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Effects of biodiversity enrichment in oil palm monocultures on pollinator diversity

Master of Science
Faculty of Agricultural Sciences
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Study focus: Resource management

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Abstract

Tropical forests harbour the highest levels of biodiversity worldwide, yet they are converted to oil palm monocultures on a daily basis. Recently, biodiversity enrichment of oil palm monocultures has been proposed as means of restoring biodiversity and ecosystem functions. Animal-mediated pollination is an important ecosystem function that plays a key role for wild plant reproduction and crop production. To date there is little knowledge on the effects of biodiversity restoration through biodiversity enrichment on pollinator communities and plant-pollinator interaction networks in oil palm plantations.

In this project, I studied the effects of biodiversity enrichment in oil palm monocultures on pollinator communities. Using sweep netting and pan traps, I assessed pollinator diversity and plant-pollinator interaction networks on 52 study plots with biodiversity enrichment through planted tree species. The plots differed in their area (25 m² - 1600 m²) and number of tree species (1 – 6 tree species).

Biodiversity enrichment successfully increased pollinator richness compared to monoculture oil palm. In particular, stand structural complexity and high canopy openness rather than enrichment area or tree diversity positively influenced pollinator diversity. In addition, variation in species composition could be attributed to differences in stand structural complexity, and the spatial position of enrichment plots. Furthermore, biodiversity enrichment led to more complex plant-pollinator interaction networks as compared to monoculture oil palm due to positive effects of enrichment area and tree diversity.

My study demonstrates that biodiversity enrichment through native tree planting is a promising approach for restoring pollinator diversity and plant-pollinator interactions in monoculture oil palm plantations. Thus, my findings could guide management recommendations for sustainable oil palm landscape that are in line with a land-sharing approach to reconcile agricultural production with biodiversity-enriched oil palm plantations.

INTRODUCTION

South-East Asia has undergone the fastest and most complete transformation of tropical lowland rainforest (Fitzherbert et al. 2008). In particular, the massive transformation of lowland rainforest into monoculture oil palm plantations has been identified as a major threat for biodiversity (see Yaap et al. 2010, Wilcove and Koh 2010, Foster et al. 2011, Drescher et al. 2016), and a potential driver of climate change (Danielsen et al. 2009). Indonesia and Malaysia have approximately 14.5 million ha under oil palm production (Foster et al. 2011).

Furthermore, pollination which is an important ecosystem function is jeopardized (Sodhi et al. 2004, Wilcove et al. 2013, Edwards et al. 2014). Animal-mediated pollination plays a key role for the sexual reproduction of 88 % of global angiosperm plant species and 70 % of the major global crop species (Klein et al. 2007, Ollerton et al. 2011). Yet, pollinators suffer from substantial losses induced by habitat loss, altered land use, alien species, and climate change (Danielsen et al. 2009, Schweiger et al. 2010, Potts et al. 2010). Threats from habitat loss are especially high in tropical areas (Sodhi et al. 2010, Foster et al. 2011).

Palm oil is of worldwide economic value (Koh and Wilcove 2007, Koh and Ghazoul 2008), therefore policy makers and researchers must find a way of merging economic interests with biodiversity conservation and management options (see Foster et al. 2011; Koh et al. 2009; Green et al. 2005).

The principle of *ecological restoration* has gained in importance for over a decade (Aronson et al. 2006). It is applied to recover ecosystems (Sala et al. 2000), to re-establish biodiversity, and ecological function (Aradottir and Hagen 2013), or to mitigate biodiversity loss (Kaiser-Bunbury et al. 2017). In a meta-analysis Rey Benayas et al. (2009) discovered the impact of ecological restoration, especially in tropical terrestrial ecosystems. In addition, well managed agroecosystems hold ecological assemblages and are comparable to unmodified habitats (Tylianakis et al. 2007). Meanwhile, there are rarely quantitative studies on ecological restoration (Kaiser-Bunbury et al. 2017).

Koh et al. (2009) introduced the concept of the so called *designer landscapes* associated with ecological restoration. Agroforestry zones enhance ecological conservation and socio-economic benefits while reducing negative impacts of oil palm monocultures. Agroforests obtain similar biodiversity as natural forests (Tylianakis et al. 2005, 2006, 2007). The idea is to restore biodiversity in intensively managed oil palm monocultures through biodiversity enrichment (Teuscher et al. 2016). Furthermore, these tree islands offer areas of recovery or recruitment to enhance biodiversity (Yarranton and Morrison 1974, Corbin and Holl 2012). Meanwhile, the introduction of tree islands results in fragmentation discussions, in which size of enrichment areas (Benedick et al. 2007, Öckinger et al. 2010, Bommarco et al. 2010) and number of planted native tree species are the key questions (Thomas 2000, Zahawi and Augspurger 2006, Franzén and Nilsson 2010). In general, species richness decreases and composition shifts with increasing habitat loss and fragmentation (McKinney and Lockwood 1999, Henle et al. 2004).

There is little knowledge about the effects of biodiversity enrichment as means of ecological restoration in oil palm monocultures (Turner et al. 2008, Foster et al. 2011, Teuscher et al. 2016), especially on pollinators and plant-pollinator networks (Kaiser-Bunbury et al. 2017, Dislich et al. 2017). To specifically address this knowledge gap, I studied pollinators. Pollination is not only an important factor to be reinstated for successful ecological restoration, but can be seen as its bio-indicator (Forup et al. 2007). Furthermore, the restoration of plant-pollinator assemblages is crucial for an ecosystem to be restored (Kaiser-Bunbury et al. 2017). Moreover, plant-pollinator interactions are only restored when habitat requirements have been met for pollinators (Gathmann and Tscharntke 2002). I analysed effects of biodiversity enrichment on insect diversity, and species composition and conducted a plant-pollinator network analysis within agroforestry patches in oil palm monocultures (Koh et al. 2009). Specifically, I studied the effects of enrichment through enrichment area and interactions with other environmental values, such as tree diversity, canopy openness, or stand structural complexity. Biodiversity data were collected using two sampling methods (pan traps and sweep netting). My hypotheses are: (1) Biodiversity enrichment restores pollinator diversity with larger enrichment areas and higher planted tree diversity both increasing pollinator richness, (2) species composition homogenizes with increasing fragmentation and poorer enrichment, and (3) plant-pollinator interaction networks become more complex with greater enrichment area and tree diversity.

METHODS

Study region and sites

I conducted my study within the framework of the collaborative project EFForTS in the subproject Biodiversity Enrichment Experiment (BEE-B11). The subproject is located in PT. Humus Indo Makmur Sejati (01.95° S and 103.25° E) in the Bungku regency in the lowlands of Jambi province, Sumatra. The overall aim of this subproject is to discern the potentials of different degrees of diversification and enrichment area on selected ecosystem functions in order to identify sustainable oil palm management options (Teuscher et al. 2016). PT. Humus Indo is a commercial medium-scale monoculture oil palm producer, with 2.8 ha area at 47 ± 11 m above sea level and a humid tropical climate. In 2013, 52 study plots were partially cleared (40 %) from oil palm and subsequently planted with multipurpose tree species (Figure 1).

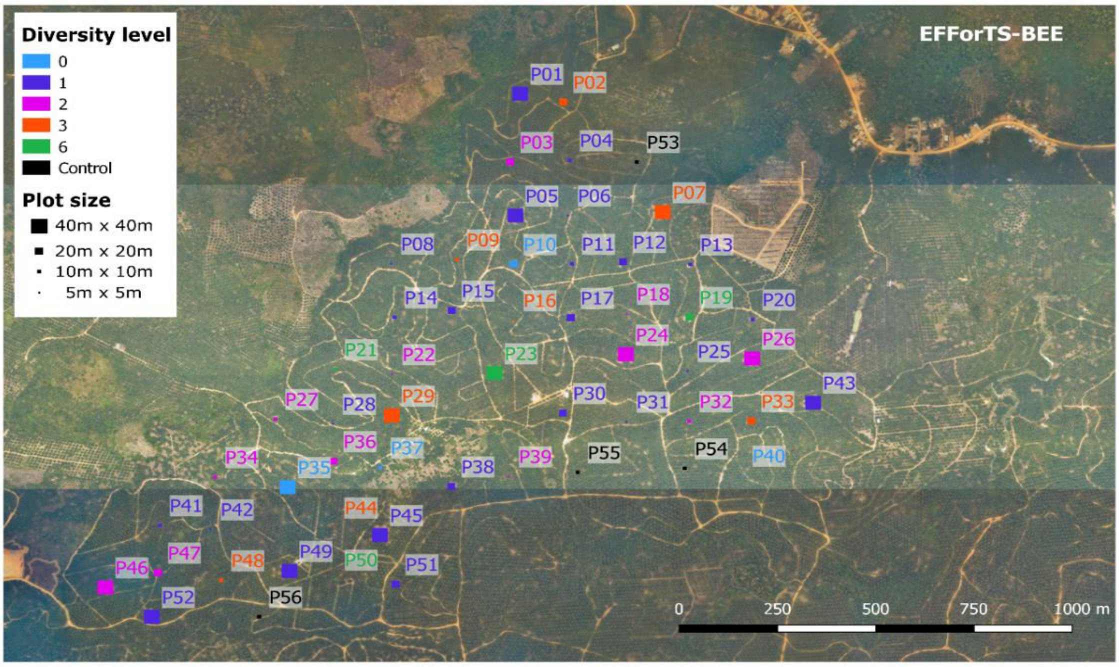

Figure 1: EFForTS-BEE (B11) subproject in PT. Humus Indo in the Bungku Regency. The experimental design randomly distributes 56 plots, whereat 52 are enriched with indigenous tree species and four remain as control plots. The enrichment plots differ in area (Plot size) and tree diversity (Diversity level). The different colours illustrate the tree diversity and the area differences are shown by varying square sizes (f.ex. P01 has 40 x 40 m and one tree species). All control plots are 10 x 10 m and remain unchanged with 'work-as-usual'. For some plots the tree diversity is zero (f.ex. P10). However, here, 40 % of oil palm trees were cut out, too, not to be confused with the control plots.

A random partitions design (Bell et al. 2009) was used that combined variation in enrichment area (plot size) and planted tree species (see Teuscher et al. 2016). The distance between the plots with the same enrichment area was maximized. Four sizes with 13 replicates each were used for enrichment areas: 5 x 5 m, 10 x 10 m, 20 x 20 m, 40 x 40 m. In addition, six native multi-purpose (either fruit, timber, or natural latex) tree species (*Parkia speciosa* (Fabaceae), *Archidendron pauciflorum* (Fabaceae), *Durio zibethinus* (Malvaceae), *Peronema cansescens* (Lamiaceae), *Shorea leprosula* (Dipterocarpaceae)), and *Dyera polyphylla* (Apocynaceae)) were planted. Here, tree diversity varied between zero (four replicates), one (24 replicates), two (12 replicates), three (eight replicates) and six (four replicates) planted tree species. Since December 2013, herbicides and fertilizer were prohibited and since May 2016, mechanical weeding was restricted to a small range around palms or small trees inside the enrichment areas. Oil palm leaves were cut as well as fruits were harvested. Four control plots remained unchanged.

Experimental design

I conducted the fieldwork during the rainy season between the end of October 2016 and the end of January 2017. In every plot, I marked five transects with 1 x 5 m each with the same geographic orientation and design (Figure 2).

Figure 2: Experimental design in PT. Humus Indo: 1) Plot 23 with 20 x 20 m in aerial view and infrared by Florian Ellsäßer (CRC990, subroject A02), modified with transects in 'N' shape, 2) control plot with design of five transects, as well as the schematic drawing of the pan traps, placed in transects 2 and 4, and 3) picture of the pan trap construct. All transects were 1 x 5 m and equally (with same distances between each transect) allocated respectively to enrichment area. (Pictures 2) and 3) by Isabelle Arimond)

Transects were organized as an 'N' shape with the same distances among them according to enrichment area. The smallest enrichment area was 25 m², and thus applied for all other enrichment areas to be statistically comparable.

Survey of plant species and flower cover

For all plots, I identified plant species (Rembold et al. 2017) and specifically counted flower units in order to analyse the flower cover inside transects. The higher the flower cover, the more pollinators were attracted due to greater foraging resources (Aleixo et al. 2017). I also assessed the vegetation cover for each plot as well as the percentage of every plant species in each plot. Zemp (CRC990, subproject B11) recorded stand structural complexity taken with a laser scanner (Ehbrecht et al. 2017) and canopy openness by hemispherical photographs (Jupp et al. 2008). Stand structural complexity values describe the number of structural attributes and their abundance inside a habitat.

Biodiversity enrichment effects on pollinator diversity

Insects, most importantly pollinators, were sampled using pan traps placed in the enrichment areas. Many studies have shown Lepidoptera and Diptera to contribute to pollination, thus are included (Potts et al. 2010, Inouye et al. 2015, Orford et al. 2015, MacGregor et al. 2015). Each plot was sampled three times with six traps per plot exposed for 45 hours (Figure 2). Traps were fixed in a holding system next to each other at the height of the surrounding plants, in order to blend in with the adjacent vegetation. For the traps, I used white plastic soup bowls covered with yellow UV spray-paint, hence mimicking a flower to attract pollinators (Westphal et al. 2008). The traps were filled with water and one drop of regular soap in order to capture insects. Subsequently, I identified all individuals to higher taxonomic groups. All hymenopterans were further identified to family and morphospecies, and categorized into functional groups (pollinators, predators, parasitoids) using different identification keys (Vecht 1957, Bohart and Menke 1976, Yamane 1990, Goulet and Huber 1993, Carpenter and Nguyen 2003, Choate 2011, Engel 2012).

Ecological restoration effects on plant-pollinator-networks

I collected pollinators between 8am and 5pm using sweep nets, only considering insects that sat on open flowers. Each plot was sampled two times with five transect walks each. In the first round, I began with plot 1, following the random design. In the second round, I switched the order and started from the back as well as shifting the plots from mornings to afternoon in order to prevent weather bias. The sweep net is suitable for all flying insect over one mm. Ants were collected by directly picking them off the flower into tubes. Even though ants or wasps are historically seen as predators (“thieves”) (Faegri and Van Der Pijl 1979), they are shown to have pollination qualities (Molbo et al. 2003). After the flower survey, as well as the weather survey, transects were always conducted by the same person with least possible movement for five minutes. The timer was paused while preserving individuals. For their determination I used Ethylene Acetate, and for conservation 70 % alcohol. Identification took place as described above.

Statistical analyses

In order to identify the effects of biodiversity enrichment on insect diversity, as well as species richness within hymenopteran functional groups (pollinators including Lepidoptera, predators and parasitoids), I used Poisson error distributed fitting generalized linear models (GLMs). Species richness was the dependent variable. I tested enrichment area and different environmental values, such as tree diversity, canopy openness, or stand structural complexity, as explanatory variables. I also tested for interactions between environmental values and enrichment area. Confidence intervals were included in all graphs. Moreover, I used non-metric multidimensional scaling (NMDS) to test if the hymenopteran families differed due to enrichment area, tree diversity, geographic location, or stand structural complexity.

In addition, I conducted plant-pollinator network analyses, in order to identify the effects of biodiversity enrichment on the complexity of these interaction networks. Furthermore, specialisation was measured with H2’ (Dormann et al. 2009) and nestedness of interactions (Bascompte et al. 2003). The H2’ and nestedness were then tested in a null model against 1000 random values (community networks), to verify if the real community differed from randomized communities. Using R^2 I tested for correlation between floral abundance and the number of flower visitor species.

I analysed data from two sampling methods, pan traps and sweep netting, performed in R version 3.4.3. (R Core Team 2017) using the packages “vegan” (Oksanen et al. 2018) for generalized linear models, as well as NMDS with the metaNMDS function, and “bipartite” (Dormann et al. 2008) for network analyses. Models and interaction networks were presented with packages “effects” (Fox 2003) and “RColorBrewer” (Neuwirth 2014).

RESULTS

Survey of plant species and flower cover

Figure 3: Most frequent flower species in PT. Humus Indo. A flower survey was conducted within all transects in each plot. The most abundant flower species are a) *Asystasia gangetica*, b) *Clidemia hirta*, c) *Ageratum conyzoides* and d) *Mikania micrantha*. Furthermore, *Asystasia gangetica* was the most frequent flowering plant species.

The plant survey delivered 67 plant species in total, whereof 23 plants actually flowered Table A1. The most abundant plant species were a) *Asystasia gangetica* (3353 floral units), b) *Clidemia hirta* (1033 floral units), c) *Ageratum conyzoides* (127 floral units), and d) *Mikania micrantha* (76 floral units), illustrated in Figure 2. Both, abundances of *Asystasia gangetica* and *Clidemia hirta* largely set themselves apart from all other flowering plant species. The weather during sampling varied from sunny to cloudy with temperatures between 20.8 °C to 37.1 °C, as well as the rainfall between 0 mm to 12.9 mm during the day and max 19.1 mm at night (Data from Z02 subproject within CRC990). Furthermore, plots with slopes / hillsides showed signs of erosion and flooding (observation by Isabelle Arimond).

Biodiversity enrichment effects on pollinator diversity

In general, I collected 20375 insects resulting in 991 different morphospecies corresponding to 14 insect orders. The six insect orders with the most morphospecies were Hymenoptera (500) Hemiptera (120), Coleoptera (95), Araneae (82), Lepidoptera (60), and Diptera (56). A total of 1630 hymenopteran individuals were collected, representing 30 families. The five most abundant families were Formicidae (631), Halictidae (219), Encyrtidae (152), Scelionidae (110), Trichogrammatidae (89). The hymenopteran functional groups with most individuals were pollinators (Lepidoptera included) (1584), predators (814), and parasitoids (586). Further information on species richness respectively to tree diversity and enrichment area are presented in Table A2.

Figure 4 presents species richness for a) and b) Hymenoptera, c) Diptera and d) Lepidoptera depending on different environmental factors.

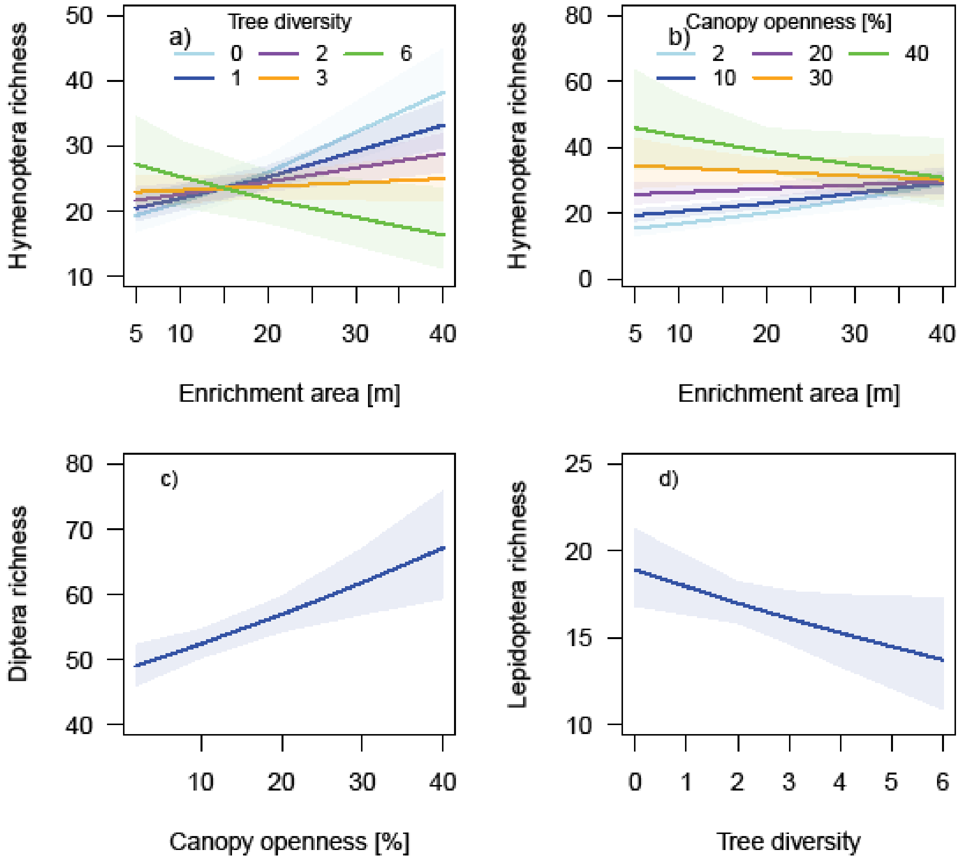

Figure 4: GLM results for models on changes in insect species richness (SR): a) Hymenoptera richness in relation to interactions between tree diversity and enrichment area [m] and b) interactions between canopy openness [%] and enrichment area [m], c) Diptera richness in relation to canopy openness [%] and d) Lepidoptera richness in relation to tree diversity. In a) the Hymenoptera richness shows no difference of tree diversity at small scale. However, it has a negative effect at big scale (40 x 40m) for a high tree diversity, but an increase for zero planted tree species. In b) a high canopy openness shows a significantly higher Hymenoptera richness at small scale than with low canopy openness, while showing no difference at big scale. The Diptera richness increases with canopy openness (c). In d) the tree diversity shows a negative effect on Lepidoptera richness. All graphs (a, b, c, d) present significant results (see Table 1).

Hymenoptera richness showed a significant negative effect for the interaction of a) enrichment area and tree diversity (Z = -3.7, $P < 0.001$) and b) enrichment area and canopy openness (Z = -2.7, $P = 0.006$). Species richness for low enrichment was significantly higher with big enrichment area, whereas for small areas highest enrichment was favoured. In contrast, high canopy openness had significantly higher species richness increases at small scale, while showing no difference at big scale. While the interaction in a) and b) had negative effects, Table 1 shows that only tree diversity (Z = 2.5, $P < 0.05$) or canopy openness (Z = 4.7, $P < 0\ .001$) significantly increased species richness. Furthermore, stand structural complexity had a significant negative effect on species richness, thus Hymenoptera favoured a less structural complex habitat. Diptera richness significantly increased with canopy openness (c) (Z = 2.8, $P = 0.005$). In d) the tree diversity shows a significant negative effect on Lepidoptera richness (Z = -2.7, $P = 0.007$). Table 1 shows the significant results, thus for Hymenoptera only enrichment area or the interaction of enrichment area and stand structural complexity were not significant, while Diptera and Lepidoptera were not significantly influenced by most environmental factors.

In addition, other insect orders were significantly influenced by biodiversity enrichment (Figure A1). In a) Hemiptera richness shows a negative significant effect of the interaction of stand structural complexity and enrichment area (Z = -2.682, $P < 0.01$). However, for big scale and low stand structural complexity Hemiptera richness was highest. In b) Coleoptera richness increases significantly (Z = 2.0, $P < 0.05$) with canopy openness. In c) Araneae richness demonstrates significant lower richness with increasing enrichment area.

Table 1: GLM results for models on changes in species richness (SR) (see Figure 4): Statistical results for a) Hymenoptera richness depending on interactions between enrichment area with tree diversity or canopy openness, b) Diptera richness depending on canopy openness and c) Lepidoptera richness depending on tree diversity. Note, that all values in bold print are significant results (min p < 0.05). For Hymenoptera richness, only the significant interactions are highlighted in Figure 4. Thus it is still to mention a significant negative effect of stand structural complexity (SSC), as well as a significant positive effect only considering tree diversity and canopy openness.

	Hymenoptera richness				**Diptera richness**				**Lepidoptera richness**			
	Estimate	SE	Z	P	Estimate	SE	Z	P	Estimate	SE	Z	P
Enrichment area	0.015	0.013	1.120	0.263	0.006	0.009	0.668	0.504	0.009	0.016	0.528	0.598
Tree diversity	**0.085**	**0.034**	**2.543**	**0.011**	-0.005	0.023	-0.193	0.847	**-0.122**	**0.045**	**-2.717**	**0.007**
SSC	**-0.165**	**0.072**	**-2.298**	**0.022**	-0.076	0.048	-1.582	0.114	-0.116	0.086	-1.348	0.178
Canopy openness	**0.032**	**0.007**	**4.653**	**< 0.001**	**0.013**	**0.005**	**2.810**	**0.005**	0.013	0.008	1.653	0.098
Enrichment area x tree diversity	**-0.006**	**0.002**	**-3.682**	**< 0.001**	-0.001	0.001	-0.948	0.343	0.004	0.002	1.872	0.061
Enrichment area x SSC	0.003	0.003	1.258	0.208	0.001	0.002	0.663	0.507	-0.004	0.003	-1.086	0.278
Enrichment area x canopy openness	**-0.001**	**0.000**	**-2.728**	**0.006**	0.000	0.000	-1.379	0.168	0.000	0.000	1.327	0.185

Next, Figure 5 demonstrates model results for species richness of the functional groups. All statistical values are presented in Table 2. Parasitoids and predators had significant interactions, while pollinators only had single environmental values that were significant. First, the interaction of enrichment area and a) tree diversity (Z = -4.4, $P < 0.0001$) had significant negative, and b) stand structural complexity (Z = 2.3, $P < 0.05$) significant positive effects on parasitoid richness. In a) species richness shows a decrease for increasing enrichment area and tree diversity, while at big scale the highest species richness was achieved with no trees planted. For 25 m² the highest enrichment had highest species richness. Regarding species richness in b) high stand structural complexity and big scale were best. Not taken into account in the graphs, but still important was the significant positive impact of tree diversity on parasitoid richness (Z= 4.1, $P < 0.0001$).

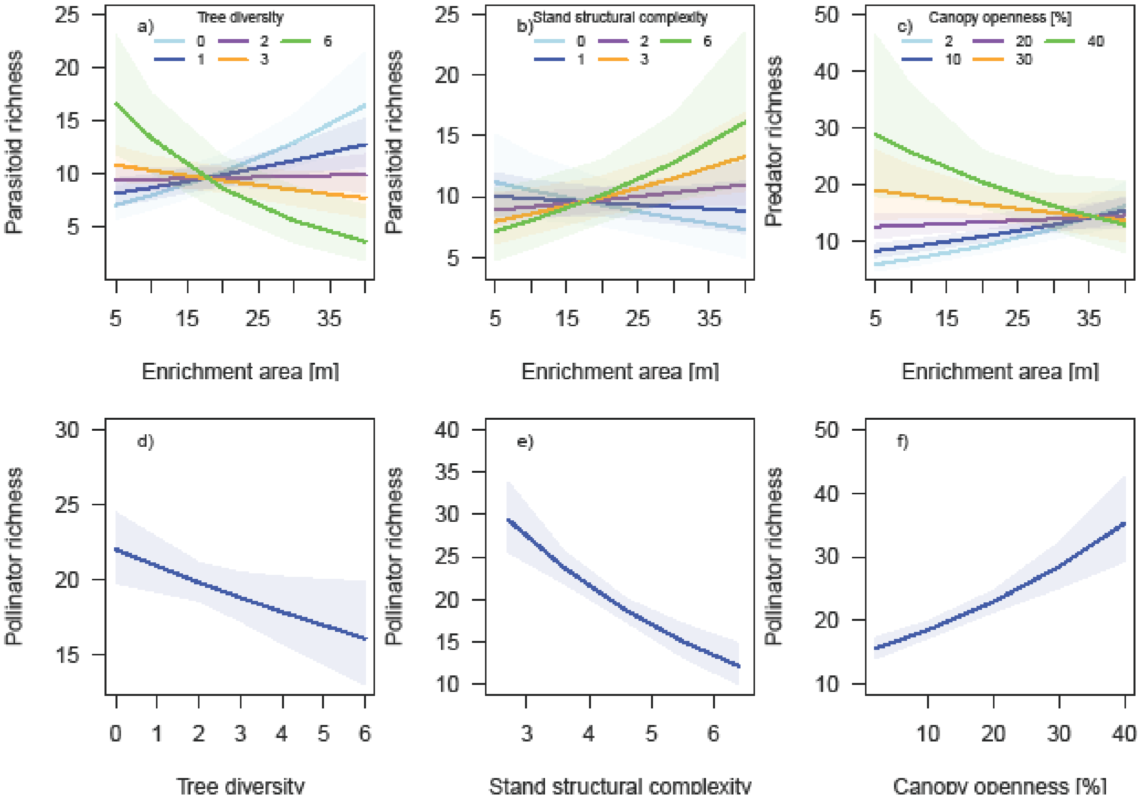

Figure 5: GLM results for models on changes in species richness (SR) of functional groups: pollinators, predators and parasitoids. All Hymenotpera and Lepidoptera species are included. First, parasitoid richness is shown in relation to a) interactions between tree diversity and enrichment area [m] and b) interactions between SSC and enrichment area. Next, c) presents predator richness in relation to the interaction between canopy openness [%] and enrichment area. Last, pollinator richness dependent on d) tree diversity, e) SSC and f) canopy openness is demonstrated. In a) the interaction of tree diversity and enrichment area show no difference at small scale, however a negative effect on big scale, while zero planted tree species suggests highest richness. For the interaction between SSC and enrichment, parasitoid richness shows no difference at small scale, but increases with enrichment area (b). In c) predator richness is highest for the interaction of high canopy openness and lowest scale, while there is no difference with at big scale. Pollinator richness significantly decreases with d) tree diversity, and e) SSC, while in f) significantly increases with canopy openness. All graphs (a, b, c, d) present significant results (Table 2).

In c) predator richness shows significant negative effects of the interaction of canopy openness and enrichment area (Z = -3.3, *P* < 0.001). Low scale showed significant differences in species richness from high to low canopy openness, while at big scale it could not be distinguished. In addition, considering enrichment area (Z = 2.0, *P* < 0.05) and canopy openness (Z = 4.6, *P* < 0.0001) individually, they showed positive significant effects on predator richness. Last, d) tree diversity (Z = -2.5, *P* < 0.05), and e) stand structural complexity (Z = -2.1, *P* < 0.05) had significant negative, and f) canopy openness (Z = 1.99, *P* < 0.05) significant positive effects on pollinator richness. Here, no interaction with enrichment area reached significance.

Furthermore, all significant interactions (Figure A2), as well as single impacts (Figure A3) of Hymenopteran families are presented. These family specific findings support the results presented in functional groups. Parasitoids were presented through significant impacts of interactions between enrichment area and other environmental values on a) Scelionidae and b) Encyrtidae richness. In addition, Mymaridae richness was significantly influenced by tree diversity (Figure A3 (b)). Parasitoid family richness decreased with tree diversity and canopy openness, but increased with stand structural complexity and enrichment area. Here predators were d) Formicidae, e-g) Mutillidae, h) Pompilidae, and i) Vespidae. Canopy openness tend to be more important at small scale, while no planted tree species were more important at big scale. Stand structural complexity influenced predators contrasting in small scale with low complexity to big scale with high complexity. However, all presented significant interactions showed strongly overlapping confidence intervals, which can partly be based on low abundances within each family. For pollinators, Halictidae richness showed significant negative effects of stand structural complexity, and also had no significant interaction.

Table 2: GLM statistical results for models on changes in species richness (SR) of functional groups (see Figure 5): Note, that all values in bold print are significant results (min p < 0.05). For parasitoid and predator richness, only the significant interactions are highlighted in Figure 5. However, parasitoid richness significantly increases with tree diversity and predator richness significantly increases with enrichment area and canopy openness, while pollinators have no significant interactions.

	Parasitoid richness (a-b)				**Predator richness (c)**				**Pollinator richness (d-f)**			
	Estimate	SE	Z	P	Estimate	SE	Z	P	Estimate	SE	Z	P
Enrichment area	-0.012	0.020	-0.610	0.542	**0.040**	**0.020**	**2.018**	**0.044**	0.012	0.015	0.781	0.435
Tree diversity	**0.199**	**0.049**	**4.068**	**<0.0001**	-0.012	0.054	-0.215	0.830	**-0.102**	**0.041**	**-2.488**	**0.013**
SSC	-0.169	0.107	-1.585	0.113	-0.046	0.109	-0.421	0.674	**-0.170**	**0.081**	**-2.102**	**0.036**
Canopy openness	0.018	0.011	1.675	0.094	**0.048**	**0.011**	**4.613**	**<0.0001**	**0.015**	**0.007**	**1.987**	**0.047**
Enrichment area x tree diversity	**-0.011**	**0.003**	**-4.364**	**<0.0001**	-0.002	0.002	-0.860	0.390	0.003	0.002	1.456	0.145
Enrichment area x SSC	**0.010**	**0.004**	**2.309**	**0.021**	-0.001	0.004	-0.272	0.786	-0.004	0.003	-1.154	0.248
Enrichment area x canopy openness	-0.0004	0.0004	-0.823	0.410	**-0.001**	**0.000**	**-3.270**	**0.001**	0.0004	0.0003	1.179	0.238

Biodiversity enrichment and species composition

Further information on species composition of hymenopteran families were produced by NMDS, where the community composition is shown dependent on enrichment area (size of the dots according to enrichment area), tree diversity (different colours describe the six enrichment levels) and other environmental factors (Figure 6).

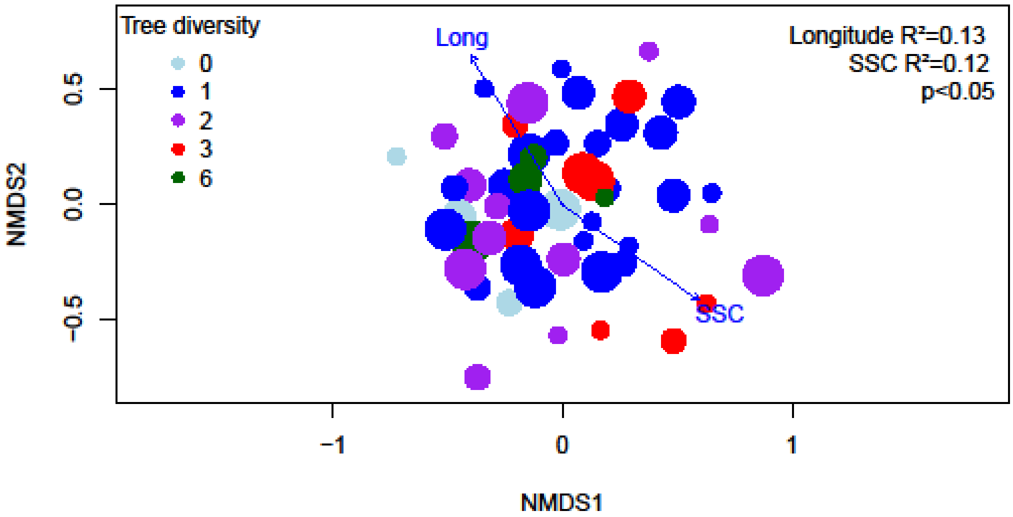

Figure 6: NMDS of community composition of hymenopteran families. The figure shows all different enrichment areas in the means of point size (with increasing plot sizes) as well as its tree diversity highlighted in the different colours (from lowest to highest tree diversity: light blue, blue, purple, red, dark green). The community composition varies in plots with low to high SSC. In addition, composition differs in longitude, so there are partly different species in the Northern community compared with the Southern community of the research area PT. Humus Indo. For statistical verification, see Table 3.

For enrichment area as well as tree diversity no similarities could be found, thus there were no explanations for specific compositions. However, longitude ($R^2 = 0.13$) and stand structural complexity ($R^2 = 0.12$) had significant implications, hence 13 % explained a difference in species composition by geographic distribution of plots, while 12 % were explained by low to high structural complex plots. These statistical values are presented in Table 3.

Table 3: Community composition of Hymenoptera families (NMDS) (see Figure 6). The table shows the different parameters tested in the NMDS whereat longitude and SSC have significant values ($p < 0.05$), shown in bold print.

	NMDS1	NMDS2	R^2	P
Latitude	0.335	0.942	0.006	0.864
Longitude	**-0.526**	**0.850**	**0.130**	**0.038**
Enrichment area	-0.940	-0.340	0.019	0.643
Tree diversity	0.691	-0.722	0.003	0.922
SSC	**0.819**	**-0.572**	**0.118**	**0.045**

Ecological restoration effects on plant-pollinator-networks

During transect walks, I collected 196 individuals, whereof 50 flower visitor species (Table A1) interacted 409 times with 23 flower species, flowering at that time. In total 66 flower species were recorded. The most abundant families were *Eumeninae* (193), *Tapinoma* (41), and *Hesperiidae* (33) present in all enrichment areas, and lowest, as well as highest diversity level (Table A3 and Table A4). Plant-pollinator interaction networks were divided by enrichment area, from small (a) to big plot size (d) (Figure 7). For 25 m² a total of 52 interactions with 5 plant species and 9 flower visitor species (a), for 100 m² with 135 interactions, 18 plant species and 18 flower visitor species (b), for 400 m² with 112 interactions, 14 plant species and 30 flower visitor species (c) and for 1600 m² with 99 interactions, 13 plant species and 21 flower visitor species (d) were found (Table 4). The networks not only show flower visitor species (red bar) and plant species (green bar), but also the abundance of every species, presented through the width of each bar. This also highlights plant species that flowered to some extent, however never have been visited, such as *Ageratum conyzoides*. In 100 m² and 400 m² areas, networks were more complex with flower visitor species not only interacting with one plant species. In addition, these areas had frequent interactions with *Larrinae* and *Lassiglossium* species. 25 m² areas had the least interactions, plant species and flower visitor species. Moreover, most flower visitor species interacted with *Asystasia gangetica* that had highest floral units, while *Clidemia hirta* that also had comparably high floral units was mostly visited by ants.

The interaction networks of control plot, zero planted tree species, and six planted tree species supported these findings (Figure A4). No planted tree species led to 28 interactions being the highest found during the investigation, followed by enrichment with six tree species having 22 interactions, and then 7 interactions for control plots. Plant species ranged from 5 (control), over 5 (zero tree species) to 8 (6 tree species), while flower visitor species counted 3 species for control plots, and both 12 species for tree diversity zero and six (Table A4).

Furthermore, 70 % in the variation of partner numbers was explained by flower abundance, hence the more flowers per plant, the more flower visitor partners. This development, however, saturated at some point.

For the measurement of specialisation in networks via H2' or interaction nestedness of interactions all plant-pollinator networks presented generalists (weigthed nestedness: 0.5 – 18.4; H2': 0.6 – 0.92). Also robustness (0.7 – 0.9) supported these findings as a reaction of insects to weeding from rarest to most frequent plant species.

Table 4: List of interactions, plant species and flower visitor species inside the plant-pollinator networks respectively to enrichment area, presented in Figure 7. Here, 10 x 10 m offer the best plant-pollinator network, followed by 20 x 20 m and then 40 x 40 m, while 5 x 5 m stays well behind.

	5 x 5 m	**10 x 10 m**	**20 x 20 m**	**40 x 40 m**
Interactions	52	135	112	99
Plant species (total)	5	18	14	13
Flower visitor species (total)	9	37	30	21

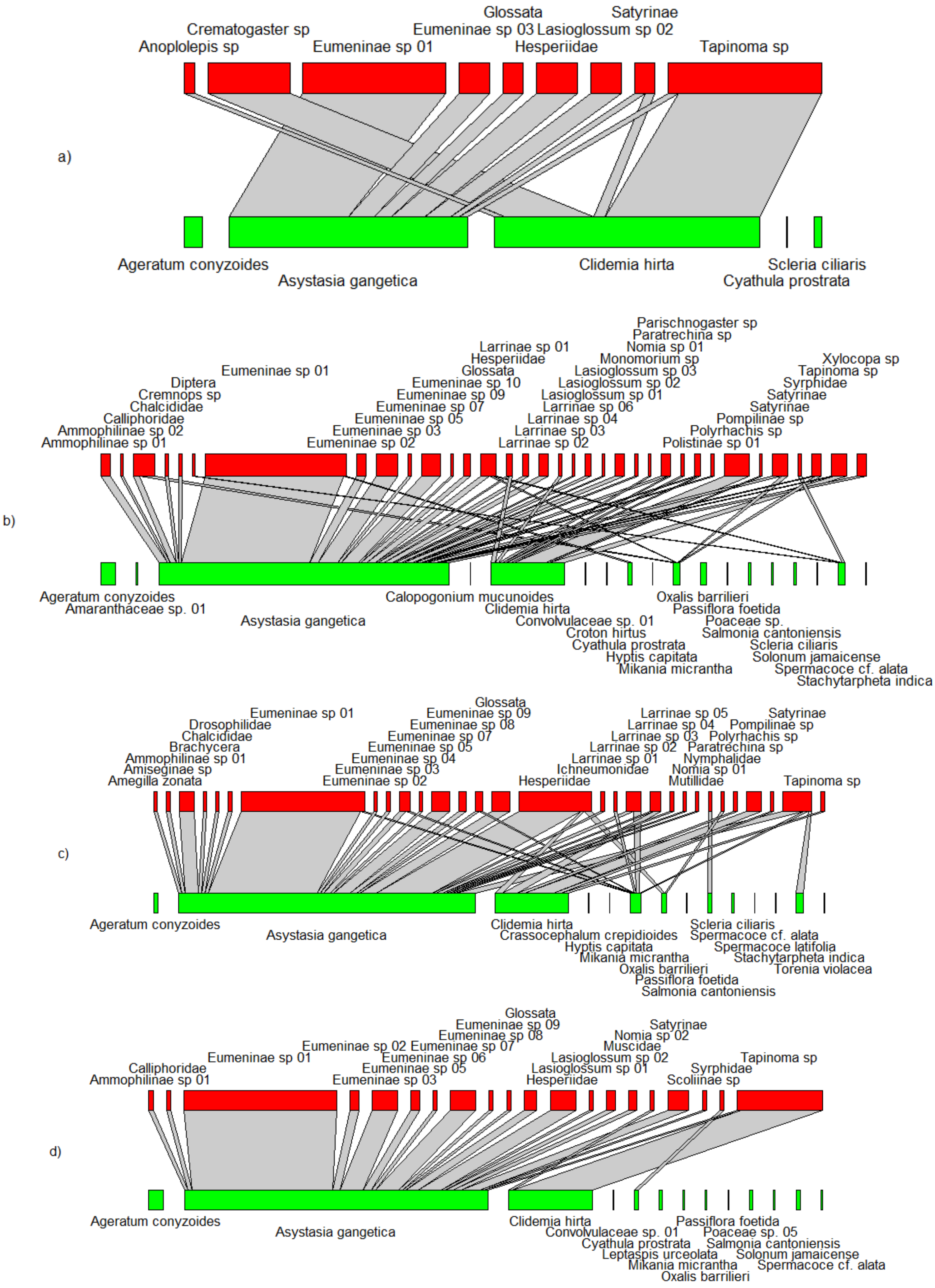

Figure 7: Plant-pollinator interaction networks for different scales. The networks are clustered into the four enrichment areas: a) 5 x 5 m, b) 10 x 10 m, c) 20 x 20 m, or d) 40 x 40 m. The red slots present flower visitor species, while the green ones are plant species. The bars vary in size to present the amount of either pollinator species or plant species. Thus plant species that flowered, but were not visited by pollinators are presented, too. The connections inside the network symbolize the interactions between plants and pollinators, hence the complexity of a network. (See also Table 4)

Comparisons with random values generated from a null model showed that the observed values of interaction nestedness and network specialization H2’ significantly differed from those expected under random interaction associations. For each size class, observed nestedness was lower and network specialization was higher than would be expected under random interaction assembly (Figure A5). Thus, the plant-pollinator interaction networks were not randomly, but systematically structured, indicating non-random associations between plant and pollinator communities in the enrichment plots.

DISCUSSION

Biodiversity enrichment as means of ecological restoration is of vital importance for biodiversity to restore (Rey Benayas et al. 2009) and an opportunity for sustainable oil palm cultivation. Particularly the re-establishment of pollinators and plant-pollinator interaction networks is crucial for its success (Forup et al. 2007, Kaiser-Bunbury et al. 2017). My findings promote a successful pollinator restoration through biodiversity enrichment and natural regeneration of wild plants. In particular, pollinator diversity responded positively to increasing canopy openness and decreasing stand structural complexity. Enrichment areas were of less importance to pollinator diversity. Pollinator species richness was highest for enrichment areas where 40 % of oil palm was cut out, but had no planted native tree species compared to those with six planted native tree species. In addition, species composition changed significantly with spatial distribution of enrichment areas, and differences in stand structural complexity. Furthermore, biodiversity enrichment restored plant-pollinator networks, and enhanced interactions for larger enrichment areas compared to control plots. Specialisation analyses revealed generalist species with non-random associations between plant and pollinator communities.

Insect species richness, especially Hymenoptera, Lepidoptera, and Diptera richness increased as a consequence of restoration efforts compared to control plots. This reveals an opportunity for tropical biodiversity and disturbed landscapes (Forup et al. 2007, Yaap et al. 2010). In fact, with oil palm monocultures organised in designer landscapes, biodiversity losses could be mitigated (Koh et al. 2009, Foster et al. 2011). Ecological restoration has highest impacts in the tropics, thus offers a win-win situation for biodiversity conservation and socio-economic development objectives (Rey Benayas et al. 2009). A variety of habitats are beneficial for biodiversity and species richness in highly disturbed tropical landscapes (Harvey et al. 2006, Franzén and Nilsson 2010).

Most insect orders had no strong preferences for enrichment area size, except that 25 m² had least species richness. Smallest fragments are prone to habitat disturbance (i.e. own observations of pesticide intrusions in PT. Humus Indo) since the relative amount of “edges” is higher

(Ewers and Didham 2006). Only predator richness significantly increased with enrichment area. Larger habitats offer higher herbivory rates that benefit predator richness (Tscharntke et al. 2008). Even though many studies show that species richness increases with habitat patch size (i.e. McKinney and Lockwood 1999, Steffan-Dewenter and Tscharntke 2000, Öckinger et al. 2009, Bommarco et al. 2010), my observations are in line with Thomas (2000) and show that enrichment areas depend more on habitat quality. This suggests that all enrichment area sizes, especially greater than 100m², may be beneficial for biodiversity with the tropical lowland forest landscape. Forest fragment sizes are not necessarily distinctive for genetic diversity or population size, however, smallest fragments are not viable for diversity in the long term (Benedick et al. 2007). Isolation of fragments or the lack of a suitable habitat have greater impacts on different insect taxa than area per se (Benedick et al. 2007). Furthermore, interpatch distances of less than 120 m can maintain sufficient pollen flow (Kormann et al. 2016).

The functional group of pollinators (including Lepidoptera) was not significantly impacted by enrichment area or any interaction of enrichment area with environmental values. Pollinator species have different preferences of habitat area (Aizen and Feinsinger 1994, Steffan-Dewenter et al. 2002, Brosi et al. 2008). In addition, life-history traits, most importantly dispersal capacity, niche breadth and reproduction are key determinants for species richness and distribution in fragmented landscapes (Ewers and Didham 2006, Prugh et al. 2008, Öckinger et al. 2010), or recovery from environmental changes (Henle et al. 2004).

In fact, Hymenoptera species richness and more importantly functional groups were influenced by environmental values, sometimes interacting with enrichment area. In general, Hymenoptera richness favoured no planted tree species over six planted tree species. More flower species can naturally regenerate. Alien plants with attractive floral displays or large rewards, such as *Asystasia gangetica*, thus enhance large pollinator populations (Schweiger et al. 2010). Only for smallest enrichment area species richness was highest with the most possible tree species planted. There were no differences between tree diversity levels 1, 2, and 3. While I did not observe any trees flowering or collected insects off trees, it is difficult to connect effects of tree species to insect diversity. Tree diversity levels within plots have changed over time; however, I used data from the original experimental design, similar to other long-term studies such as the Jena experiment (Weigelt et al. 2010, Teuscher et al. 2016, Gérard et al. 2017).

Only parasitoids responded positively to tree diversity, regardless of enrichment area. In fragmented landscapes, parasitoids are more strongly influenced in their foraging behaviour than predators, due to enhanced natural selection (van Alphen and Visser 1990). While predators have no preferences, pollinators (including Lepidoptera) were significantly negatively affected by planted tree diversity. Lepidoptera tend to have high host specificity for particular herbivore lineages (Weiss 1991, Dyer et al. 2007). At the same time, higher pressure of natural enemy communities exists, especially in the tropics (Dyer et al. 2007).

More importantly, canopy openness and stand structural complexity determined species richness. Hymenoptera richness (predators and pollinators including Lepidoptera) as well as Diptera richness generally increased with high canopy openness. Pollinators in particular responded positively to canopy openness. High canopy openness ensures more light intrusion (Gérard et al. 2017), hence more understory vegetation. This is especially important for Hymenoptera (predators) in the smallest 25 m² plots. These plots are more influenced by shadow, due to close surrounding oil palm trees and no thinning (Gérard et al. 2017). Parasitoid richness responded positively to stand structural complexity, except for smallest enrichment areas. In a meta-analysis, Langellotto and Denno (2004) found a positive correlation between habitat complexity and parasitoid richness increase. However, pollinator richness significantly decreased with increasing stand structural complexity. High vegetation complexity might mislead species from their specific hosts (Weiss 1991). Moreover, flowers are able to change colours, thus influence visitors in a preferential behaviour among pollinators to follow colour phases of colour-changing plants (Weiss 1991). In addition, insect species rely on a few plant species (Smith et al. 2012).

In general, monocultures are vulnerable for invasions of pests and weeds (Foster et al. 2011). Parasitoids are important as biological control (van Alphen and Visser 1990, Basri et al. 1995, Dislich et al. 2017), accompanied by predators that influence herbivory rates (Rosumek et al. 2009). Moreover, non-native species can be valuable as biological controls (Blüthgen and Feldhaar 2010), for example *Anoplolepis gracilipes* (Fayle et al. 2010), which was also present in the study site.

Apart from species richness, these findings present differences in species composition. Habitat area and tree diversity were not important, however, longitude and stand structural complexity had significant impacts on species compositions. Flower diversity and geographical separation are accounted for changes in community composition (Potts et al. 2003). This marks the necessity of implementing diverse enrichment islands spread out through oil palm cultivations, in order to support different species compositions (Aizen and Feinsinger 1994, Henle et al. 2004, Prugh et al. 2008). In addition, different species may generally coexist better with some than with others, due to preferable interactions or habitat modifications (Tylianakis et al. 2007). Moreover, the implementation of enrichment areas counters the risk of homogenization of species composition (McKinney and Lockwood 1999, Ekroos et al. 2010).

In addition to patterns in pollinator diversity, plant-pollinator networks were restored by biodiversity enrichment. A recent study also found a very strong impact of ecological restoration on pollinator abundance, their behaviour, performance, and enhanced network structures (Kaiser-Bunbury et al. 2017). Among enrichment area and tree diversity (zero or six tree species planted) plant-pollinator networks were not very distinct. However, 25 m² areas had the lowest and simplest impact. Smallest areas have increased demographic stochasticity or a lack of suitable habitats (Benedick et al. 2007). Yet 100 m² had the most interactions, plant species, or flower visitor species. Otherwise, 400 m² had higher floral abundances than the other enrichment area sizes, especially of *Asystasia gangetica.* In addition, 100m² and 400m² presented a slightly higher connectance, which increases function and stability (Tylianakis et al. 2010).

In general, I found a dependency of floral abundance and flower visitor species. Habitats that contain higher flower abundances offer more resources, thus are linked to higher pollinator abundances (Potts et al. 2003). Plant biodiversity procreates animal diversity (Novotny et al. 2006, Dyer et al. 2007, Condon et al. 2008), such as herbivorous insects. Furthermore, especially understory vegetation is important (Turner and Foster 2009, Fayle et al. 2010). However, there is also a risk of pteridophytes (Danielsen et al. 2009). The plant surveys showed that only one third of all plants actually flowered, whereas not all flowering plants, such as *Ageratum conyzoides* were visited by flower visitor species. Hence, some flowers, for example *Asystasia gangetica* with highest floral units, or *Clidemia hirta* that especially supported ant diversity, are more important for restoring plant-pollinator networks and should be protected from weeding. Smith et al. (2012) state a reliance of insects on few flower species, which however varies throughout species (Carreck and Williams 2002, Williams and Tepedino 2003). Below certain habitat sizes, for example bees even choose specific host plants, regardless of the distance to their nest, as long as they are available (Smith et al. 2012).

Meanwhile, I observed *Melastoma malabathricum,* an originally native plant, present in most plots, attractive for many pollinators, but which did not appear or flower yet inside transects. I used standardized transect walks with permanently marked corridors (Dafni et al. 2005: cited in Westphal et al. 2008). Since the enrichment area varied in the experimental design, this ensured the same areas were tested in all presented plot sizes and thus enabled statistical comparison. However, this leads to an underrepresentation of temporal and spatial foraging, hence a reduced capture of pollinator communities (Westphal et al. 2008). A possible solution would be variable transects on the most attractive resource patches (Sutherland 1996, Dafni et al. 2005: cited in Westphal et al. 2008).

Furthermore, biodiversity enrichment favoured generalist species instead of specialists (nestedness and H2’). Meanwhile, a null model demonstrated preferable plant-pollinator associations. Restored landscapes promote more generalized native plants that attract more pollinator species (Kaiser-Bunbury et al. 2017). Generalists thrive in secondary habitats (Yaap et al. 2010). Kaiser-Bunbury et al. (2017) discovered pollinators to be more generalized. Moreover, they implied the development of so-called super-generalists: pollinator performance increases (Blüthgen and Klein 2011, Kaiser-Bunbury and Blüthgen 2015). In addition, they stated that these generalized networks and species have higher functional redundancy and lower mutual dependencies. This supports ecosystem resilience (Potts et al. 2010, Devoto et al. 2012) and functional robustness to local species loss to a greater extent (Memmott et al. 2004). Specialists are first to go extinct in a network (Henle et al. 2004). Moreover, specialists sense their habitat areas as even more fragmented than generalists, and increase sensitivity to fragmentation in the first place (With and Crist 1995, Ewers and Didham 2006). In fact, generalists use a broader range of resources, as well as areas outside their habitat. Therefore, they are less susceptible even to small habitat area sizes (Öckinger et al. 2010). Studies have found a connection between niche breadth and extinction risk for Lepidoptera (Kotiaho et al. 2005) and other taxa (Goulson et al. 2005, Boyles and Storm 2007).

This dominance of generalists might influence ecosystem functioning profoundly (Schweiger et al. 2010) cascading to other trophic levels (Dunn et al. 2009). However, the enrichment project has only been carried out since 2013, so biodiversity restoration is still in an early stage. Thus, biodiversity enrichment may favour opportunistic generalists in the beginning and only promote specialist species at later stages.

Overall, my study demonstrates that biodiversity enrichment, and with a variety of habitat types (Franzén and Nilsson 2010), is a promising approach for restoring pollinator diversity and plant-pollinator interactions in monoculture oil palm plantations. In addition to the importance of protecting high value areas from further conversions (Yaap et al. 2010), the implementation of enrichment areas in monoculture oil palm plantations (designer landscapes) is of vital importance for biodiversity conservation (Koh et al. 2009, Foster et al. 2011). Moreover, increased biodiversity provides ecosystem functioning (Balvanera et al. 2006), such as pollination, biological control or additional economic value (Zhang et al. 2007, Gérard et al. 2017). While more specific research to support this opportunity is necessary (Rey Benayas et al. 2009, Kaiser-Bunbury et al. 2017, Dislich et al. 2017), my findings could guide management recommendations for sustainable oil palm landscape that are in line with a land-sharing approach to reconcile agricultural production with biodiversity-enriched oil palm plantations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the **Appendix**:

Table A1: Plant (floral units) and flower visitor (abundance) species from transect walks

Table A2: Species richness (mean SD) respectively to enrichment area and tree diversity

Table A3: Plant-pollinator assemblages (floral units and abundance) of different enrichment areas

Table A4: Plant-pollinator assemblages (floral units and abundance) of different enrichment levels

Figure A1: GLM results for other insect taxa

Figure A2: GLM results for Hymenoptera family species richness and interactions

Figure A3: GLM results for Hymenoptera family species richness and environmental values

Figure A4: Plant-pollinator networks of different enrichment levels

Figure A5: Specialisation nullmodel with random community assemblages

Appendix

Table A1: List and floral units (FU) of all plant species (native/alien) and their family name (Rembold et al. 2017) found within the plant surveys as well as all flower visitor species and abundance of transect walks. The plants species with highest FU abundance are in bold print, hence *Asystasia gangetica* (alien), as well as *Clidemia hirta* (alien) offer the highest flower resource by far. Flower visitor species with highest abundance (all *Eumeninae sp.*) are in bold print. (see Figure 7).

Plant species	Origin	Plant family	FU (total)	Flower visitor species	Abundance
Asystasia gangetica	**alien**	**Acanthaceae**	**3353**	***Eumeninae sp. 01***	**134**
Clidemia hirta	**alien**	**Melastomataceae**	**1033**	***Tapinoma sp.***	**41**
Ageratum conyzoides	**alien**	**Asteraceae**	**127**	***Hesperiidae***	**33**
Mikania micrantha	**alien**	**Asteraceae**	**76**	*Satyrinae*	20
Oxalis barrelieri	alien	Oxalidaceae	49	***Eumeninae sp. 03***	**18**
Stachytarpheta indica	alien	Verbenaceae	34	***Eumeninae sp. 07***	**18**
Spermacoce cf. alata	-	Rubiaceae	31	*Glossata*	15
Salmonia cantoniensis	native	Polygalaceae	27	*Polyrhachis sp.*	13
Scleria ciliaris	native	Cyperaceae	27	*Ammophilinae sp. 01*	8
Cyathula prostrata	native	Amaranthaceae	26	*Calliphoridae*	8
Solonum jamaicense	-	Solanaceae	13	*Crematogaster sp.*	8
Poaceae sp. 01 + 02	-	Poaceae	10	*Larrinae sp. 02*	8
Poaceae sp. 05	-	Poaceae	7	*Lasioglossum sp. 02*	**8**
Amaranthaceae sp. 01	-	Amaranthaceae	7	***Eumeninae sp. 02***	**6**
Leptaspis urceolata	native	Poaceae	7	*Nomia sp. 01*	5
Passiflora foetida	alien	Passifloraceae	6	***Eumeninae sp. 05***	**4**
Convolvulaceae sp. 01	-	Convolvulaceae	3	***Eumeninae sp. 09***	**4**
Crassocephalum crepidioides	alien	Asteraceae	2	*Larrinae sp. 03*	4
Hyptis capitata	alien	Lamiaceae	2	*Syrphidae*	4
Torenia violacea	native	Linderniaceae	2	***Eumeninae sp. 04***	**3**
Spermacoce latifolia	-	Rubiaceae	2	***Eumeninae sp. 08***	**3**
Calopogonium munucoides	alien	Fabaceae	1	*Larrinae sp. 01*	3
Croton hirtus	alien	Euphorbiaceae	1	*Xylocopa sp.*	3
Poaceae sp. 03	-	Poaceae	0	*Chalcididae*	2
Poaceae sp. 04	-	Poaceae	0	***Eumeninae sp. 10***	**2**
Euphorbiaceae sp. 01	-	Euphorbiaceae	0	*Larrinae sp. 04*	2
Phyllanthus urinaria	native	Phyllanthaceae	0	*Larrinae sp. 06*	2
Cyperus cf. diffuses	-	Cyperaceae	0	*Lasioglossum so. 01*	2
Nephrolepis biserrata	native	Nephrolepidaceae	0	*Muscidae*	2
Lygodium sp. 01	-	Lygodiaceae	0	*Paratrechina sp.*	2
Lygodium sp. 02	-	Lygodiaceae	0	*Parischnogaster sp.*	2
Paspalum conjugatum	-	Poaceae	0	*Pompilinae sp.*	2
Rhynchospora colorata	alien	Cyperaceae	0	*Amegilla zonata*	1
Mimosa pudica	alien	Fabaceae	0	*Amiseginae sp.*	1
Imperata cylindrica	native	Poaceae	0	*Ammophilinae sp. 02*	1
Chromolaena odorata	alien	Asteraceae	0	*Anoplolepis sp.*	1
Lygodium cf. circinatum	native	Lygodiaceae	0	*Brachycera*	1
Adiantum latifolium	native	Pteridaceae	0	*Cremnops sp.*	1
Trema orientalis	-	Cannabaceae	0	*Diptera*	1
Selaginella cf. plana	native	Selaginellaceae	0	*Drosophilidae*	1
Christella sp. 01	-	Thelypteridaceae	0	***Eumeninae sp. 06***	**1**
Christella sp. 02	-	Thelypteridaceae	0	*Ichneumonidae*	1
Christella sp. 03	-	Thelypteridaceae	0	*Larrinae sp. 05*	1
Microlepia cf. hance	-	Dennstaedtiaceae	0	*Lasioglossum sp. 03*	1
Centrosema pubescens	alien	Fabaceae	0	*Monomorium sp.*	1
Pteridophyta sp. 01	-	Pteridophyta	0	*Mutillidae*	1
Melastoma malabathricum	native	Melastomataceae	0	*Nomia sp. 02*	1

Dioscorea cf. hispida	-	Dioscoreaceae	0	*Nymphalidae*	1
UI	-	UI	0	*Polistinae sp. 01*	1
Poaceae sp. 06	-	Poaceae	0	*Scoliinae sp.*	1
Pouzolzia zeylanica	native	Urtiaceae	0	-	-
Schizostachium brachycladum	-	Poaceae	0	-	-
Poaceae sp. 07	-	Poaceae	0	-	-
Rubiaceae sp. 01	-	Rubiaceae	0	-	-
Pityrogramma calomelanos	alien	Pteridaceae	0	-	-
Axonopus compressus	alien	Poaceae	0	-	-
Pericampylus glaucus	-	Menispermaceae	0	-	-
Urena lobate	native	Malvaceae	0	-	-
Centotheca lappaceae	native	Poaceae	0	-	-
Pennisetum polystachion	alien	Poaceae	0	-	-
Bauhinia sembifidia	native	Fabaceae	0	-	-
Araceae sp. 01	-	Araceae	0	-	-
Cuphea carthaginensis	alien	Lythraceae	0	-	-
Macaranga bancana	native	Euphorbiaceae	0	-	-
Rolandra fructicosa	native	Asteraceae	0	-	-
Pteridophyta sp. 01	-	Pteridophyta	0	-	-

Table A2: Species richness (mean SD) in every enrichment area and tree diversity.

25m^2	100m^2	400m^2	1600m^2	
28.54 ± 5.62	48.54 ± 21.01	46.92 ± 18.7	49.62 ± 18.61	
Tree diversity 0	Tree diversity 1	Tree diversity 2	Tree diversity 3	Tree diversity 6
41.75 ± 22.69	46.33 ± 19.27	47.25 ± 23.12	33.13 ± 6.72	36.5 ± 8.02

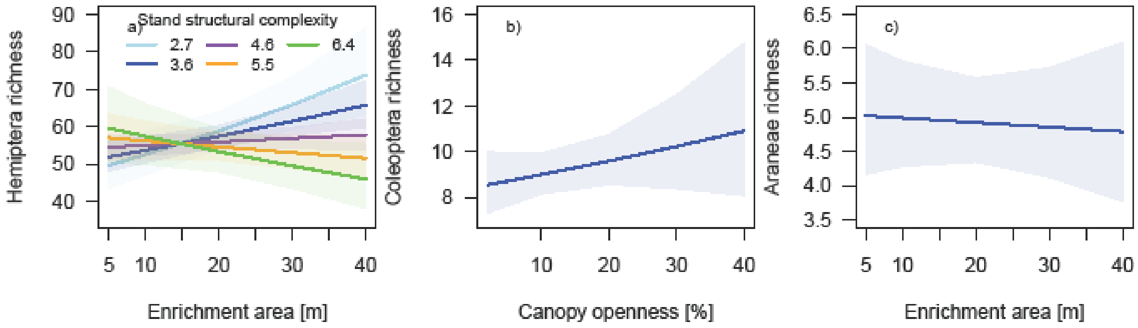

Figure A1: GLM results for insect SR: a) Hemiptera richness in relation to interaction between SSC and enrichment area [m], b) Coleoptera richness in relation to canopy openness [%] and c) Araneae richness in relation to enrichment area. In a) the interaction of SSC and enrichment area have a negative significant effect ($Z = -2.682$, $p < 0.01$) on Hemiptera richness. However, for big enrichment area and low SSC Hemiptera richness is highest. In b) Coleoptera richness is increasing significantly ($Z = 2.0$, $p < 0.05$) with increasing canopy openness. For Araneae richness c) demonstrates significant lower richness with increasing enrichment area, however richness has high confidence intervals and narrow changes.

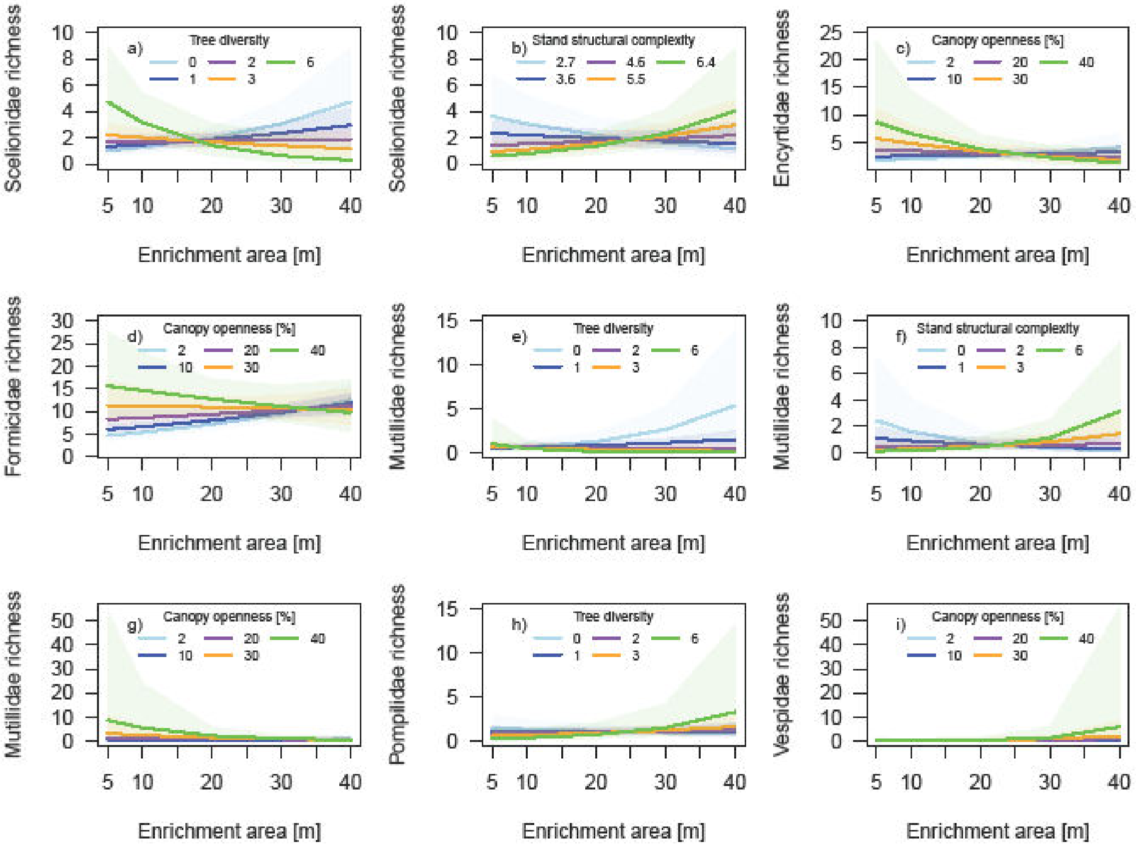

Figure A2: GLM results for Hymenoptera family SR: a) Scelionidae richness in relation to interactions between tree diversity and enrichment area [m] and b) interactions between SSC and enrichment area, c) Encyrtidae richness in relation to to interactions canopy openness [%] and enrichment area, d) Formicidae richness in relation to interactions between canopy openness and enrichment area, Mutillidae richness in relation to interactions between e) tree diversity and enrichment area, f) SSC and enrichment area and g) canopy openness and enrichment area, h) Pompilidae richness in relation to interactions between tree diversity and enrichment area and i) Vespidae richness in relation to interactions between canopy openness and enrichment area.

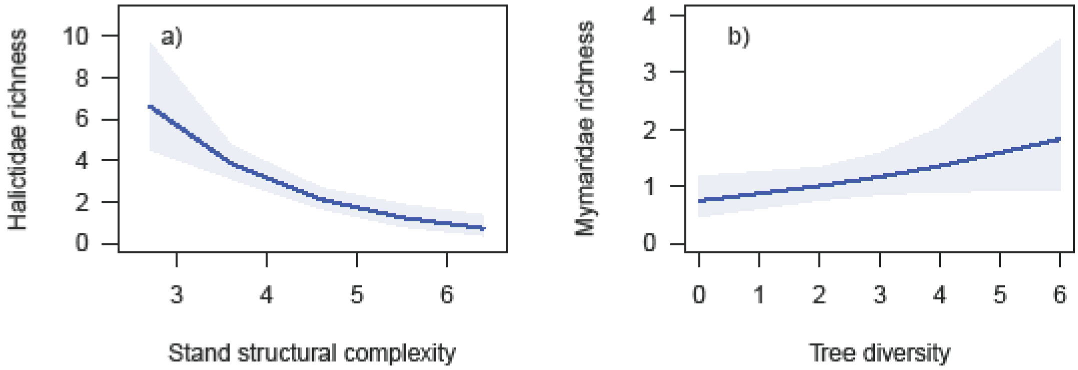

Figure A3: GLM of insect richness (family level) in relation to SSC and tree diversity. Halictidae richness a) is significantly decreasing with increasing SSC and Mymaridae richness b) is significantly increasing with higher tree diversity.

Table A3: List of plant species with floral units (FU) respectively and flower visitor species with abundance for different enrichment areas (5 x 5 m, 10 x 10 m, 20 x 20 m, 40 x 40 m). Plant species that actually had an interaction with a flower visitor species is put in bold print. This table supports the results demonstrated in Figure 7.

Enrichment area	Plant species	FU	Flower visitor species	Abundance
5 x 5 m			*Anoplolepis sp.*	1
			Crematogaster sp.	8
	Clidemia hirta	220	*Eumeninae sp. 01*	14
	Asystasia gangetica	197	*Eumeninae sp. 03*	3
	Ageratum conyzoides	15	*Glossata*	2
	Scleria ciliaris	6	*Hesperiidae*	4
	Cyathula prostrata	1	*Lasioglossum sp. 02*	3
			Satyrinae	2
			Tapinoma sp.	15
10 x 10 m			*Ammophilinae sp. 01*	3
			Ammophilinae sp. 02	1
			Calliphoridae	7
			Chalcididae	1
			Cremnops sp.	1
			Diptera	1
			Eumeninae sp. 01	50
			Eumeninae sp. 02	3
	Asystasia gangetica	1113	*Eumeninae sp. 03*	7
	Clidemia hirta	289	*Eumeninae sp. 05*	1
	Ageratum conyzoides	58	*Eumeninae sp. 07*	7
	Spermacoce cf. alata	27	*Eumeninae sp. 09*	1
	Mikania micrantha	25	*Eumeninae sp. 10*	2
	Oxalis barrilieri	24	*Glossata*	5
	Cyathula prostrata	16	*Hesperiidae*	4
	Poaceae sp.	10	*Larrinae sp. 01*	2
	Scleria ciliaris	10	*Larrinae sp. 02*	3
	Amaranthaceae sp. 01	7	*Larrinae sp. 03*	1
	Salmonia cantoniensis	6	*Larrinae sp. 04*	1
	Solonum jamaicense	3	*Larrinae sp. 06*	2
	Convolvulaceae sp. 01	2	*Lasioglossum sp. 01*	1
	Calopogonium mucunoides	1	*Lasioglossum sp. 02*	3
	Croton hirtus	1	*Lasioglossum sp. 03*	1
	Hyptis capitate	1	*Monomorium sp.*	1
	Passiflora foetida	1	*Nomia sp. 01*	4
	Stachytarpheta indica	1	*Paratrechina sp.*	1
			Parischnogaster sp.	2
			Polistinae sp. 01	1
			Polyrhachis sp.	8
			Pompilinae sp.	1
			Satyrinae	7
			Syrphidae	3
			Tapinmoa sp.	5
			Xylocopa	3
20 x 20 m			*Amegilla zonata*	1
			Amiseginae sp.	1
	Asystasia gangetica	1292	*Ammophilinae sp. 01*	4
	Clidemia hirta	318	*Brachycera*	1
	Mikania micrantha	48	*Chalcididae*	1
	Stachytarpheta indica	33	*Drosophilidae*	1
	Oxalis barrilieri	21	*Eumeninae sp. 01*	34
	Ageratum conyzoides	18	*Eumeninae sp. 02*	1
	Salmonia cantoniensis	17	*Eumeninae sp. 03*	1
	Scleria ciliaris	11	*Eumeninae sp. 04*	3
	Passiflora foetida	4	*Eumeninae sp. 05*	1
	Crassocephalum crepidioides	2	*Eumeninae sp. 07*	5
	Spermacoce latifolia	2	*Eumeninae sp. 08*	2
	Torenia violacea	2	*Eumeninae sp. 09*	2
	Hyptis capitate	1	*Glossata*	5
	Spermacoce cf. alata	1	*Hesperiidae*	20
			Ichneumonidae	1
			Larrinae sp. 01	1

			Larrinae sp. 02	5
			Larrinae sp. 03	3
			Larrinae sp. 04	1
			Larrinae sp. 05	1
			Mutillidae	1
			Nomia sp. 01	1
			Nymphalidae	1
			Paratrechina sp.	1
			Polyrhachis sp.	6
			Pompilinae sp.	1
			Satyrinae	8
			Tapinoma sp.	1
40 x 40 m	***Asystasia gangetica***	751	*Ammophilinae sp. 01*	1
	Clidemia hirta	206	*Eumeninae sp. 01*	36
	Ageratum conyzoides	36	*Eumeninae sp. 02*	2
	Solonum jamaicense	10	*Eumeninae sp. 03*	7
	Cyathula prostrata	9	*Eumeninae sp. 05*	2
	Leptaspis urceolata	7	*Eumeninae sp. 07*	6
	Poaceae sp. 05	7	*Eumeninae sp. 08*	1
	Oxalis barrilieri	4	*Eumeninae sp. 09*	1
	Salmonia cantoniensis	4	*Glossata*	3
	Mikania micrantha	3	*Hesperiidae*	6
	Spermacoce cf. alata	3	*Satyrinae*	4
	Convolvulaceae sp. 01	1	*Tapinoma sp.*	20
	Passiflora foetida	1		

Table A4: List of plant species with floral units (FU) respectively and flower visitor species with abundance for control plots and tree diversity zero and six, as well as total interactions, total plant species and total flower visitor species. This table supports the results demonstrated graphically in Figure A4.

Tree diversity	Plant species	FU	Flower visitor species	Abundance	Interactions
Control	*Ageratum conyzoides*	35	*Eumeninae sp. 01*	6	**7**
	Asystasia gangetica	33	*Eumeninae sp. 07*	1	
	Cythula prostrata	14	*Nomia sp. 01*	1	
	Spermacoce cf. alata	2	*Syrphidae*	1	
	Clidemia hirta	1	*Tapinoma sp.*	1	
Tree diversity 0	***Clidemia hirta***	132	*Crematogaster sp.*	1	**28**
	Asystasia gangetica	65	*Eumeninae sp. 01*	6	
	Mikania micrantha	24	*Eumeninae sp. 03*	1	
	Scleria ciliaris	14	*Eumeninae sp. 07*	1	
	Passiflora foetida	3	*Eumeninae sp. 09*	2	
			Glossata	1	
			Hesperiidae	3	
			Larrinae sp. 02	1	
			Larrinae sp. 05	1	
			Mutillidae	1	
			Paratrechina sp.	1	
			Polyrhachis sp.	1	
			Tapinoma sp	9	
Tree diversity 6	***Asystasia gangetica***	162	*Ammophilinae sp. 01*	2	**22**
	Clidemia hirta	46	*Eumeninae sp. 01*	3	
	Oxalis barrilieri	9	*Eumeninae sp. 02*	1	
	Ageratum conyzoides	6	*Eumeninae sp. 03*	1	
	Mikania micrantha	2	*Glossata*	3	
	Spermacoce latifolia	2	*Hesperiidae*	4	
	Convolvulaceae sp. 01	2	*Lasioglossum sp. 02*	1	
	Spermacoce cf. alata	2	*Nomia sp. 01*	1	
			Paratrechina sp.	1	
			Polyrhachis sp.	1	
			Satyrinae	1	
			Tapinoma sp.	3	

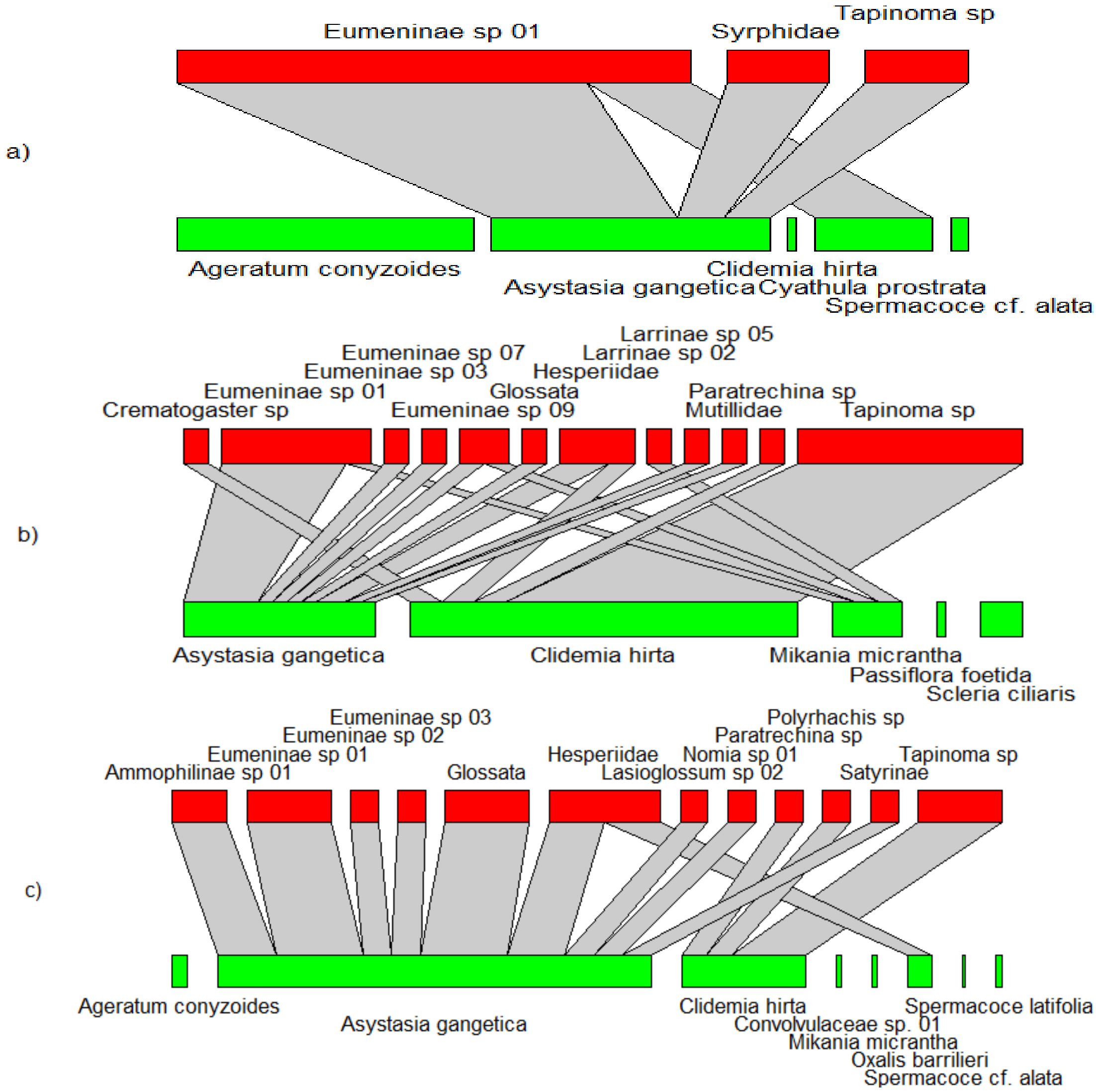

Figure A4: Plant-pollinator interaction networks of a) control plots, b) zero, and c) six planted tree species. It shows higher interactions, and abundances of plant species and flower visitor species for enrichment (zero and six tree species) compared to control plots. There are few differences within enrichment levels. While with zero enrichment there are more interactions, there are however, fewer plant species. However flower visitor species are equally occurring.

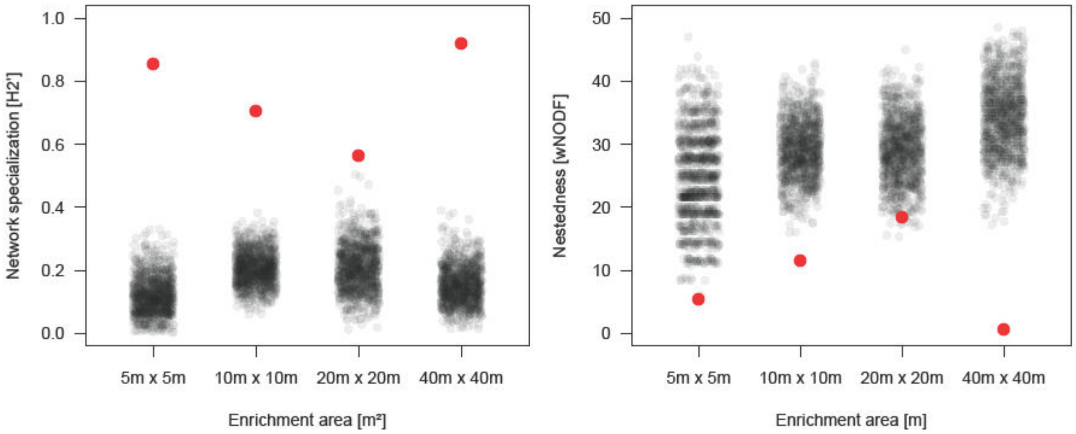

Figure A5: Both graphs demonstrate a null model with 1000 random communities and their average H2' and nestedness compared to the originally observed value in the existing network. In both calculations the actual values were significantly different to the random values ($p < 0.0001$), thus plant-pollinator interaction networks were not randomly, but systematically structured, indicating non-random associations between plant and pollinator communities in the enrichment plots.

Verification of examination registration in FlexNow

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Module: Ressourcenmanagement
Exam: Agrar - Abschlussarbeit
Lecturer: Dr. Ingo Grass

Declaration

I hereby declare that I have produced this work independently and without outside assistance, and have used only the sources and tools stated.

I have clearly identified the sources of any sections from other works that I have quoted or given in essence.

I have complied with the guidelines on good academic practice at the University of Göttingen.

If a digital version has been submitted, it is identical to the written one.

I am aware that failure to comply with these principles will result in the examination being graded “nicht bestanden”, i.e. failed.

Göttingen, 06.08.2018 Isabelle Arimond