (i.e., extensive rubber cultivation), and monoculture plantations of 3) rubber or 4) oil palm. Smallholder plantations of rubber and oil palm support less than 25% of the abundance and less than 50% of the canopy ant species richness in lowland rainforest, with intermediate levels in jungle rubber. Canopy ant communities from rainforest and jungle rubber were similar and differed from those in monoculture rubber and oil palm plantations, which each hosted distinct communities. Nestedness and turnover also differed between rainforest and jungle rubber on the one hand and rubber and oil palm on the other. This pattern was in part due to significantly greater proportions of tramp ants in the monoculture plantations: While virtually absent in forest (< 1%), six tramp ant species accounted for 9.8% of the collected ant individuals in jungle rubber, 26.6% in rubber and 41.1% in oil palm plantations (up to 88.1% in one studied plantation). Overall, this study improves our understanding of the effects of rainforest conversion to cash crop plantations of rubber and oil palm on ant communities by incorporating smallholder systems in one of the most important regions for oil palm and rubber production worldwide.

Key words: Deforestation, agriculture, biodiversity, canopy fogging, tramp ants, Southeast Asia.

Received 13 February 2020; revision received 11 May 2020; accepted 29 June 2020

Subject Editor: Nicholas J. Gotelli

Rizky Nazarreta, Purnama Hidayat, Damayanti Buchori, Department of Plant Protection, Faculty of Agriculture, IPB University, Jl. Kamper, Kampus IPB Dramaga, Bogor, 16680 Indonesia.

*Tamara Hartke, Stefan Scheu, Jochen Drescher (contact author), Department of Animal Ecology, JFB-Institute of Zoology and Anthropology, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany.
E-mail: jochen.drescher@biologie.uni-goettingen.de*

**These authors contributed equally to this work.*

Introduction

Habitat loss is among the most important drivers of biodiversity decline worldwide. Biodiversity is particularly high in tropical lowland rainforests, which mainly occur in the Amazon region, the Congo basin, and the Indo-Malayan Archipelago. Indonesia comprises much of Southeast Asia's rainforest and hence has often been referred to as biologically "mega-diverse" (PERSON & VAN WEERD 2006). While Indonesian rainforests have been exposed to moderate human activity for centuries, the impact of humans has increased strongly over the last decades. From 1990 to 2005, over 40% of the lowland rainforests

of Sumatra and Kalimantan were cleared (HANSEN & al. 2009), leaving less than 30% of the original area covered by rainforest in Sumatra (MARGONO & al. 2012). Moreover, Indonesia had the highest deforestation rate worldwide in 2012 (MARGONO & al. 2014), with loss of primary forest twice that of the Congo basin and triple that of the Amazon by the end of 2014 (TURUBANOVA & al. 2018).

Primary tropical rainforests harbor much of the world's biodiversity, and their decline leads to dramatic, irreversible species loss (GIBSON & al. 2011). This also applies to ants (Hymenoptera: Formicidae), which are among the

most conspicuous taxa in tropical rainforest canopies, both in abundance and biomass (HÖLLDOBLER & WILSON 1990). Estimates from Borneo suggest that ca. 50% of all tropical ant species may be at least partially associated with the canopy (FLOREN & al. 2014). Consequently, ants can account for up to 94% of all arthropod specimens in canopy fogging samples and up to 96% of the biomass of these samples (TOBIN 1995, DAVIDSON & PATRELL-KIM 1996, DAVIDSON & al. 2003). Ants are thus arguably “the dominant arthropod family in the canopies of tropical lowland rainforests” (DAVIDSON 1997). Being predators, prey, detritivores, plant mutualists, cryptic herbivores, coprovores, fungivores, and possibly more, ants have far-reaching impacts on the structure of arboreal arthropod communities and the ecological functions they provide (DAVIDSON 1997, FLOREN & LINSÉNMAIR 2001, FLOREN & al. 2002, DAVIDSON & al. 2003, PHILPOTT & ARMBRECHT 2006). Notably, the abundance and diversity of ants may change abruptly with habitat disturbance or loss (ATKINS 1980, PHILPOTT & ARMBRECHT 2006, BOS & al. 2008, RIZALI & al. 2013), thus serving as biotic indicators of habitat changes (KING & al. 1998, ANDERSEN 2000, ANDERSEN & MAJER 2004).

Global demand for cash-crop plantation products has risen dramatically in the past decades. Two of the most important cash crops worldwide are rubber and oil palm. Since 1960, plantation area has tripled for rubber (3.9 Mio ha to 11.8 Mio ha) and quintupled for oil palm (3.6 Mio ha to ca. 18.9 Mio ha) (Food and Agriculture Organization 2020). It has repeatedly been shown that the ant community in SE Asian rainforests is much more diverse than in oil palm plantations, across microhabitats (e.g., PFEIFFER & al. 2008, BRÜHL & ELTZ 2010, FAYLE & al. 2010, FOSTER & al. 2011, LUCEY & al. 2014, LUKE & al. 2014). The same pattern has been reported for rubber plantations (BICKEL & WATANASIT 2005, THONGPAK 2014, ALCANTARA & al. 2019 and references therein). Previous studies are geographically restricted, however: In SE Asia, the vast majority of studies comparing ant diversity in forests and oil palm have been conducted in Malaysian Borneo (specifically Sabah, some in Sarawak) while comparisons between forests and rubber are largely from China and Thailand (see references above). We found only a single study on ant diversity in SE Asian forest versus cash crop systems which includes both oil palm and rubber (ROOM 1975, Papua New Guinea). Curiously, similar research from Indonesia, the leading producer of oil palm and the second largest producer of natural rubber (Food and Agriculture Organization 2020), and by far the largest SE Asian country in both size and population, is still largely lacking.

In the present study, we address these research gaps by comparing canopy ant abundance, diversity and community composition from rainforest and monoculture plantations of both rubber and oil palm in Jambi Province, Sumatra, Indonesia. We include a fourth land-use system, “jungle rubber”, which is an extensively managed rubber agroforestry system with remnant rainforest tree species (REMBOLD & al. 2017). The production of rub-

ber in Indonesia is dominated by individual farmers or households; smallholders also account for ca. 40% of the oil palm plantation area (EULER & al. 2017, ABAZUE & al. 2019). Consequently, the present study utilizes smallholder cash-crop plantations of ca. 2 - 5 ha, which contribute to a more heterogeneous landscape mosaic and are subjected to more heterogeneous management than large, company owned estates. Based on the results of previous studies on a range of taxa in the same research plots (SCHNEIDER & al. 2015, DRESCHER & al. 2016, BARNES & al. 2017), we expected (1) higher abundance and (2) higher species richness of canopy ants in lowland rainforest than in smallholder plantations, with jungle rubber in an intermediate position. We also expected (3) the canopy ant community of lowland rainforest and jungle rubber to be similar, but significantly different from rubber and oil palm plantations. Based on the observation that disturbance promotes the establishment of invasive alien species (EARLY & al. 2016), and that the expansion of agriculture is one of the most important disturbance factors globally (CHYTRÝ & al. 2009), we (4) expected higher numbers of invasive ant species in the smallholder plantations of rubber and oil palm than in forest and jungle rubber. As the status (native vs. invasive) of some generally considered invasive ant species in Southeast Asia is not clear (e.g., DRESCHER & al. 2011), we use the term “tramp ants”, which we define as confirmed Linnéan species which have been reported to form invasive populations in other parts of the world.

Materials and methods

Study region: Canopy ants were collected in the dry season of 2013 within and adjacent to two forest reserves in the lowlands of Jambi Province, Sumatra, Indonesia: Bukit Duabelas National Park and Harapan Rainforest / (see Fig. S1, as digital supplementary material to this article, at the journal’s web pages). The natural vegetation of the study area is lowland dipterocarp rainforest (LAUMONIER 1997). The vast majority of lowland rainforest in Jambi Province has vanished, however, and remaining primary and secondary forests are mostly found in mountainous regions (DRESCHER & al. 2016, MELATI 2017). Remaining pockets of lowland forests, such as Bukit Duabelas National Park and Harapan Rainforest, generally contain degraded primary forest. According to MARGONO & al. (2014), this term refers to “primary forest that has been fragmented or subjected to forest utilization, for example by selective logging or other human disturbances resulting in partial canopy loss and altered forest composition and structure”. While both reserves contain forests in many stages, the study plots did not show any direct sign of disturbance (REMBOLD & al. 2017).

The land adjacent to the reserves has largely been taken into cultivation, mainly by smallholder plantations of rubber and oil palm. Henceforth, each forest reserve and the area surrounding it are referred to as the Bukit Duabelas landscape and the Harapan landscape. The landscapes have contrasting soil textures, with clay-dominated

Acrisols in the Bukit Duabelas landscape, and loamy Acrisols in the Harapan landscape (ALLEN & al. 2015, GUILLAUME & al. 2018). As different basal fertility between the two soil types (ALLEN & al. 2015) may indirectly influence canopy arthropods living on plants growing on these differing soils, “landscape” was considered a fixed factor in statistical analyses.

Sampling: Sampling followed the nested standardized plot design of the EForTS project (“Ecological and socioeconomic functions of tropical lowland rainforest transformation systems, Sumatra, Indonesia”; <http://www.uni-goettingen.de/EForTS>) (DRESCHER & al. 2016). In each landscape, arboreal ants were collected from four plots in each of four different land-use systems, lowland rainforest in the reserves (referred to as “forest”), jungle rubber (GOUYON & al. 1993), and rubber or oil palm smallholder plantations, resulting in 32 plots in total (all < 100 m above sea level). In each of these 32 plots, canopy ants were collected by canopy fogging from three target canopies (not the 1-m² subplots from DRESCHER & al. 2016), using the Swingfog® SN50 (Swingtec GmbH, Germany) to apply a mixture of 50 ml DECIS 25 EC® (Bayer Crop Science, active ingredient deltamethrin, 25 g / L) dissolved in four liters of petroleum white oil to each target canopy. The target canopies were chosen by visually identifying three locations with dense canopies, that is, canopy gaps and damaged trees were avoided. Beneath each target canopy, sixteen square 1 × 1 m collection funnels were suspended from ropes tied to height-adjustable tent poles, each fitted with a 250 ml wide neck PE flask containing 100 ml 96% ethanol. The collecting traps and bottles were removed two hours after fogging. Arthropod samples were then cleaned of debris, the ethanol exchanged and samples stored at -20 °C until further use. Worker ants were identified to genera using SHATTUCK (1999), BOLTON (1994) and FAYLE (2014). If possible, workers were then determined to Linnéan species using online keys and resources available from ANTWIKI (2019) and ANTWEB (2019). When no determination to Linnéan species was possible, morphospecies were defined based on a variety of morphological traits and trait states documented in ECOTAXONOMY (2019). Images of all species and morphospecies are documented in “A Guide to the Ants of Jambi” (NAZARRETA & al. 2019). Preliminary data on species richness per plot were published in DRESCHER & al. (2016) in a collated form with preliminary, unrevised species richness from a collection in rainy season 2013 / 2014.

Abundance data in social insects are typically skewed and this is especially pronounced if nests are sampled. Abundance data in this study are based on a trap area per plot of 3 × 16 m² = 48 m². Ants collected in the traps stem from branches and leaves in the canopy above, and predominantly comprise foragers outside the nest. This is reflected by the complete absence of callow workers, and the very low number of pupa and larva in our samples (< 0.4% of all collected individuals).

Statistical Analysis: Statistical analysis was performed using R v 3.6.1 (R CORE TEAM 2020) and visualized

using ggplot2 (WICKHAM 2016). Exploratory data analysis was performed using boxplots, dotplots, conditional boxplots, histograms, QQ-plots, and Cullen and Frey graphs for each response variable to ensure the data met underlying assumptions of the statistical tests (ZUUR & al. 2010) using $\alpha = 0.05$. The response variables abundance per m², species richness, species richness rarefied to the lowest number of individuals recovered in a plot, inverse Simpson Index (calculated using `vegan::diversity`; OKSANEN & al. 2019), and abundance of tramp species per m² were analyzed using `lm` or `glm` (family Gaussian with the log link function), as indicated by data exploration.

Initial models included land use (4 levels: forest, jungle rubber, rubber, oil palm), landscape (2 levels: Bukit Duabelas and Harapan), and their interaction as fixed factors. Models were simplified in a step-wise manner using AIC to arrive at the minimal adequate model for each response variable. Model fit was checked, then multiple comparisons were made using pairwise t-tests with Holm corrections (`multcomp::glht`; HOTHORN & al. 2008), as appropriate for each final model. Rank abundances were compared (`vegan::radrit`) and visualized (`RankAbund`; HARTKE 2019).

Beta diversity was partitioned into turnover, nestedness, and overall beta diversity using Sørensen pairwise dissimilarities (`betapart::beta.pair`; BASELGA & al. 2018). Multivariate dispersions were tested for each partition for land use and landscape, then differences in community composition were compared using permutational manova (`vegan::adonis`) and pairwise multilevel comparisons (`pairwiseAdonis::pairwise.adonis`; MARTINEZ ARBIZU 2019). Each partition was also used for non-metric multidimensional scaling (NMDS, `vegan::metaMDS`). Multivariate anova (`manova`, Wilk’s lambda) was used to test how well land use and landscape predicted the variability in nmDS scores; pair-wise contrasts were FDR adjusted (FDR = False Discovery Rate; BENJAMINI & HOCHBERG 1995).

Results

In total, 76 641 ant specimens were collected, belonging to 177 species from seven subfamilies and 54 genera (Tab. S1). Formicinae ($N_{sp} = 71$) and Myrmicinae ($N_{sp} = 66$) were by far the most species-rich subfamilies, accounting for more than three quarters of the species. The three most species-rich genera were *Crematogaster* ($N_{sp} = 24$), *Polyrhachis* ($N_{sp} = 24$) and *Camponotus* (excl. *Colobopsis*, $N_{sp} = 24$). There was considerable canopy ant community overlap between the Bukit Duabelas and the Harapan landscape (112 species), but the Bukit Duabelas landscape had 56 exclusive species, while the Harapan landscape only 10 (Fig. S2). A total of 44 species occurred in all four land-use systems; 39 species were exclusively found in forest, ten in jungle rubber, three in oil palm and two in rubber (Fig. S3).

Abundance and alpha diversity: Rubber and oil palm plantations had comparatively low levels of species richness and low total abundance, and differed from jungle rubber (intermediate) and forest, which had high levels

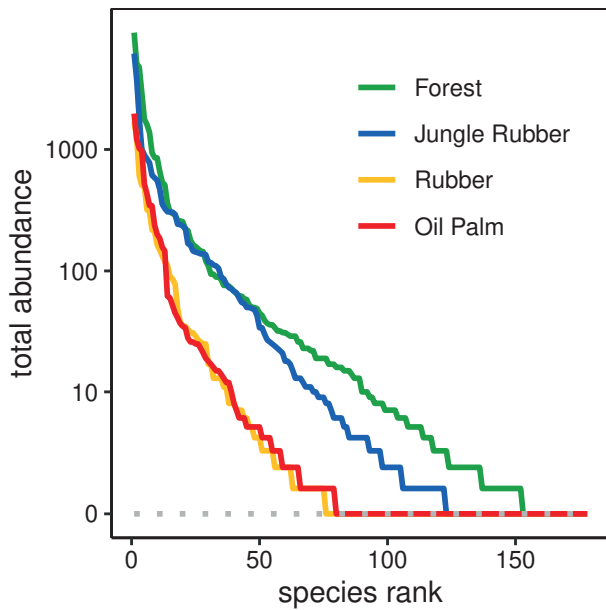


Fig. 1: Rank abundance curves of canopy ants in four land-use systems in Jambi, Sumatra.

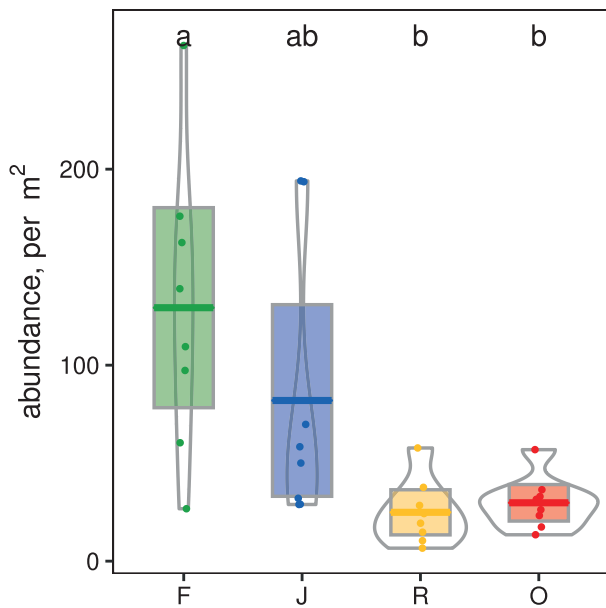


Fig. 2: Canopy ant abundance per square meter in four land-use systems in Jambi, Sumatra (F = forest, J = jungle rubber, R = rubber, O = oil palm). Different letters indicate significant differences of ant abundance between the land-use systems (dots = data points, bars = means, boxes = 95% confidence intervals, violins = density).

of total abundance and species richness (Fig. 1). Rank abundance distributions of forest differed significantly from rubber or oil palm (Tukey's HSD, both $t > 2.9$, both $p < 0.05$; Fig. 1) but not jungle rubber (Tukey's HSD, both $t > 1.74$, both $p > 0.15$).

Per square meter, canopy ant abundance N/m^2 in forest was more than four times higher than in oil palm and more than five times higher than in rubber, while

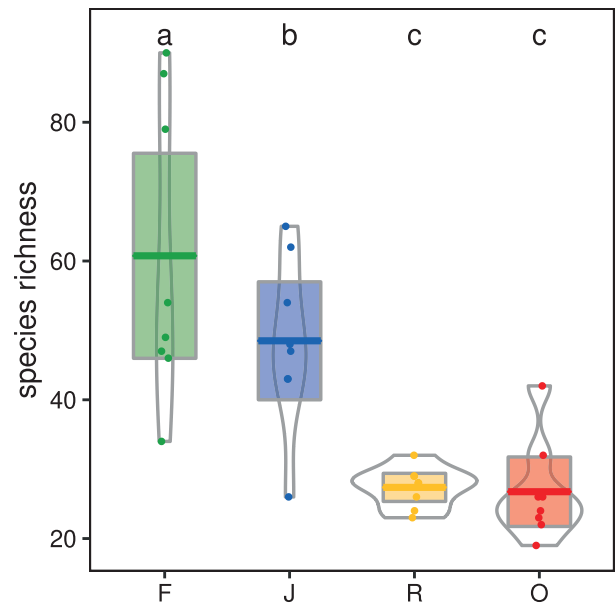


Fig. 3: Canopy ant species richness in four land-use systems in Jambi, Sumatra (F = forest, J = jungle rubber, R = rubber, O = oil palm). Different letters indicate significant differences of ant abundance between the land-use systems (dots = data points, bars = means, boxes = 95% confidence intervals, violins = density).

abundance in jungle rubber was intermediate (Fig. 2). As a consequence, canopy ant abundance N/m^2 varied significantly among land-use systems (glm, $F_{3,28} = 11.32$, $p < 0.0001$, Tukey's HSD pairwise test). Canopy ant abundance N/m^2 in the Bukit Duabelas landscape was on average more than twice that in the Harapan landscape ($N_{[BD]}/m^2 = 205.4 \pm 185.2$; $N_{[HR]}/m^2 = 94.0 \pm 66.0$; mean \pm s.d.; glm: $F_{1,27} = 19.91$, $p < 0.001$). However, no interaction between the factors land use and landscape were detected (glm, $F_{3,24} = 0.17$, $p = 0.9$).

A similar pattern was found for species richness N_{sp} . On average, species richness in forest was more than twice that of rubber and oil palm plantations, and intermediate in jungle rubber (glm: $F_{3,28} = 27.3$, $p < 0.0001$; Fig. 3). Similar to abundance, species richness in the Bukit Duabelas landscape was higher than in the Harapan landscape ($N_{sp[BD]} = 46.8 \pm 23.2$; $N_{sp[HR]} = 34.9 \pm 10.2$; glm: $F_{1,27} = 24.6$, $p < 0.0001$). Again, no significant interaction between the factors land use and landscape was detected (glm, $F_{3,24} = 2.8$, $p = 0.059$). When rarefied to the smallest number of individuals observed in a plot, there is no effect of landscape, and land use is marginally significant ($F_{3,28} = 2.512$, $p = 0.0789$), with species richness of forest most similar to jungle rubber and higher than rubber and oil palm plantations (Fig. S4, S5). By contrast, inverse Simpson diversity did not vary significantly with land use or landscape, not even marginally ($f < 1.0$, $p > 0.5$ for both). Both canopy ant abundance and canopy ant species richness were positively correlated to tree biomass (Pearson's correlation; both $t > 3.6$, both $r^2 > 0.5$, both $p < 0.001$; Fig. S6). Tree biomass was highest in forest, intermediate in jungle rubber and

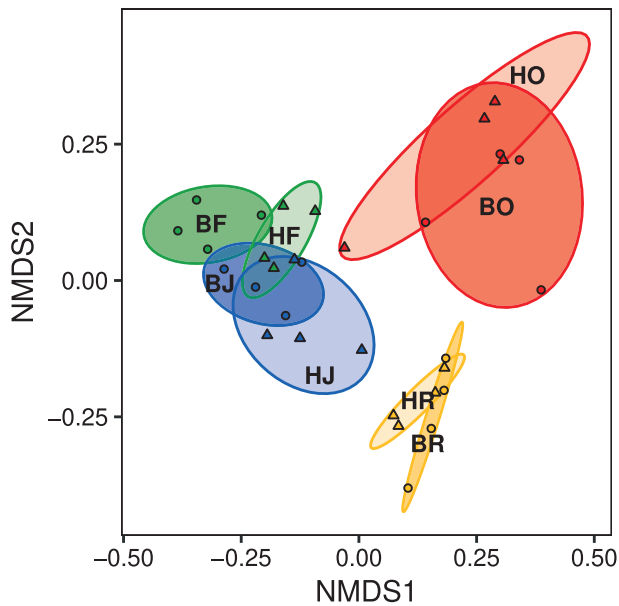


Fig. 4: NMDS of canopy ant community composition in four land-use systems and two landscapes in Jambi, Sumatra, based on Sørensen dissimilarities (F = forest, J = jungle rubber, R = rubber, O = oil palm, B = Bukit Duabelas, H = Harapan Rainforest). Community composition is influenced by both land use and landscape, with significant interaction between the factors.

lowest in plantations of oil palm and rubber (DRESCHER & al. 2016).

Beta diversity: Overall beta diversity differed significantly among land-use systems (Wilk's lambda = 0.005, $F_{3,24} = 22.06$, $p < 0.001$) and between landscapes (Wilk's lambda = 0.328, $F_{1,24} = 8.18$, $p < 0.001$). The two factors interacted significantly (Wilk's lambda = 0.214, $F_{3,24} = 2.76$,

$p = 0.003$), as visualized in the nmDS of overall beta diversity (Fig. 4). Canopy ant community composition differed significantly between the Bukit Duabelas and Harapan landscapes only in forest and rubber plantations (pairwise adonis, $F_{BF*HF} = 2.84$, $p = 0.043$ and $F_{BR*HR} = 2.26$, $p = 0.048$, respectively), but not in jungle rubber and oil palm plantations (pairwise adonis, both $F_{BJ*HJ} = 0.91$, $p = 0.6$ and $F_{BO*HO} = 1.54$, $p = 0.09$). Overall, however, community composition in forest and jungle rubber from both landscapes were more similar to each other than to communities in other land-use systems from either landscape. Nestedness of communities was also affected by land use (Wilk's lambda = 0.13, $F = 4.14$, $p < 0.001$) and landscape (Wilk's lambda = 0.49, $F = 4.04$, $p = 0.011$), with the interaction also being significant (Wilk's lambda = 0.31, $F = 1.94$, $p = 0.034$). While rubber and oil palm communities had similar degrees of nestedness irrespective of landscape, nestedness in forest and jungle rubber differed between the landscapes (Fig. 5A). Turnover differed among land-use systems (Wilk's lambda = 0.03, $F = 7.84$, $p < 0.001$) and between landscapes (Wilk's lambda = 0.29, $F = 7.68$, $p < 0.001$), but the interaction was not significant (Fig. 5B). In all land-use systems, turnover contributed more to overall beta diversity than nestedness (Fig. S7). Geographic distance among plots correlated with Sørensen dissimilarities when all possible plot comparisons were considered (Pearson's product-moment correlation, $t = 2.68$, $p = 0.01$), but not when tested only within landscape and land use ($t = 0.15$, $p = 0.88$).

Tramp ants: Among the 177 ant species encountered, six are commonly classified as "tramp ants", which form invasive populations in other parts of the world. The six species were *Anoplolepis gracilipes* (F. SMITH, 1857), *Cardiocondyla wroughtonii* (FOREL, 1890), *Monomorium*

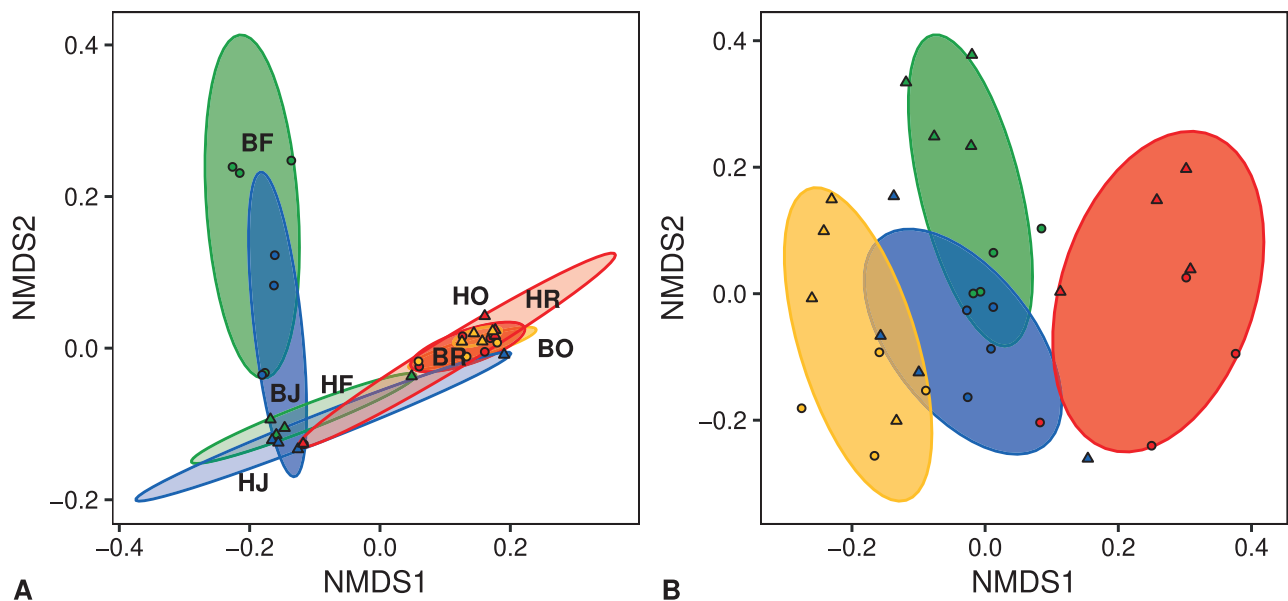


Fig. 5: NMDS of nestedness (A) and turnover (B) of canopy ant communities in four land-use systems and two landscapes in Jambi, Sumatra, based on Sørensen dissimilarities (F = forest, J = jungle rubber, R = rubber, O = oil palm, B = Bukit Duabelas / circles, H = Harapan Rainforest / triangles). Land-use systems and landscapes were significant predictors for both turnover and nestedness, while an interaction between land use and landscape was only found in nestedness.

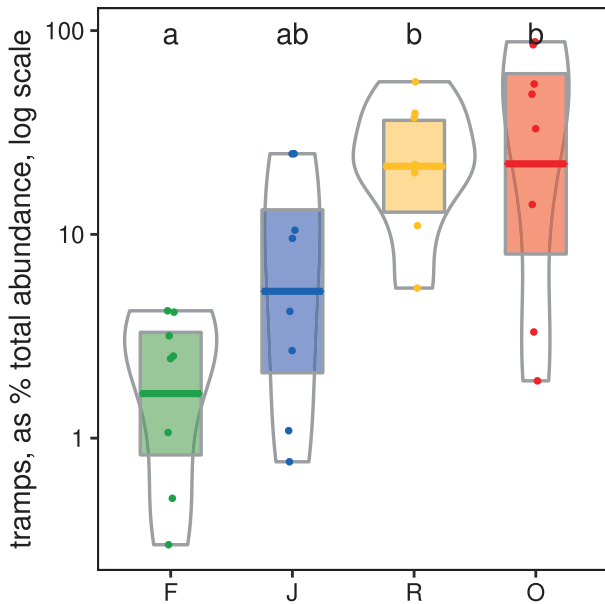


Fig. 6: Abundance per m² of six tramp ant species (*Anoplolepis gracilipes*, *Cardiocondyla wroughtonii*, *Monomorium floricola*, *Paratrechina longicornis*, *Tapinoma melanocephalum* and *Technomyrmex albipes*) as log percentage of the overall abundance per m² of canopy ants across four land-use systems in Jambi, Sumatra (F = forest, J = jungle rubber, R = rubber, O = oil palm, dots = data points, bars = means, boxes = 95% confidence intervals, violins = density). Different letters indicate significant differences.

floricola (JERDON, 1851), *Paratrechina longicornis* (Latreille, 1802), *Tapinoma melanocephalum* (Fabricius, 1793) and *Technomyrmex albipes* (F. Smith, 1861). In total, 7562 individuals of these six tramp species were collected, representing almost 10% of all ants collected.

The proportion of tramp ants varied strongly with land use ($\text{lm: } F_{3,28} = 9.11, p = 0.0002$) and was significantly lower in forest ($\text{TP}_F = 2.3 \pm 1.5\%$) than in monoculture plantations of rubber ($\text{TP}_R = 26.6 \pm 16.6\%$) and oil palm ($\text{TP}_O = 41.1 \pm 34.1\%$, Fig. 6). Tramp ant proportions in jungle rubber were intermediate. Abundance and relative proportion of tramp ants were highly correlated in each land-use system (Pearson rank correlation prc , all $r^2 > 0.7$, all $t > 2.5$, all $p < 0.05$; Fig. 7A), indicating that the high proportions of tramp ants in the plantation systems are not merely an artifact of lower absolute abundance of other ants. In fact, the abundance of tramp ants only correlated with total ant abundance in rubber (prc , $r^2 = 0.8, t = 3.2, p < 0.0176$), but not the other land-use systems (Fig. 7B). The projected linear correlations in rubber and oil palm plantations were very similar, though not significant in the latter, likely due to high variability of the relative abundance of tramp ants in oil palm plantations.

Discussion

This study investigated effects of tropical lowland rainforest conversion into rubber and oil palm smallholder plantations on abundance, species richness and community composition of arboreal ants in Sumatra, Indonesia. This represents the first in-depth analysis of canopy ant community response to conversion of rainforest into two of the world's most important cash crops. While extending the geographic scope of canopy ant investigations to the largest SE Asian nation (Indonesia), which produces the most palm oil, and the second-most natural rubber worldwide, this study is also the first to compare lowland rainforest to the common practice of comparatively extensive small-scale plantations of smallholder rubber and oil palm rather than vast, intensively managed, company-owned

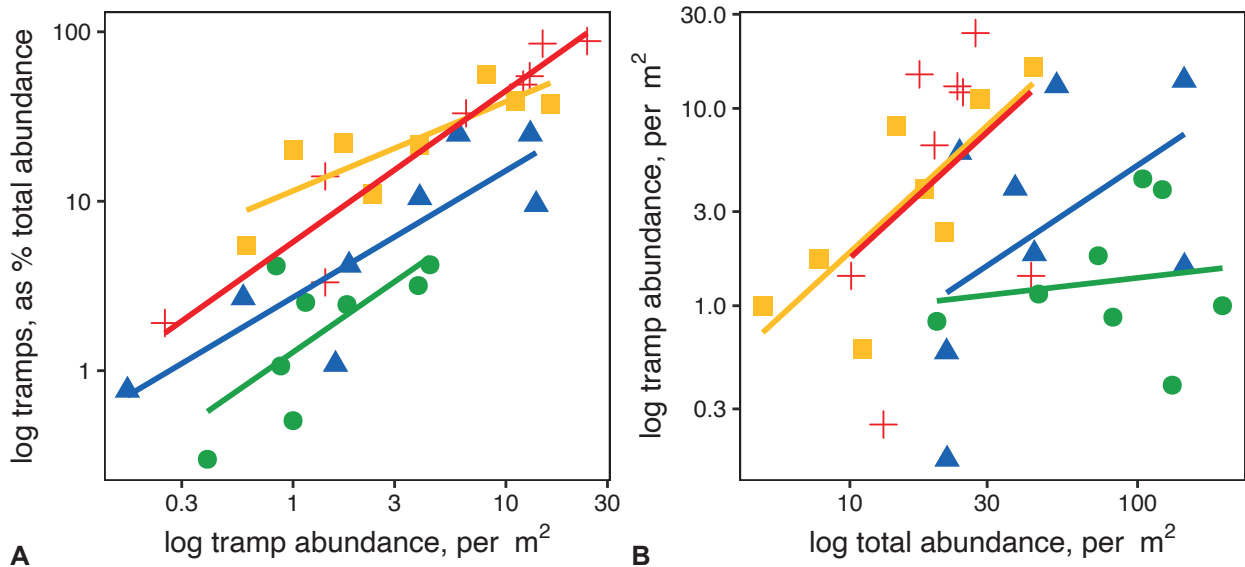


Fig. 7: (A) log tramp ant percentage vs. log tramp abundance per m² and (B) log tramp abundance per m² vs. log total ant abundance per m² in four land-use systems in Jambi, Indonesia (green circles = forest, blue triangles = jungle rubber, yellow squares = rubber, red crosses = oil palm).

estate plantations. This work thus offers a new perspective on the rainforest-to-cash-crop conversion process that has not been offered by the previous literature.

The results confirmed the expectation that (1) canopy ant abundance is much lower in monocultures of rubber and oil palm than in lowland rainforest, corresponding to an average abundance reduction of > 75% from forest to oil palm, and > 80% from forest to rubber. These values are reminiscent of recent reports of drastic insect population declines over the past decades (e.g., CEBALLOS & al. 2017, HALLMANN & al. 2017), sparking the term “Ecological Armageddon” (LEATHER 2018). These results are similar to those of many previous studies which report reduced ant abundance or occurrence in oil palm plantations compared to forest (e.g., BRÜHL & ELTZ 2010, FAYLE & al. 2010, LUKE & al. 2014, FAYLE & al. 2015). Reduced worker ant abundance in smallholder rubber and oil palm is not surprising, however, as agriculture is known to affect arthropod population sizes, for example, through pesticide use, fertilization (KYTÖ & al. 1996), habitat fragmentation (TSCHARNTKE & al. 2005), light pollution (GRUBISIC & al. 2018), higher temperatures due to climate change (LISTER & GARCIA 2018) or associated higher levels of atmospheric CO₂ (AUCOTT 2019). Other potential factors contributing to these severe abundance declines may include an increase in canopy openness, which influences aboveground temperature, and reductions in aboveground biomass and plant species richness, which coincide with reduced canopy ant species richness (DRESCHER & al. 2016). Declines in worker ant numbers should cause particular concern as the far-reaching effects of ants on the environment are often attributed to their high abundance (TUMA & al. 2020). Being among the main scavengers in many tropical ecosystems (FAYLE & al. 2011, TAN & CORLETT 2012), ants can be responsible for up to 61% of invertebrate-mediated resource removal from rainforest floors (GRIFFITHS & al. 2018). The reduced numbers of canopy ants along the rainforest conversion gradient in our study likely affects the performance of the remaining ant community in this and other abundance-related ecosystem functions. It is as of yet unclear whether differences in canopy ant abundance between forest and monoculture plantations remain stable over time, or may even increase as the agricultural systems age (KRAUSS & al. 2010). Abundance of ants, or all social insects for that matter, must be interpreted with caution as the building blocks of social insect populations are colonies, not mostly infertile worker individuals (HÖLLDOBLER & WILSON 2009). Colony and individual body sizes of ants vary profoundly (HÖLLDOBLER & WILSON 1990), as does the ecological significance of individual ant species, or an entire community. Although unable to be quantified here, the differences in ant abundance between forest and the smallholder plantations are striking, and suggest a significant ecological impact.

These results also confirmed the expectation (2) that canopy ant species richness was significantly lower in monoculture plantations of rubber and oil palm than in lowland rainforest, and (3) that community composition

differed significantly between lowland rainforest and monoculture plantations. As with abundance, these findings support those from previous studies on changes in ant species richness and community composition from rainforest to agricultural systems in Southeast Asia, particularly oil palm (PFEIFFER & al. 2008, BRÜHL & ELTZ 2010, FAYLE & al. 2010). The total and average ant species numbers vary greatly between our study and existing literature. This is partially due to differing sampling methods, but also stratum: While we used canopy fogging for ant specimen on trees from 5 m upwards, other studies used baiting (e.g., BRÜHL & ELTZ 2010) or pitfall traps (e.g., LUCEY & al. 2014) to sample soil- and litter-dwelling ant species. Yet others used a combination of direct and indirect sampling to collect ants from different strata and microhabitats (e.g., FAYLE & al. 2010). Forest type, plantation system and geographic region also have to be taken into account when comparing this study to previous work. Among other differences, the current study sampled ants from primary degraded lowland rainforest (*sensu* MARGONO & al. 2014) and smallholder oil palm and rubber plantations in central Sumatra. In comparison, most previous studies contrasted ant communities between primary rainforests and large company-owned plantations in northern Borneo, specifically Sabah, Malaysia (e.g., TURNER & FOSTER 2009, BRÜHL & ELTZ 2010, FAYLE & al. 2010, LUCEY & HILL 2012, FAYLE & al. 2013, LUCEY & al. 2014). Smallholder plantations, however, differ greatly from large company-owned estates in terms of management (DARRAS & al. 2019) and the ecosystem functions they provide (DISLICH & al. 2017). Also, a mosaic of relatively little smallholder plantations of different crops contribute much more to heterogeneity on the landscape scale than large company-owned estates. The current findings also highlight the need to consider sampling strategy when comparing ant community patterns between rainforest and cash crop monocultures. Two previous studies focusing on litter- and shrub-layer ants in the same research plots did not detect differences in species richness between rainforest and monoculture plantations (RUBIANA & al. 2015, SHOLIH & al. 2019). In contrast to this study, ants in the two previous studies were sampled using food baits. Baiting disproportionately attracts behaviorally and numerically dominant species over subordinate species with small colony sizes (J. Drescher, unpubl.) and is generally known to yield lower species numbers than non-baiting sampling methods like pitfall traps (WANG & al. 2001, LOPES & VASCONCELOS 2008, DRESCHER & al. 2011). Canopy fogging as done in the present study, on the other hand, is largely indiscriminate within the size range of ants and yields datasets containing many rare species. In fact, among the 76 641 specimens from 177 species collected in this study, 37 species (20%) were represented by less than five individuals per species. Notably, the majority of rare species were found in forest, driving the species richness contrast to the monoculture plantations.

Finally, the results confirm the expectation (4) that the relative abundance of six tramp ant species increased with habitat disturbance, that is, from being virtually

absent in forest to contributing about 10% in jungle rubber, more than 25% in rubber and more than 40% of total ant individuals in oil palm plantations. These numbers likely underestimate the actual proportion of tramp ants in rubber and oil palm monoculture plantations, because we only categorized ant species as “tramp” if they were a confirmed Linnéan species for which invasive populations had been reported elsewhere. Generally, this assumption is supported by a growing body of evidence that invasive species, a subset of tramp ants, are highly abundant in agricultural systems, causing substantial ecological and economic damage (partially reviewed in PAINI & al. 2016). This highlights that rubber and oil palm monocultures are numerically dominated by highly generalist ant species, which are largely absent in lowland rainforest.

It might be tempting to consider jungle rubber a sustainable option for rubber production as it combines economic revenue with considerable biodiversity and a high proportion of “forest species” across taxa (DRESCHER & al. 2016, REMBOLD & al. 2017, GRASS & al. 2020, POTAPOV & al. 2020). But as jungle rubber combines relatively high labor intensity with relatively low gross margins (CLOUGH & al. 2016, DRESCHER & al. 2016, GRASS & al. 2020), it continues to be converted to higher profit land-use systems such as monocultures of rubber or oil palm. One possible method for ecologically upgrading rubber monocultures might be the establishment of “biodiversity islands”, that is, the introduction of other tree and shrub species into the plantations, similar to a design currently being investigated in oil palm plantations in Sumatra (TEUSCHER & al. 2016, GÉRARD & al. 2017). It is unclear to what degree such biodiversity islands impact overall yield, the prime concern of the smallholder farmers that dominate rubber production in Jambi Province, as opposed to large estate plantations dominating oil palm production (EULER & al. 2017, KOPP & BRÜMMER 2017, BPS PROVINSI JAMBI 2018, BPS INDONESIA 2019).

This study expands our understanding of rainforest conversion effects on the largely understudied arboreal ant communities in the fast-changing tropical ecosystems of Southeast Asia in general, and Sumatra in particular. Using primary degraded rainforest as control, and smallholder plantations of both rubber and oil palm as treatment, the present study offers new insights into ant community changes after rainforest conversion to cash crop agriculture. Important to note is that, most likely, much more pronounced differences between control and treatment would have been detected if undisturbed, pristine lowland rainforest had been the control, or intensively managed, large estate crops had been the treatment. This aspect is important to keep in mind when comparing similar land-use systems elsewhere. Future research should also include ant communities from different strata, such as litter and soil, to uncover different strategies that may help to mitigate the challenges posed by intensively managed tropical agricultural ecosystems. Further, seasonal dynamics of canopy ant communities need to be investigated as well as the long-term response of ant abundance

in relatively new ecosystems such as rubber and oil palm plantations. Lastly, applying a community phylogenetic perspective may allow linkage of phylogenetic differences between local communities to key ecological traits such as feeding biology or nesting behavior, deepening our understanding of biodiversity-ecosystem functioning relationships in a changing world. These insights will be essential for establishing future sustainable management strategies maintaining the functioning and integrity of tropical land-use systems.

Author contributions

Study design: JD, SS; sample collection: JD; species sorting: RN, JD; data analysis: TRH, JD; all authors contributed to and acknowledged the final version of this manuscript.

Acknowledgments

We thank Dmitry Dubovikoff, Brian Fisher, Shingo Hosoi-chi, Weejawat Jaitrong, Petr Klimes, Dirk Mezger, Wendy Wang, Phil Ward, and Seiki Yamane for invaluable help in verification of selected groups of canopy ant morphospecies. Adha Sari, Anik Larasati, Herry Marta Saputra, Ratna Rubiana, and Susilawati are thanked for help during administration and sorting ant specimens, and Nop, Yohanes Bayu Suharto, Yohanes Toni Rohaditomo, and Zulfi Kamal are thanked for help during sample collection. This study was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) project number 192626868 – SFB 990 in the framework of the collaborative German - Indonesian research project CRC990 - EF-ForTS. We thank the following persons and organizations for granting us access to and use of their properties: village leaders, local plot owners, PT Humusindo, PT Perkebunan Nusantara VI, Harapan Rainforest, and Bukit Duabelas National Park. This study was conducted using samples / organisms collected based on Collection Permit No. S.710 / KKH-2 / 2013 (23. Dec. 2013) issued by the Ministry of Forestry (PHKA) based on recommendation No. 2122 / IPH.1 / KS.02 / X / 2013 (31.Oct. 2013) by the Indonesian Institute of Sciences (LIPI), and export permit No. 773 / KKH / SDG / KSA.2 / 2017 (PHKA, 04. Aug. 2017) based on recommendation B-1885 / IPH.1 / KS.02.04 / VII / 2017 (LIPI, 07. Jul. 2017). Nicholas Gotelli and two anonymous reviewers are acknowledged for valuable comments and criticism of a previous version of the manuscript.

References

- ABAZUE, C.M., CHOY, E.A. & LYDON, N. 2019: Oil palm smallholders and certification: exploring the knowledge level of independent oil palm smallholders to certification. – *Journal of Bioscience and Agriculture Research* 19: 1589-1596.
- ALCANTARA, M.J.M., MODI, S., LING, T.C., MONKAI, J., XU, H., HUANG, S. & NAKAMURA, A. 2019: Differences in geographic distribution of ant species (Hymenoptera: Formicidae) between forests and rubber plantations: a case study in Xishuangbanna, China, and a global meta-analysis. – *Myrmecological News* 29: 135-145.
- ALLEN, K., CORRE, M.D., TJOA, A. & VELDKAMP, E. 2015: Soil nitrogen-cycling responses to conversion of lowland forests

- to oil palm and rubber plantations in Sumatra, Indonesia. – *Public Library of Science One* 10: art. e0133325.
- ANDERSEN, A.N. 2000: Global ecology of rainforest ants: functional groups in relation to environmental stress and disturbance. In: AGOSTI, D., MAJER, J.D., ALONSO, L.E. & SCHULTZ, T.R. (Eds.): *Ants: standard methods for measuring and monitoring biodiversity*. – Smithsonian Institution Press, Washington, DC, pp. 25-34.
- ANDERSEN, A.N. & MAJER, J.D. 2004: Ants show the way down under: invertebrates as bioindicators in land management. – *Frontiers in Ecology and the Environment* 2: 291-298.
- ANTWEB 2019: AntWeb. – <<https://www.antweb.org>>, retrieved on 1 September 2019.
- ANTWIKI 2019: AntWiki. – <<https://www.antwiki.org>>, retrieved on 1 September 2019.
- ATKINS, M.D. 1980: *Introduction to insect behaviour*. – Macmillan Publishing, New York NY, 237 pp.
- AUCOTT, M. 2019: Are changes in plants due to enhanced CO₂ contributing to insect population declines? – *Environmental Entomology* 48: 274-275.
- BARNES, A.D., ALLEN, K., KREFT, H., CORRE, M.D., JOCHUM, M., VELDKAMP, E., CLOUGH, Y., DANIEL, R., DARRAS, K., DENMEAD, L.H., FARIKHAH HANEDA, N., HERTEL, D., KNOHL, A., KOTOWSKA, M.M., KURNIAWAN, S., MELJIDE, A., REMBOLD, K., EDHO PRABOWO, W., SCHNEIDER, D., TSCHARNTKE, T. & BROSE, U. 2017: Direct and cascading impacts of tropical land-use change on multi-trophic biodiversity. – *Nature Ecology and Evolution* 1: 1511-1519.
- BASELGA, A., ORME, D., VILLEGGER, S., BORTOLI, J. DE & LEPRIEUR, F. 2018: betapart: partitioning beta diversity into turnover and nestedness components. R package version 1.5.1. – <<https://cran.r-project.org/package=betapart>>, retrieved on 1 September 2019.
- BENJAMINI, Y. & HOCHBERG, Y. 1995: Controlling the false discovery rate: a practical and powerful approach to multiple testing. – *Journal of the Royal Statistical Society Series B Methodological* 57: 289-300.
- BICKEL, T.O. & WATANASIT, S. 2005: Diversity of leaf litter ant communities in Ton Nga Chang Wildlife Sanctuary and nearby rubber plantations, Songkhla, Southern Thailand. – *Songklanakarin Journal of Science and Technology* 27: 943-955.
- BOLTON, B. 1994: *Identification guide to the ant genera of the world*. – Harvard University Press, Cambridge, MA, 222 pp.
- BOS, M.M., TYLIANAKIS, J.M., STEFFAN-DEWENTER, I. & TSCHARNTKE, T. 2008: The invasive yellow crazy ant and the decline of forest ant diversity in Indonesian cacao agroforests. – *Biological Invasions* 10: 1399-1409.
- BADAN PUSAT STATISTIK (BPS) PROVINSI JAMBI 2018: *Provinsi Jambi Dalam Angka 2018*. – Badan Pusat Statistik Provinsi Jambi, Jambi, 650 pp.
- BADAN PUSAT STATISTIK (BPS) INDONESIA 2019: *Statistical Yearbook of Indonesia*. – Badan Pusat Statistik Indonesia, Jakarta, 738 pp.
- BRÜHL, C.A. & ELTZ, T. 2010: Fuelling the biodiversity crisis: species loss of ground-dwelling forest ants in oil palm plantations in Sabah, Malaysia (Borneo). – *Biodiversity and Conservation* 19: 519-529.
- CEBALLOS, G., EHRLICH, P.R. & DIRZO, R. 2017: Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. – *Proceedings of the National Academy of Sciences of the United States of America* 114: E6089-E6096.
- CHYTRÝ, M., PYŠEK, P., WILD, J., PINO, J., MASKELL, L.C. & VILÀ, M. 2009: European wild of alien plant invasions based on the quantitative assessment across habitats. – *Diversity and Distributions* 15: 98-107.
- CLOUGH, Y., KRISHNA, V.V., CORRE, M.D., DARRAS, K., DENMEAD, L.H., MELJIDE, A., MOSER, S., MUSSHOF, O., STEINEBACH, S., VELDKAMP, E., ALLEN, K., BARNES, A.D., BREIDENBACH, N., BROSE, U., BUCHORI, D., DANIEL, R., FINKELDEY, R., HARAHAP, I., HERTEL, D., HOLTkamp, A.M., HÖRANDL, E., IRAWAN, B., JAYA, I.N.S., JOCHUM, M., KLARNER, B., KNOHL, A., KOTOWSKA, M.M., KRASHEVSKA, V., KREFT, H., KURNIAWAN, S., LEUSCHNER, C., MARAUN, M., MELATI, D.N., OPFERMANN, N., PÉREZ-CRUZADO, C., PRABOWO, W.E., REMBOLD, K., RIZALI, A., RUBIANA, R., SCHNEIDER, D., TJITROSOEDIRJO, S.S., TJOA, A., TSCHARNTKE, T. & SCHEU, S. 2016: Land-use choices follow profitability at the expense of ecological functions in Indonesian smallholder landscapes. – *Nature Communications* 7: art. 13137.
- DARRAS, K.F.A., CORRE, M.D., FORMAGLIO, G., TJOA, A., POTAPOV, A., BRAMBACH, F., SIBHATU, K.T., GRASS, I., RUBIANO, A.A., BUCHORI, D., DRESCHER, J., FARDIANSAH, R., HÖLSCHER, D., IRAWAN, B., KNEIB, T., KRASHEVSKA, V., KRAUSE, A., KREFT, H., LI, K., MARAUN, M., POLLE, A., RYADIN, A.R., REMBOLD, K., STIEGLER, C., SCHEU, S., TARIGAN, S., VALDÉS-URIBE, A., YADI, S., TSCHARNTKE, T. & VELDKAMP, E. 2019: Reducing fertilizer and avoiding herbicides in oil palm plantations – ecological and economic valuations. – *Frontiers in Forests and Global Change* 2: art. 65.
- DAVIDSON, D.W. 1997: The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. – *Biological Journal of the Linnean Society* 61: 153-181.
- DAVIDSON, D.W., COOK, S.C., SNELLING, R.R. & CHUA, T.H. 2003: Explaining the abundance of ants in lowland tropical rainforest canopies. – *Science* 300: 969-972.
- DAVIDSON, D.W. & PATRELL-KIM, L. 1996: Tropical arboreal ants: why so abundant? In: GIBSON, A.C. (Ed.): *Neotropical biodiversity and conservation*. – Mildred E. Mathias Botanical Garden, Los Angeles, CA, pp. 127-149.
- DISLICH, C., KEYEL, A.C., SALECKER, J., KISEL, Y., MEYER, K.M., AULIYA, M., BARNES, A.D., CORRE, M.D., DARRAS, K., FAUST, H., HESS, B., KLASSEN, S., KNOHL, A., KREFT, H., MELJIDE, A., NURDIANSYAH, F., OTTEN, F., PE'ER, G., STEINEBACH, S., TARIGAN, S., TÖLLE, M.H., TSCHARNTKE, T. & WIEGAND, K. 2017: A review of the ecosystem functions in oil palm plantations, using forests as a reference system. – *Biological Reviews* 92: 1539-1569.
- DRESCHER, J., FELDHAAR, H. & BLÜTHGEN, N. 2011: Interspecific aggression and resource monopolization of the invasive ant *Anoplolepis gracilipes* in Malaysian Borneo. – *Biotropica* 43: 93-99.
- DRESCHER, J., REMBOLD, K., ALLEN, K., BECKSCHÄFER, P., BUCHORI, D., CLOUGH, Y., FAUST, H., FAUZI, A.M., GUNAWAN, D., HERTEL, D., IRAWAN, B., JAYA, I.N.S., KLARNER, B., KLEINN, C., KNOHL, A., KOTOWSKA, M.M., KRASHEVSKA, V., KRISHNA, V., LEUSCHNER, C., LORENZ, W., MELJIDE, A., MELATI, D., NOMURA, M., PÉREZ-CRUZADO, C., QAIM, M., SIREGAR, I.Z., STEINEBACH, S., TJOA, A., TSCHARNTKE, T., WICK, B., WIEGAND, K., KREFT, H. & SCHEU, S. 2016: Ecological and socio-economic functions across tropical land use systems after rainforest conversion. – *Philosophical Transactions of the Royal Society B-Biological Sciences* 371: art. 20150275.
- EARLY, R., BRADLEY, B.A., DUKES, J.S., LAWLER, J.J., OLDEN, J.D., BLUMENTHAL, D.M., GONZALEZ, P., GROSHOLZ, E.D., IBANEZ, I., MILLER, L.P., SORTE, C.J.B. & TATEM, A.J. 2016: Global threats from invasive alien species in the twenty-first century and national response capacities. – *Nature Communications* 7: art. 12485.

- ECOTAXONOMY 2019: Ecotaxonomy database. – <<http://ecotaxonomy.org>>, retrieved on 1 September 2019.
- EULER, M., KRISHNA, V., SCHWARZE, S., SIREGAR, H. & QAIM, M. 2017: Oil palm adoption, household welfare, and nutrition among smallholder farmers in Indonesia. – *World Development* 93: 219-235.
- FAYLE, T.M., BAKKER, L., CHEAH, C., CHING, T.M., DAVEY, A., DEM, F., EARL, A., HUAIMEI, Y., HYLAND, S., JOHANSSON, B., LIGTERMOET, E., LIM, R., LIN, L.K., LUANGYOTHA, P., MARTINS, B.H., PALMEIRIM, A.F., PANINHUAN, S., ROJAS, S.K., SAM, L., SAM, P.T.T., SUSANTO, D., WAHYUDI, A., WALSH, Y., WEIGL, S., CRAZE, P.G., JEHL, R., METCALFE, D. & TREVELYA, R. 2011: A positive relationship between ant biodiversity (Hymenoptera: Formicidae) and rate of scavenger-mediated nutrient redistribution along a disturbance gradient in a south-east Asian rain forest. – *Myrmecological News* 14: 5-12.
- FAYLE, T.M., EDWARDS, D.P., FOSTER, W.A., YUSAH, K.M. & TURNER, E.C. 2015: An ant-plant by-product mutualism is robust to selective logging of rain forest and conversion to oil palm plantation. – *Oecologia* 178: 441-450.
- FAYLE, T.M., TURNER, E.C. & FOSTER, W.A. 2013: Ant mosaics occur in SE Asian oil palm plantation but not rain forest and are influenced by the presence of nest-sites and non-native species. – *Ecography* 36: 1051-1057.
- FAYLE, T.M., TURNER, E.C., SNADDON, J.L., CHEY, V.K., CHUNG, A.Y.C., EGGLETON, P. & FOSTER, W.A. 2010: Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. – *Basic and Applied Ecology* 11: 337-345.
- FAYLE, T.M., YUSAH, K. & HASHIMOTO, Y. 2014: Key to the ant genera of Borneo in English and Malay. – <<http://www.tomfayle.com/Ant%20key.htm>>, retrieved on 1 May 2020.
- FLOREN, A., BIUN, A. & LINSÉNMAIR, E.K. 2002: Arboreal ants as key predators in tropical lowland rainforest trees. – *Oecologia* 131: 137-144.
- FLOREN, A. & LINSÉNMAIR, K.E. 2001: The influence of anthropogenic disturbances on the structure of arboreal arthropod communities. – *Plant Ecology* 153: 153-167.
- FLOREN, A., WETZEL, W. & STAAB, M. 2014: The contribution of canopy species to overall ant diversity (Hymenoptera: Formicidae) in temperate and tropical ecosystems. – *Myrmecological News* 19: 65-74.
- Food and Agriculture Organization 2020: Food and Agriculture Organization of the United Nations Statistical Database; <<http://www.fao.org/faostat/en/#data/QC>>, retrieved on 1 May 2020.
- FOSTER, W.A., SNADDON, J.L., TURNER, E.C., FAYLE, T.M., COCKERILL, T.D., ELLWOOD, M.D.F., BROAD, G.R., CHUNG, A.Y.C., EGGLETON, P., KHEN, C.V. & YUSAH, K.M. 2011: Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. – *Philosophical Transactions of the Royal Society B-Biological Sciences* 366: 3277-3291.
- GÉRARD, A., WOLLNI, M., HÖLSCHER, D., IRAWAN, B., SUNDAWATI, L., TEUSCHER, M. & KREFT, H. 2017: Oil-palm yields in diversified plantations: initial results from a biodiversity enrichment experiment in Sumatra, Indonesia. – *Agriculture, Ecosystems and Environment* 240: 253-260.
- GIBSON, L., LEE, T.M., KOH, L.P., BROOK, B.W., GARDNER, T.A., BARLOW, J., PERES, C.A., BRADSHAW, C.J.A., LAURANCE, W.F. & LOVEJOY, T.E. 2011: Primary forests are irreplaceable for sustaining tropical biodiversity. – *Nature* 478: 378-381.
- GOUYON, A., FORESTA, H. DE & LEVANG, P. 1993: Does "jungle rubber" deserve its name? An analysis of rubber agroforestry systems in southeast Sumatra. – *Agroforestry Systems* 22: 181-206.
- GRASS, I., KUBITZA, C., KRISHNA, V., CORRE, M.D., MUSSHOF, O., PÜTZ, P., DRESCHER, J., REMBOLD, K., ARIYANTI, E.S., BARNES, A.D., BRINKMANN, N., BROSE, U., BRÜMMER, B., BUCHORI, D., DANIEL, R., DARRAS, K., FAUST, H., FEHRMANN, L., HEIN, J., HENNINGS, N., HIDAYAT, P., HÖLSCHER, D., JOCHUM, M., KNOHL, A., KOTOWSKA, M.M., KRASHEVSKA, V., KREFT, H., LEUSCHNER, C., LOBITE, N.J.S., PANJAITAN, R., POLLE, A., POTAPOV, A.M., PURNAMA, E., QAIM, M., RÖLL, A., SCHEU, S., SCHNEIDER, D., TJOA, A., TSCHARNTKE, T., VELDKAMP, E. & WOLLNI, M. 2020: Trade-offs between multifunctionality and profit in tropical smallholder landscapes. – *Nature Communications* 11: art. 1186.
- GRIFFITHS, H.M., ASHTON, L.A., WALKER, A.E., HASAN, F., EVANS, T.A., EGGLETON, P. & PARR, C.L. 2018: Ants are the major agents of resource removal from tropical rainforests. – *Journal of Animal Ecology* 87: 293-300.
- GRUBISIC, M., GRUNSVEN, R.H.A. VAN, KYBA, C.C.M., MANFRIN, A. & HÖLKER, F. 2018: Insect declines and agroecosystems: does light pollution matter? – *Annals of Applied Biology* 173: 180-189.
- GUILLAUME, T., KOTOWSKA, M.M., HERTEL, D., KNOHL, A., KRASHEVSKA, V., MURTLAKSONO, K., SCHEU, S. & KUZYAKOV, Y. 2018: Carbon costs and benefits of Indonesian rainforest conversion to plantations. – *Nature Communications* 9: art. 2388.
- HALLMANN, C.A., SORG, M., JONGEJANS, E., SIEPEL, H., HOFFLAND, N., SCHWAN, H., STENMANS, W., MÜLLER, A., SUMSER, H., HÖRREN, T., GOULSON, D. & DE KROON, H. 2017: More than 75 percent decline over 27 years in total flying insect biomass in protected areas. – *Public Library of Science One* 12: art. e0185809.
- HANSEN, M.C., STEHMAN, S. V., POTAPOV, P. V., ARUNARWATI, B., STOLLE, F. & PITTMAN, K. 2009: Quantifying changes in the rates of forest clearing in Indonesia from 1990 to 2005 using remotely sensed data sets. – *Environmental Research Letters* 4: art. 034001.
- HARTKE, T. 2019: RankAbund: Calculate rank abundances and plot rank abundance curves. R package version 0.1.0. – <<https://github.com/tamarahartke/RankAbund>>, retrieved on 1 September 2019.
- HÖLLDOBLER, B. & WILSON, E.O. 1990: *The ants*. – Harvard University Press, Cambridge, MA, 745 pp.
- HÖLLDOBLER, B. & WILSON, E.O. 2009: *The superorganism*. – W.W. Norton & Company, New York, NY, 522 pp.
- HOTHORN, T., BRETZ, F. & WESTFALL, P. 2008: Simultaneous inference in general parametric models. – *Biometrical Journal* 50: 346-363.
- KING, J.R., ANDERSEN, A.N. & CUTTER, A.D. 1998: Ants as bio-indicators of habitat disturbance: validation of the functional group model for Australia's humid tropics. – *Biodiversity & Conservation* 7: 1627-1638.
- KOPP, T. & BRÜMMER, B. 2017: Traders' market power along Indonesian rubber value chains. – *China Agricultural Economic Review* 9: 169-187.
- KRAUSS, J., BOMMARCO, R., GUARDIOLA, M., HEIKKINEN, R.K., HELM, A., KUUSSAARI, M., LINDBORG, R., ÖCKINGER, E., PÄRTEL, M., PINO, J., PÖYRY, J., RAATIKAINEN, K.M., SANG, A., STEFANESCU, C., TEDER, T., ZOBEL, M. & STEFFANDEWENTER, I. 2010: Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. – *Ecology Letters* 13: 597-605.
- KYTÖ, M., NIEMELÄ, P. & LARSSON, S. 1996: Insects on trees: population and individual response to fertilization. – *Oikos* 75: 148-159.

- LAUMONIER, Y. 1997: The vegetation and physiography of Sumatra. – Kluwer Academic Publishers, Dordrecht, 222 pp.
- LEATHER, S.R. 2018: “Ecological Armageddon” – more evidence for the drastic decline in insect numbers. – *Annals of Applied Biology* 172: 1-3.
- LISTER, B.C. & GARCIA, A. 2018: Climate-driven declines in arthropod abundance restructure a rainforest food web. – *Proceedings of the National Academy of Sciences of the United States of America* 115: E10397-E10406.
- LOPES, C.T. & VASCONCELOS, H.L. 2008: Evaluation of three methods for sampling ground-dwelling ants in the Brazilian Cerrado. – *Neotropical Entomology* 37: 399-405.
- LUCEY, J.M. & HILL, J.K. 2012: Spillover of insects from rain forest into adjacent oil palm plantations. – *Biotropica* 44: 368-377.
- LUCEY, J.M., TAWATAO, N., SENIOR, M.J.M., CHEY, V.K., BENEDICK, S., HAMER, K.C., WOODCOCK, P., NEWTON, R.J., BOTTRELL, S.H. & HILL, J.K. 2014: Tropical forest fragments contribute to species richness in adjacent oil palm plantations. – *Biological Conservation* 169: 268-276.
- LUKE, S.H., FAYLE, T.M., EGGLETON, P., TURNER, E.C. & DAVIES, R.G. 2014: Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. – *Biodiversity and Conservation* 23: 2817-2832.
- MARGONO, B.A., POTAPOV, P. V, TURUBANOVA, S., STOLLE, F. & HANSEN, M.C. 2014: Primary forest cover loss in Indonesia over 2000-2012. – *Nature Climate Change* 4: 730-735.
- MARGONO, B.A., TURUBANOVA, S., ZHURAVLEVA, I., POTAPOV, P., TYUKAVINA, A., BACCINI, A., GOETZ, S. & HANSEN, M.C. 2012: Mapping and monitoring deforestation and forest degradation in Sumatra (Indonesia) using Landsat time series data sets from 1990 to 2010. – *Environmental Research Letters* 7: art. 034010.
- MARTINEZ ARBIZU, P. 2019: pairwiseAdonis: Pairwise multilevel comparison using adonis.R package version 0.3. – <<https://github.com/pmartinezarbizu/pairwiseAdonis>>, retrieved on 1 September 2019.
- MELATI, D.N. 2017: The use of remote sensing data to monitor land use systems and forest variables of the tropical rainforest landscape under transformation in Jambi Province, Sumatra, Indonesia. – PhD thesis, Georg-August University of Göttingen, Göttingen, 126 pp.
- NAZARRETA, R., BUCHORI, D., HIDAYAT, P., FARDIANSAH, R., SCHEU, S. & DRESCHER, J. 2019: A guide to the ants of Jambi (Sumatra, Indonesia) – identification key to common ant genera and images of the EFForTS collection. Version 4.0 beta, October 2019. – <<https://www.uni-goettingen.de/de/handbooks+and+guides/605977.html>>, retrieved on 1 September 2019.
- OKSANEN, J., BLANCHET, G., FRIENDLY, M., KINDT, R., LEGENDRE, P., MCGLINN, D., MINCHIN, P.R., O'HARA, R.B., SIMPSON, G.L., SOLYMOS, P., STEVENS, M.H.H., SZOEC, E. & WAGNER, H. 2019: vegan: Community Ecology Package. R package version 2.5.6. – <<https://cran.r-project.org/package=vegan>>, retrieved on 1 September 2019.
- PAINI, D.R., SHEPPARD, A.W., COOK, D.C., BARRO, P.J. DE, WÖRNER, S.P. & THOMAS, M.B. 2016: Global threat to agriculture from invasive species. – *Proceedings of the National Academy of Sciences of the United States of America* 113: 7575-7579.
- PERSOON, G.A. & WEERD, M. VAN 2006: Biodiversity and natural resource management in insular Southeast Asia. – *Island Studies Journal* 1: 81-108.
- PFEIFFER, M., TUCK, H.C. & LAY, T.C. 2008: Exploring arboreal ant community composition and co-occurrence patterns in plantations of oil palm *Elaeis guineensis* in Borneo and Peninsular Malaysia. – *Ecography* 31: 21-32.
- PHILPOTT, S.M. & ARMBRECHT, I. 2006: Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. – *Ecological Entomology* 31: 369-377.
- POTAPOV, A.M., DUPÉRRÉ, N., JOCHUM, M., DREZKO, K., KLARNER, B., BARNES, A.D., KRASHEVSKA, V., REMBOLD, K., KREFT, H., BROSE, U., WIDYASTUTI, R., HARMS, D. & SCHEU, S. 2020: Functional losses in ground spider communities due to habitat structure degradation under tropical land-use change. – *Ecology* 101: art e02957.
- R CORE TEAM 2020: R: A language and environment for statistical computing. – <<https://www.r-project.org>>, retrieved on 1 September 2019.
- REMBOLD, K., MANGOPO, H., TJITROEDIRDO, S.S. & KREFT, H. 2017: Plant diversity, forest dependency, and alien plant invasions in tropical agricultural landscapes. – *Biological Conservation* 213: 234-242.
- RIZALI, A., CLOUGH, Y., BUCHORI, D., HOSANG, M.L.A., BOS, M.M. & TSCHARNTKE, T. 2013: Long-term change of ant community structure in cacao agroforestry landscapes in Indonesia. – *Insect Conservation and Diversity* 6: 328-338.
- ROOM, P.M. 1975: Diversity and organization of the ground foraging ant faunas of forest, grassland and tree crops in Papua New Guinea. – *Australian Journal of Zoology* 23: 71-89.
- RUBIANA, R., RIZALI, A., DENMEAD, L.H., ALAMSARI, W., HIDAYAT, P., PUJJIANTO HINDAYANA, D., CLOUGH, Y., TSCHARNTKE, T. & BUCHORI, D. 2015: Agricultural land use alters species composition but not species richness of ant communities. – *Asian Myrmecology* 7: 73-85.
- SCHNEIDER, D., ENGELHAUPT, M., ALLEN, K., KURNIAWAN, S., KRASHEVSKA, V., HEINEMANN, M., NACKE, H., WIJAYANTI, M., MERYANDINI, A., CORRE, M.D., SCHEU, S. & DANIEL, R. 2015: Impact of lowland rainforest transformation on diversity and composition of soil prokaryotic communities in sumatra (Indonesia). – *Frontiers in Microbiology* 6: art. 1339.
- SHATTUCK, S.O. 1999: Australian ants: their biology and identification. – CSIRO Publishing, Collingwood, VIC, 226 pp.
- SHOLIH, M.B., BUCHORI, D., SAKTI HARAHAP, I. & RIZALI, A. 2019: Pengaruh tipe penggunaan lahan dalam membentuk komunitas semut dan layanan ekosistem yang diberikan. – *Jurnal Entomologi Indonesia* 16: 83-90.
- TAN, C.K.W. & CORLETT, R.T. 2012: Scavenging of dead invertebrates along an urbanisation gradient in Singapore. – *Insect Conservation and Diversity* 5: 138-145.
- TEUSCHER, M., GÉRARD, A., BROSE, U., BUCHORI, D., CLOUGH, Y., EHBRECHT, M., HÖLSCHER, D., IRAWAN, B., SUNDAWATI, L., WOLLNI, M. & KREFT, H. 2016: Experimental biodiversity enrichment in oil-palm-dominated landscapes in Indonesia. – *Frontiers in Plant Science* 7: art. 1538.
- THONGPAK, D. 2014: Diversity and community composition of ants in the mixed deciduous forest, the pine forest and the para rubber plantation at Chulaborn Dam, Chaiyaphum Province, the Northeastern Thailand. – *International Journal of Environmental and Rural Development* 5: 72-76.
- TOBIN, J.E. 1995: Ecology and diversity of tropical forest canopy ants. In: LOWMAN, M.D. & NADKARNI, N.M. (Eds.): *Forest canopies*. – Academic Press, New York, NY, pp. 129-147.
- TSCHARNTKE, T., KLEIN, A.M., KRUESS, A., STEFFAN-DEWENTER, I. & THIES, C. 2005: Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. – *Ecology Letters* 8: 857-874.

- TUMA, J., EGGLETON, P. & FAYLE, T.M. 2020: Ant-termite interactions: an important but under-explored ecological linkage. – *Biological Reviews* 95: 555-572.
- TURNER, E.C. & FOSTER, W.A. 2009: The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. – *Journal of Tropical Ecology* 25: 23-30.
- TURUBANOVA, S., POTAPOV, P.V., TYUKAVINA, A. & HANSEN, M.C. 2018: Ongoing primary forest loss in Brazil, Democratic Republic of the Congo, and Indonesia. – *Environmental Research Letters* 13: art. 74028.
- WANG, C., STRAZANAC, J. & BUTLER, L. 2001: A comparison of pitfall traps with bait traps for studying leaf litter ant communities. – *Journal of Economic Entomology* 94: 761-765.
- WICKHAM, H. 2016: *ggplot2 - Elegant graphics for data analysis* (2nd edn.). – Springer-Verlag, New York, NY, 260 pp.
- ZUUR, A.F., IENO, E.N. & ELPHICK, C.S. 2010: A protocol for data exploration to avoid common statistical problems. – *Methods in Ecology and Evolution* 1: 3-14.