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Rainforest transformation reduces parasitoid wasp diversity—Can the enrichment of flowering vegetation alleviate this?

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Abstract

1. In Indonesia, the rapid expansion of oil palm and rubber plantations replaces large areas of tropical rainforest. Rainforest transformation alters the diversity and composition of parasitoid wasp communities, but appropriate management strategies to buffer their decline in rainforest transformation landscapes are not yet developed.
2. Here, we studied the effects of rainforest conversion to smallholder rubber and oil palm plantations on parasitoid wasp species richness, abundance and species composition. We also conducted a flowering vegetation enrichment experiment using the flowering weed *Asystasia gangetica* in all land-uses to investigate potential mitigation effects on parasitoid wasp diversity and composition.
3. Rainforest transformation to rubber plantations caused a large decrease in species richness (46%) and abundance (59%) of parasitoid wasps. Community structure of parasitoid wasps differed between forest and monoculture habitats with more habitat-specialised species in forest and a higher proportion of common species in the monoculture.
4. The experimental flowering vegetation enrichment increased parasitoid wasp species richness by 18% and abundance by 127%. Enrichment also enhanced the presence of unique parasitoid species in plantation and furthermore increased differences in community composition between rainforest and plantations. However, the enrichment experiment was confounded by time, meaning that a multi-year experiment with targeted controls is necessary for statistically more reliable statements.
5. Our study shows the effect of rainforest transformation to oil palm and rubber plantations on parasitoid wasp communities. Although providing additional flowering vegetation in plantations seems to potentially mitigate diversity loss, further research is needed to confirm and to investigate the mechanisms how flowering plants alleviate negative effects of rainforest transformation on parasitoid communities. Thereby, efficient conservation strategies for parasitoids

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wasps and their biological control services can be developed for rapidly changing tropical landscapes.

KEYWORDS
Asystasia gangetica, land-use change, oil palm, rubber, species composition

INTRODUCTION

Parasitoids are beneficial insects that provide biological control services to suppress phytophagous insect populations. Parasitoids kill their hosts by living inside or on the body of their hosts and by eating part of hosts' bodies. Compared with predators and pathogens, parasitoids are able to kill a wider spectrum of host and cause high mortality at various life stages of the host (Hawkins et al., 1997; Pennacchio & Strand, 2006). Parasitoid wasps are being utilised as biological control agent of major insect pest such as lepidopteran larvae, whitefly and aphids in high-value cash crop plantations (Boivin et al., 2012; Halim et al., 2018; Liu et al., 2015; Lou et al., 2013; Wang et al., 2019).

Parasitoid wasps are sensitive to disturbance and habitat fragmentation. In particular, intensive agriculture replacing natural habitats can reduce parasitoid richness and simplify food webs, which impairs the capacity of parasitoids to provide biological control services (Kruess & Tscharntke, 1994; Tylianakis et al., 2007). In tropical areas, rainforests typically harbour greater parasitoid wasps species richness and abundance than agroecosystem (Ruiz-Guerra et al., 2015). Agricultural intensification in turn negatively affects host–parasitoid interactions, decreasing parasitism rates in highly intensively managed agroecosystem (Jonsson et al., 2012). In addition to limited host availability, lack of flowering resources in agroecosystems can result in decreased parasitoid species richness and abundance (Kishinevsky et al., 2018).

Engineering agroecosystems by providing shelters for natural enemies was suggested to provide suitable conditions for natural enemies populations and support the conservation of biological control on agricultural land (Gontijo, 2019; Landis, 2017). Since parasitoid diversity has been shown to correlate positively with vegetation diversity and habitat complexity (Nugraha et al., 2014; Ulina et al., 2019), increasing floral resources in simplified agroecosystem through enrichment plantings may thus enhance parasitoid diversity and parasitism rates (Jonsson et al., 2012; Tscharntke et al., 2012). Promoting flowering vegetation in agroecosystems is crucial for parasitoids as it provides nectar as feeding source and habitat for alternative hosts (Hogg & Daane, 2011; Landis et al., 2000; Perović et al., 2010). Growing flowering vegetation successfully enhanced parasitoid presence and parasitism rates in oil palm (Harjotedjo et al., 2016; Kamarudin & Basri, 2010), coffee (Rezende et al., 2014) and also gave various benefits for many parasitoids of the tomato moth (Arnó et al., 2018). Likewise, increasing the amount of flowering weeds increases the number of parasitoids of the coffee berry borer in coffee plantation (Daniati et al., 2018).

In this study, we want to investigate how rainforest transformation to cash crop plantations affects the diversity and community composition of parasitoids. Rubber and oil palm are two commodities that have contributed to vast deforestation in Southeast Asia, and particularly Indonesia, in the last three decades (FAO, 2020; Tsujino et al., 2016; Wilcove et al., 2013). Indonesia has around 14.9 million hectares of oil palm plantation and 3.7 million hectares of rubber plantation (Badan Pusat Statistik, 2020a, 2020b), which makes it the global main producer of these commodities (Foster et al., 2011). A previous study reported that rainforest conversion to oil palm and rubber plantations reduced canopy parasitoid wasp diversity and affected the species composition (Azhar, Hartke, et al., 2022). However, little is known about the effects of tropical rainforest conversion to oil palm and rubber plantations on terrestrial parasitoid diversity and community structure. Parasitoid species such as *Apanteles* sp., *Brachymeria carinata* Joseph, *Pediobius anomalus* Gahan and *Euplectrus* sp. have been reported to attack bagworms *Metisa plana* Walker, *Mahasena corbetti* Tams and *Darna trima* (Moore) in oil palm plantations (Cheong et al., 2010; Egonyu et al., 2022; Sahari et al., 2019), but information on parasitoid utilisation in rubber plantations is still lacking. Established tree islands in oil palm plantations contributed to a higher arthropods biodiversity and their ecosystem functioning (Zemp et al., 2023) and were associated with the higher vegetation abundance compared with conventional oil palm (Azhar, Tawakkal, et al., 2022). The management of flowering weeds in oil palm plantation has been reported to have a positive impact on predators and parasitoids in Malaysia (Kamarudin & Basri, 2010). Flowering vegetation in cash crop plantations could increase parasitoid wasp abundance because the flowers provide high-quality food for parasitoid wasps (Damien et al., 2020; Zytynska et al., 2023). The potential of enhanced flowering vegetation for promoting parasitoid diversity in oil palm and rubber plantations has been little explored. Here, we compared the diversity and community of terrestrial parasitoid wasps in different land-use systems, from natural rainforest to managed smallholder rubber and oil palm plantations, with the aim of investigating the response of parasitoid wasp community assembly to natural habitat conversion to a cash crop monoculture. We experimentally enhanced flowering resources for parasitoids in the plantation systems and monitored parasitoid communities before and after flowering vegetation enhancement. We expected that rainforest transformation leads to parasitoid decline in plantations but that providing additional flower vegetation can mitigate the loss of parasitoid diversity. This study aims to investigate the effect of different land use types and flowering vegetation enrichment on the species composition of parasitoid wasps. The comparison of parasitoid community structure in tropical rainforest, oil palm and rubber plantation due to flowering vegetation enrichment can provide new insights into host–parasitoid interactions and land use. Therefore, we would like to test the enrichment experimentally on parasitoid species composition, without a priori prediction.

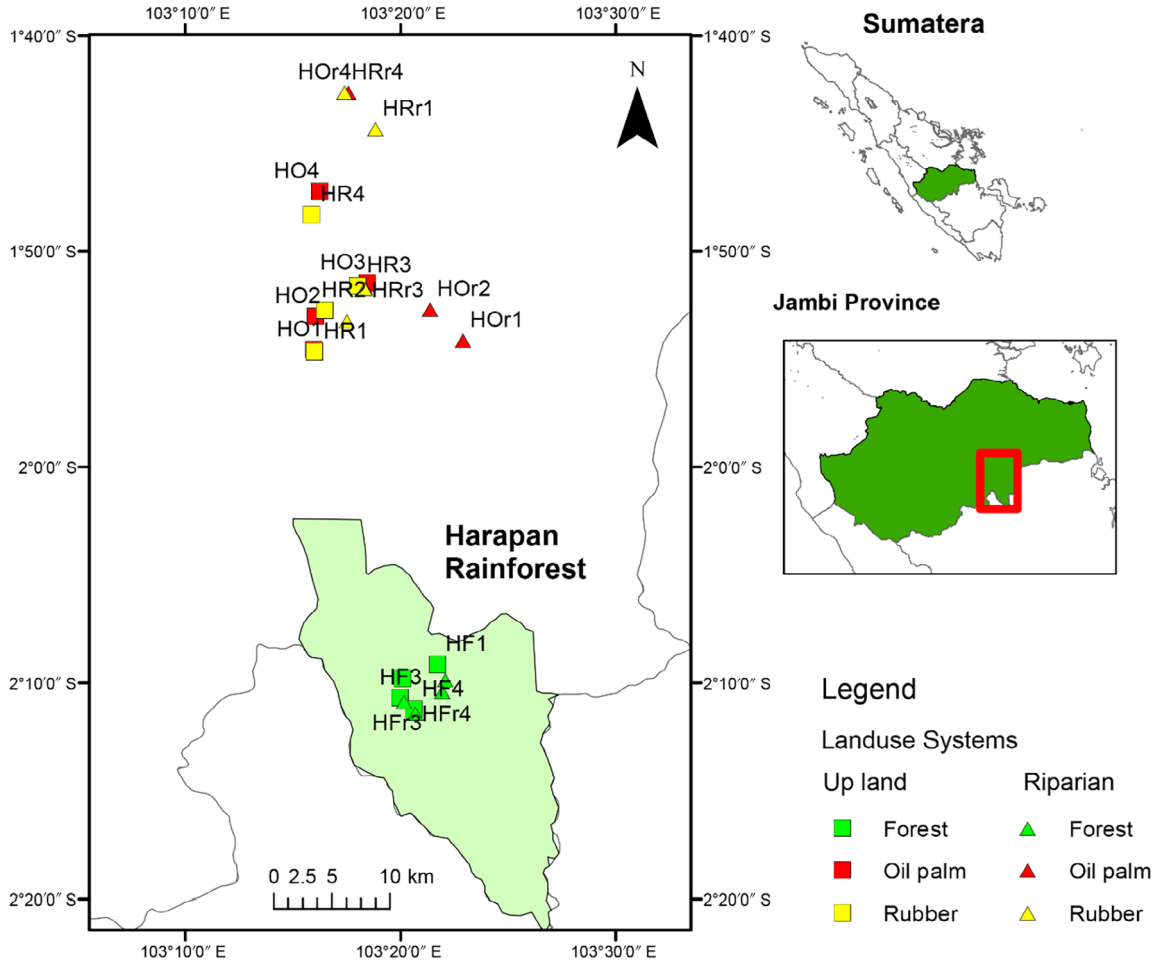


FIGURE 1 Study sites location in Jambi Province, Sumatra, Indonesia. Study sites located in Harapan Landscape within EFForTS project's core plots and riparian plots.

MATERIALS AND METHODS

Study site

Our study was conducted in the Harapan landscape of Jambi Province, Central Sumatra, Indonesia (Figure 1). Three different land use types were investigated: rainforest, smallholder oil palm (*Elaeis guineensis* Jacq.) and rubber (*Hevea brasiliensis* Müll.Arg.) plantations, the study sites were part of the EFForTS project and each land-use type has a plot size of 50 m × 50 m (Barnes et al., 2014; Drescher et al., 2016). We subdivided each plot into a 10 m × 20 m sized area to do the flower enrichment and parasitoid sampling (Figure 2). For each land use, four plots were located in the upland core plot area (Drescher et al., 2016), and four plots were located in riparian area (Paoletti et al., 2018). A total of eight plots were established in each land use system, for a total of 24 study plots. The minimum distance between the plots was 60 m, and the altitudes varied between 9 and 81 m above sea level. The plantation plots were located far from the forest. The age of oil palm plantations was between 10 and 20 years and rubber plantations from 8 to 28 years at the time of sampling. Less intensive plantation management (weeding and fertilisation) was applied in smallholder plantations compared with company estates. Field sampling was conducted from July to November 2017. The study area had a dryer period during July–August, with the highest rainfall during March and December (Drescher et al., 2016). We assumed that this study was conducted during the dry season. The El Nino Southern Oscillation (ENSO) caused hotter and drier seasons in Indonesia, which affected the rainfall on August, September and October (Meijide et al., 2018).

Sampling methods

Insects were collected by direct sampling and traps. Four transect areas of 10 m length and 2 m width were established in the study site (Figure 2). Direct sampling using a sweep net was performed by walking the transect lines for 10 min, along the transect lines (Vaissière et al., 2011). Sweep net was conducted three times to represent the daytimes: morning (09:00–10:00), midday (12.00–13.00) and afternoon (15:00–16:00). To avoid collecting the same species and ensure a better representation of the insect communities, sampling was done in different time windows on different days in each plot. Four yellow

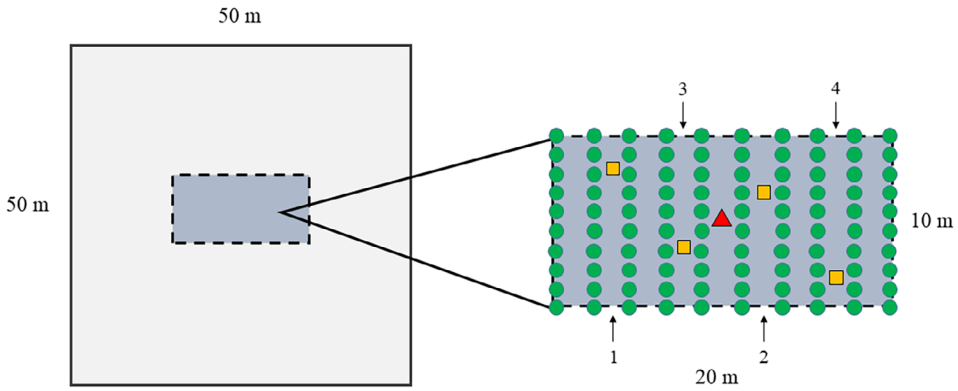


FIGURE 2 Study sites design. A study plot sized 10 × 20 m was established inside the 50 × 50 m sized of EFForTS study plots (Drescher et al., 2016). Green circles indicated flowering vegetation positions, yellow rectangles indicated yellow pan trap positions, and red triangle indicated malaise trap position. Transect walk directions and rows were pointed by the arrows then the numbers indicated the sequences.

pans and one malaise trap were installed in each plot (Figure 2), and all traps were set up in the field for 48 h. All collected specimens were stored in 70% ethanol. We identified the specimen to morphospecies level using common reference literature (Goulet & Huber, 1993; Wharton et al., 1997). Parasitoid wasps were sampled before and after the flowering vegetation enrichment. The second sampling round occurred 2 weeks after flowering vegetation was placed in the plots. The sampling plots and methodologies were the same, both before and after flower vegetation enrichment.

Flowering vegetation enrichment

After completion of the first round of insect sampling, we conducted an enrichment of the flowering vegetation in each study plot. For the enrichment, we used the pan-tropical weedy species *Asystasia gangetica* (*L.*) T.Anderson, which was the most dominant flowering species in our study plots. *A. gangetica* was collected from surrounding plot areas and then planted in the polybag nursery. After 2 weeks in the nursery, the plants were transferred to the study plots. We put 100 plants in each plot with 1 m × 2 m spacing between planted individuals (Figure 2).

Data analysis

The three land use systems and the field enrichment condition (before and after flowering vegetation enrichment), site conditions (upland and riparian) and any possible interactions were chosen as fixed factors in the analyses. Parasitoid wasp abundance and species richness were compared between land-use systems and enrichment conditions using generalised linear models. Pairwise differences were calculated using Tukey's HSD (Honest Significant Difference) multiple comparisons with Holm's correction (Hothorn et al., 2008). The community structure of parasitoid between land use, flowering vegetation and their interaction was compared using permutational multivariate analysis of variance (PERMANOVA) (Vicente-Gonzalez et al., 2022). The community structure of parasitoids was compared between before and after flowering vegetation enrichment in each land-use type based on Bray–Curtis dissimilarities and non-metric multidimensional scaling (Kruskal, 1964). Analysis of similarity (ANOSIM) was performed to test for differences in parasitoid community structure between the land-use types and flowering vegetation enrichment. Pairwise contrasts were performed using pairwise Adonis to detect differences between each land use (Martinez Arbizu, 2020). All analyses were done using R (R Core Team, 2022), with R-package 'vegan' for species richness and beta diversity indices (Oksanen et al., 2022) and visualised using ggplot2 (Wickham, 2016).

RESULTS

Parasitoid wasp diversity

We sampled 5879 individuals from 254 morphospecies of parasitoid wasps in this study. We collected 1798 individuals from 195 morphospecies before the flowering vegetation enrichment experiment. After the flowering vegetation enrichment experiment had been conducted in all plots, we collected 4081 individuals from 232 morphospecies. We sampled a total of 29 families of parasitoid wasps in this study. The family with the highest number of species was Braconidae (species richness = 35), but the most abundant family was Scelionidae ($N = 1196$ parasitoid individuals). Some families were found only in specific land uses, including Dryinidae, Figitidae and Megasipilidae, which were found only in rubber plantations, and Chrysididae, which was sampled only in rainforest. The remaining 25 families were found in all land-use types.

The dominance structure of parasitoid wasp families differed between rainforest and plantation systems (Table 1). Braconidae were most dominant in rainforest, whereas Scelionidae were most dominant in oil palm and rubber plantations. Although the species richness and abundance of parasitoids increased after the flowering vegetation

TABLE 1 Parasitoid wasps family abundance before and after flower vegetation enrichment in different land use types.

	Forest		Oil palm		Rubber		
Family	Before	After	Before	After	Before	After	Total abundance
Aphelinidae	4	31	11	9	4	8	76
Bethylidae	25	36	3	7	3	9	90
Braconidae	151	363	34	43	32	133	804
Ceraphronidae	135	288	68	85	14	272	901
Chalcididae	6	9	12	10	4	8	50
Chrysididae	6	12	0	0	0	0	19
Diapriidae	57	55	39	45	22	77	301
Dryinidae	0	0	0	0	1	1	2
Elasmidae	5	4	3	4	0	5	21
Encyrtidae	37	104	75	73	19	78	402
Eucharitidae	5	14	3	2	2	0	33
Eucoilidae	10	142	3	3	2	52	357
Eulophidae	53	184	123	118	34	191	781
Eupelmidae	3	0	2	7	2	4	21
Eurytomidae	0	2	2	7	1	3	15
Evaniidae	11	11	1	1	0	3	27
Figitidae	0	0	0	0	1	0	1
Ichneumonidae	42	23	48	20	43	34	214
Megaspilidae	0	0	0	0	0	1	1
Mymaridae	15	40	15	24	9	65	179
Mymarommatidae	0	1	1	0	0	1	3
Ormyridae	1	1	2	4	2	2	12
Platygastridae	53	148	27	64	23	76	424
Pteromalidae	43	103	9	20	7	11	213
Scelionidae	129	184	174	253	92	328	1196
Signiphoridae	0	5	0	12	0	59	76
Tiphiidae	1	1	7	4	1	7	21
Torymidae	4	5	4	8	4	6	31
Trichogrammatidae	0	31	14	12	0	16	82
Total	796	1796	680	835	322	1450	6353

enrichment, the dominance structure of parasitoid families remained little changed. Nevertheless, some families were found only after the flowering vegetation enrichment, including Dryinidae, Evaniidae, Megaspilidae and Elasmidae in rubber plantations, Trichogrammatidae and Mymarommatidae in rainforest and rubber plantations, and Signiphoridae in all three land-use systems.

We did not find a significant interaction between land use, enrichment treatments and site conditions to abundance ($F_{2,36} = 0.611$, $p = 0.548$) and richness ($F_{2,36} = 0.658$, $p = 0.524$) of parasitoid wasp. A significant interaction between land use and flowering vegetation enrichment was found for parasitoid wasp abundance ($F_{2,41} = 5.165$, $p = 0.011$) and species richness ($F_{2,41} = 3.330$, $p = 0.047$). The other interactions between land use and site condition (abundance: $F_{2,39} = 2.829$, $p = 0.073$; richness: $F_{2,39} = 1.545$, $p = 0.227$) and enrichment treatment and site (abundance: $F_{1,38} = 1.281$; $p = 0.265$, richness: $F_{1,38} = 1.566$; $p = 0.219$) did not affect parasitoid abundance and species richness. The same result was shown in different site conditions, neither parasitoid abundance ($F_{1,43} = 1.209$; $p = 0.279$) nor species richness ($F_{1,43} = 0.362$; $p = 0.551$).

Parasitoid wasp abundance ($F_{2,45} = 5.297$; $p = 0.005$) and species richness ($F_{2,45} = 6.07$; $p = 0.005$) differed significantly between land-use systems. The highest abundance and species richness of parasitoid wasps were found in rainforest, which was the case both before and after the flowering vegetation enrichment (Figure 3). Rubber plantations had contrasting abundances and species richness of parasitoid wasps compared with rainforest, but not to oil palm plantations. In the unenriched study plots, parasitoid abundance was reduced by 59% in the rubber plantations compared with the rainforest. The same pattern was also found for the species richness. Rainforest conversion to rubber also resulted in

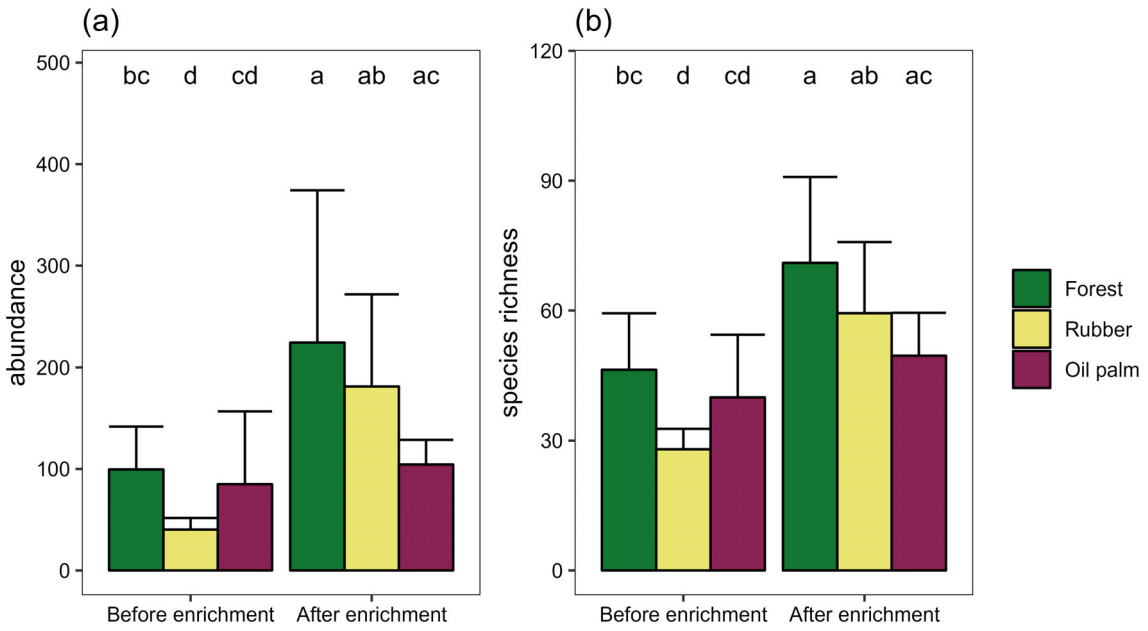


FIGURE 3 Parasitoid wasp (a) abundance and (b) species richness on various land use types and flowering vegetation enrichment conditions.

lower parasitoid species richness, with more than 40% less in rubber plantations but not in oil palm plantations.

Flowering vegetation enrichment altered parasitoid wasp abundance ($F_{1,44} = 41.67$; $p < 0.001$) and species richness ($F_{1,44} = 34.148$; $p < 0.001$). The sampling phase after the enrichment resulted in an increase in parasitoid richness and abundance in all land use types (Figure 3). [Correction added on 08 June 2024, after first online publication: The in-text citation Figure 1 has been corrected to Figure 3]. Rubber plantation had the highest increase of parasitoid abundance with 350% after the enrichment, followed by rainforest with 126%, respectively. A slight increase was only found in oil palm plantations, with a 23% increase in abundance. Even though parasitoid abundance increased strongly in rubber plantations after treatment, overall parasitoid abundance was still highest in forest. The same pattern was found for species richness, which increased by112% in rubber plantations after enrichment, followed by 53% in rainforest, and a slight increase of 24% in oil palm plantations.

Parasitoid wasp species composition

The PERMANOVA showed that the interaction between land use and flowering vegetation enrichment significantly affected to parasitoid wasp composition ($F_{2,42} = 2124$, $R^2 = 0.713$, $p = 0.001$). Land use as a single factor also showed significant effect on parasitoid wasp composition ($F_{2,42} = 4.128$, $R^2 = 0.139$, $p = 0.001$). In addition, the enrichment of flowering vegetation affected the species composition ($F_{1,41} = 5.081$, $R^2 = 0.085$, $p = 0.001$). We exclude the site condition as a factor in species composition analyses because the difference between upland and riparian site condition did not significantly affect parasitoid wasp abundance and species richness. The species composition of parasitoid wasp communities differed between land-use types, both before (ANOSIM, $R = 0.486$; $p = 0.001$) and after ($R = 0.714$; $p = 0.001$) enrichment with flowering *A. gangetica*. Pairwise Adonis test result showed no differences in parasitoid species composition in oil palm and rubber plantations before the enrichment (Table 2). The community structure of parasitoid communities was similar in oil palm and rubber plantations, as indicated by overlapping ellipses, but separated from rainforest (Figure 4). After flowering vegetation enrichment, all three land use types differed significantly in community composition (Table 2), as indicated by the differences in ellipses in each land use type (Figure 4). This means that although flowering vegetation enrichment promoted parasitoid abundance and richness in oil palm and rubber plantations, the resulting communities are not necessarily the same as in rainforest.

Dominating species of some families contributed to differences of parasitoid community structure between land-use types (Figure 4). Dominating species of Scelionidae, Diapriidae, Encyrtidae and Eulophidae on oil palm and rubber plantation contributed to higher similarity of these habitats. In forest, the great abundance of Braconids species contributed to the different community compositions from those in oil palm and rubber plantations. The difference in the parasitoid community structure between forest and monoculture habitats also contributed by the difference in the abundance of Ceraphronidae, Pteromalidae, Platygastridae and Eucoilidae between forest and oil palm or rubber plantation (Table 1).

Venn diagrams depict the number of overlapping species between different land-use types and also the habitat specialist species, henceforth unique species, of parasitoid wasp. Rainforest had much higher number of unique parasitoids than oil palm or rubber plantations both before and after flowering vegetation enrichment (Figure 5). The number of unique parasitoids in the forest increased after the enrichment. Likewise, the number of shared species increased after the enrichment, as suggested also by the higher proportion of shared species among three land-use systems

TABLE 2 Pairwise Adonis test with Bonferroni correction on parasitoid wasp species composition between land-use types before and after flowering vegetation enrichment.

	Before enrichment			After enrichment		
	F_1	R^2	Adjusted p	F_1	R^2	Adjusted p
Forest vs. oil palm	2.940	0.174	0.003	5.760	0.291	0.003
Forest vs. rubber	3.541	0.202	0.003	3.192	0.186	0.006
Oil palm vs. rubber	1.431	0.093	0.108	2.799	0.167	0.006

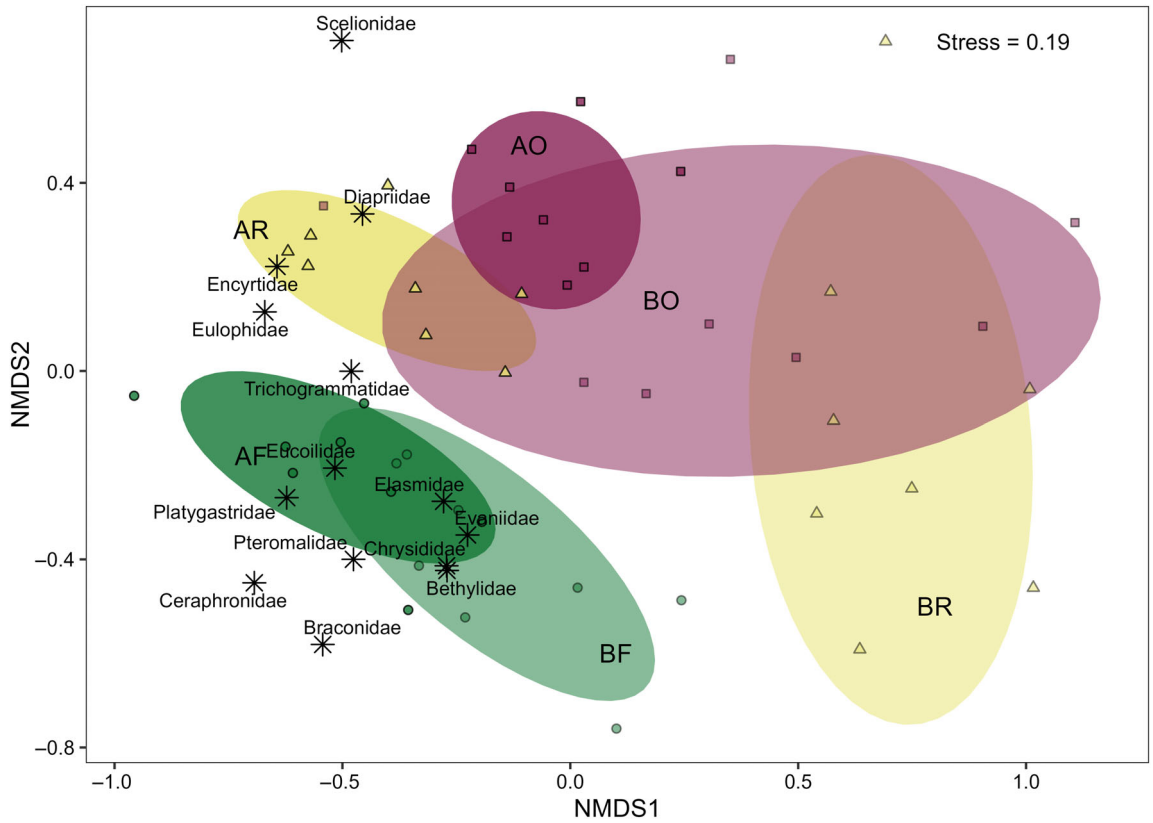


FIGURE 4 NMDS of parasitoid wasp community composition in the three land-uses, before and after the flowering vegetation enrichment, based on Bray Curtis dissimilarity. The most frequent families are shown in asterisks. First letter code indicates: B (faded colours) = before the enrichment; A (bold colours) = after the enrichment. Second letter indicates: F = rainforest (green/circles); R = rubber (yellow/triangles); O = oil palm (magenta/squares). NMDS, non-metric multidimensional scaling.

(Figure 5b). In contrast, the number of exclusive parasitoids in oil palm and rubber plantations decreased after the enrichment. After enrichment, we sampled 59 new species that had not been found in the first round of sampling, which mainly included Braconids species (10 species).

DISCUSSION

The results showed that rainforest transformation altered parasitoid species richness and abundance. Rainforests are richer than oil palm and rubber plantations and harbour more parasitoid wasps (abundance) than other land-use types. This shows that rainforest transformation into plantation agriculture in Indonesia contributes to declining parasitoid wasp diversity. In particular, rubber plantations showed much increased parasitoid richness and a fourfold increase in parasitoid abundance after the enrichment as compared to before. Our study thereby confirms previous findings from Mexico that parasitoid wasp diversity decreases as a result of forest transformation into simpler land use types (Ruiz-Guerra et al., 2015). These findings provide important novel perspectives on conservation of parasitoid diversity and their biocontrol potential in tropical transformation landscapes.

Effects of rainforest transformation on parasitoid diversity

Parasitoid species richness and abundance was highest in rainforest than those on rubber and oil palm monoculture. This may be related to

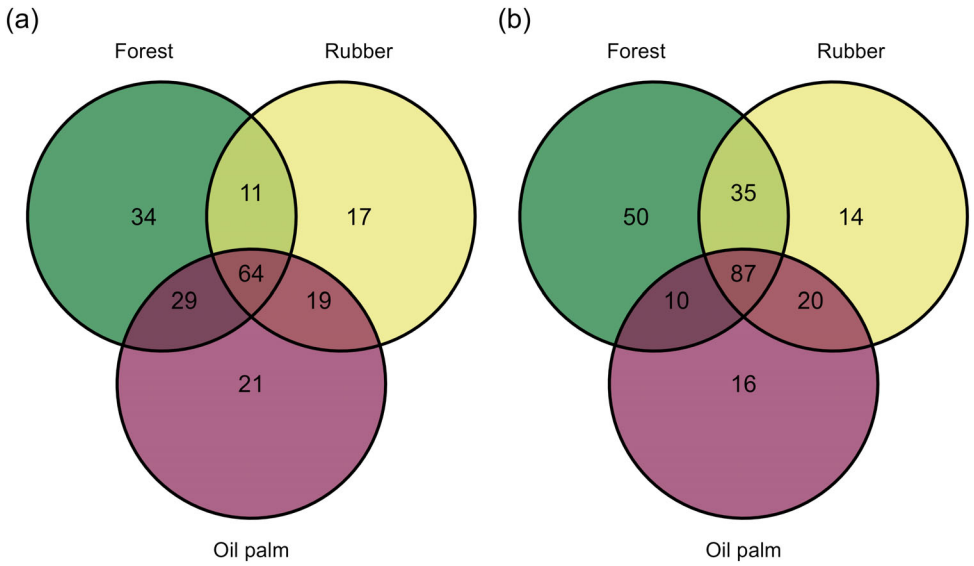


FIGURE 5 Parasitoid wasp species overlapping between different land use systems and flowering vegetation enrichment treatments. (a) Overlapping parasitoid wasp species before the enrichment; (b) overlapping parasitoid wasp species after the enrichment.

the generally much higher plant and herbivore diversity, such as by Lepidoptera and Hemiptera, in rainforest compared with the studied plantation systems (Azhar, Hartke, et al., 2022; Panjaitan et al., 2020; Rembold et al., 2017), which allows for greater niche differentiation and thus higher parasitoid richness and abundance (Rodríguez et al., 2019). Forest plants may also provide a greater variety and amount of floral resources (e.g., nectar) for parasitoids that result in greater parasitoid abundance in forests than in simplified habitats (Kishinevsky et al., 2018). Parasitoid presence often depends on the presence of their hosts (Tylianakis & Binzer, 2014). Hence, we assume that exaggeration of weed and pest control for long periods may further contribute to declining parasitoid populations in these systems. It is strengthened by the studies that showed that parasitoid diversity and food web structure became lower and simpler with increasing oil palm age (Rizali et al., 2023; Sahari et al., 2020). Decreasing in terrestrial parasitoid wasps also in line with previous biodiversity assessment that reported rainforest conversion reduced diversity of biological control agents, such as ants (Nazarreta et al., 2020), spiders (Junggebauer et al., 2021; Potapov et al., 2020) and the multidiversity and multifunctionality in the ecosystem (Grass et al., 2020).

Effect of flowering vegetation enrichment on parasitoid wasp abundance and diversity

We found that, as expected, an increase in parasitoid species richness and abundance occurred in the second round of sampling after flowering vegetation enrichment. Previous research has shown that parasitoids prefer *A. gangetica* to other wildflower plants and that maintaining *A. gangetica* in pepper plantations increased longevity, fecundity and parasitism by the pepper bug parasitoid, *Anastatus dasyni* Ferr (Trisawa, 2011). Maintaining or establishing patches or strips of weedy flowering vegetation in simplified agroecosystems such as the studied oil palm and rubber plantations may result in more suitable microclimate, increased availability of food resources for adult parasitoids and enhanced host availability for parasitoid development (Marino et al., 2006). *A. gangetica* is a common flowering weed in oil palm plantations and is a major contributor to the herbaceous understory biomass particularly at the edges of oil palm plantations (Luke et al., 2019). Therefore, management practices that promote this species, particularly at plantation edges (e.g., through manual weeding instead of chemical herbicides application (Darras et al., 2019)), could promote habitat for parasitoids and attract them to plantations. Thus, increasing resource availability by establishing strips of weedy vegetation is thus an efficient way to mitigate the decline of parasitoids in simplified agricultural systems and may foster their biological pest control services alike. The presence of *A. gangetica* in this study showed that common vegetation surrounding the plantation area could be considered to support parasitoid communities in the plantation system. In general, using native trees (Zemp et al., 2023) and flowers (Muñoz et al., 2021), monoculture plantations could support beneficial insects that provide ecosystem services and local biodiversity.

We realise that our enrichment experiment could not fully explain the effect of flowering vegetation on parasitoid wasp abundance and species richness. The enrichment was performed at different times than the natural condition, so temporal variability of parasitoid wasps was likely to occur. Temporal variability of parasitoid activity was influenced by seasonal variability, host density and host community (Elizalde et al., 2018; Scheiner & Martin, 2020). Despite the significant effect of flowering vegetation enrichment on parasitoid wasp abundance and diversity in this study, we are unable to claim that this flowering plant species fully mitigates the loss of parasitoid wasp diversity.

Species composition of parasitoids

We also found that parasitoid species composition was different between forest and monoculture habitats. Generally, rubber and oil palm plantation had similar parasitoid species composition, indicating that, in particular, the loss in vegetation complexity with rainforest transformation contributed towards changes in species composition, with similar outcomes in both plantation systems. The low similarity of species composition was contributed to the difference in dominant parasitoid families between land-uses. Oil palm and rubber had more open canopy than forest (Junggebauer et al., 2021), which may explain the domination of Scelionidae that are known to prefer open and sunny areas (Masner, 1993). In contrast, Braconidae was the most dominant family that was found in the forest possibly driven by their species-specific preference on specific hosts (Hrcek et al., 2013). These findings confirm those by Shaw (2006) who found that habitats with high vegetation complexity support specialist parasitoids and oligophage herbivores as hosts.

The higher number of unique species that can only be found in rainforest contributed to the differences in species composition between land-use types. Rainforest harboured the highest number of habitat specialist species than that on the monoculture plantations. The result was similar to previous studies in plants (Rembold et al., 2017), ants (Kreider et al., 2021; Nazarreta et al., 2020) and butterfly (Panjaitan et al., 2020). The decline of unique species reflects the vulnerability of these parasitoid species to rainforest conversion to monoculture plantations. Our experimental flower vegetation enrichment strongly modified species composition and community differences between land-use types. In fact, community composition of parasitoid wasp within study sites either in oil palm or rubber plantations became even more similar than before. This may be explained by increasing abundance of common parasitoid species occurring both in oil palm and rubber plantations. For example, some species from Scelionidae, that is, *Trissolcus* spp., *Eumocrosoma* sp. and *Telenomus* spp., increased on both sites. In contrast, the differences in community composition between forest and plantations became even stronger after the flowering vegetation enrichment (Supporting Information S3). This may be related to the positive effect on unique parasitoids species that are restricted to natural forests especially species from Braconidae, which increased higher after flower vegetation enrichment in forest than other land-use type.

Flowering vegetation enrichment contributed in conservation biological control since the important parasitoid became more abundant on monoculture habitats than the control condition. We found that the abundance of Braconidae, Chalcididae and Eulophidae increased after flowering vegetation enrichment was applied in rubber and oil palm plantation. Species that belongs to Braconidae such as *Dolichogenida metesae* (Nixon), *Aulosaphes psydivorus* Muesebeck and *Apanteles* spp., and the *Brachymeria* spp. and *Peidobius* spp. which part of Chalcididae and Eulophidae, known as importance parasitoid since they could provide essential services to decrease bagworm population in oil palm plantations (Cheong et al., 2010; Halim et al., 2018).

Finally, rainforest is irreplaceable in maintaining higher parasitoid wasp abundance, richness and preserving genuine species, which it holds vital part in conservation biological control. Rainforest conversion to profitable cash crop plantations causes strong losses of parasitoid wasp diversity. Thus, integrating land-sparing and land-sharing approaches by protecting the natural rainforest as biodiversity source and by providing flower strips or cultivating native trees in monoculture plantation to increase its habitat complexity and quality (Grass et al., 2019; Zemp et al., 2023), can potentially promotes biodiversity and biological control in tropical agricultural landscapes.

CONCLUSIONS

This study compares the diversity and community of parasitoid wasps in the transformation land-use systems from tropical rainforest to managed smallholder oil palm and rubber plantations. The results reported here show that rainforest transformation strongly affects parasitoid diversity and community compositions. Our study confirmed our hypothesis that rainforest transformation to monoculture plantations leads to a decline in the abundance and species richness of terrestrial parasitoid. This decline is likely caused by the loss of food resources and host availability. In addition, community composition of parasitoid wasps changed with rainforest conversion to oil palm and rubber plantations, in particular driven by the loss of tropical rainforest habitat specialists. Our experimental enrichment with flowering vegetation suggests that parasitoid diversity can be at least partially restored. However, as the experiment was conducted after initial sampling, confounding the effects of enrichment on parasitoids over time, follow-up experiments are needed, also to establish the mechanisms linking flower resources to parasitoid communities in rainforest transformation landscapes. Our study highlights the great importance of rainforest for parasitoid conservation and the provisioning of ecosystem services, in particular biological control.

AUTHOR CONTRIBUTIONS

Azru Azhar: Writing – original draft; methodology; conceptualization; writing – review and editing; visualization; software; formal analysis; data curation; investigation. **Ingo Grass:** Writing – review and editing; validation; investigation. **Akhmad Rizali:** Conceptualization; investigation; methodology; validation. Investigation; conceptualization; funding acquisition; validation; supervision; resources. **Pudjianto:** Investigation; conceptualization; funding acquisition; validation; supervision; resources. **Damayanti Buchori:** Conceptualization; investigation; funding acquisition; methodology; validation; project administration; supervision; resources.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Göttingen Research Online Data Repository at https://doi.org/10.25625/HKKCDA.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Supporting Information.

Figure S1. Species accumulation curve of parasitoid from various sampling methods.

Supporting Information S2. Observed and estimated species richness (based on ACE value) in different land use type.

Supporting Information S3. Dissimilarity of parasitoid species (Bray-Curtis index) between different land use types and treatment.

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