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The Filtering Effect of Oil Palm Plantations on Potential Insect Pollinator Assemblages from Remnant Forest Patches

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Abstract: Extensive oil palm plantations worldwide are dependent on insect pollination, specifically by introduced African weevils (*Elaidobius* spp.). The effectiveness of these weevils has been questioned following poor pollination and yield loss in Malaysia. Indigenous thrip (Thysanoptera) species, and moths (Lepidoptera) in the genus *Pyroderces,* may also be pollinators of oil palm, while the role of bees (Hymenoptera) and flies (Diptera) is unknown. The potential of native pollinators remains uncertain because of the almost total clearing of forest habitat from oil palm landscapes. In this study, we investigate the value of small high conservation value (HCV) forests as sources of potential native insect pollinators of oil palm in northern Sarawak. We further examine the filtering effect of oil palm-dominated landscapes on the species assemblages of six potential pollinator insect orders: Blattodea, Coleoptera, Diptera, Hemiptera, Hymenoptera and Lepidoptera. Orders differed in both species composition and abundance between forest and oil palm plantations, with an average of 28.1% of species unique to oil palm. Oil palm presented a soft permeable boundary to Coleoptera, Hymenoptera and Lepidoptera. Their species richness and abundance differed little between habitats with distance, despite species turnover. In contrast, oil palm presented a harder boundary to Diptera with a decline in both species richness and abundance with distance into oil palm. The abundance of the oil palm weevil (*Elaedobius kamerunicus*) was low compared to the native dominants, but similar to levels displayed by native thrips that may be pollinators of oil palm. The functional diversity of well-known pollinator guilds—bees and flies—was similar in forest and oil palm, suggesting that potential pollinators may yet exist among native orders of insects. Contrary to the prevailing opinion, even small forest patches in oil palm landscapes may provide native pollinator pressure.

Keywords: pollination biology; boundary effect; ecological filter; fragmentation ecology; functional diversity; introduced weevil; landscape ecology; native pollinators

1. Introduction

The increasing global demand for palm oil (*Elaeis guineensis*) has caused landscape-scale deforestation and expansion of oil palm estates in Malaysia since 1917 [1], such that Malaysia and Indonesia retain only 3% of their primary forest [2]. Oil palm establishment since the 1980s in Sarawak, Malaysian Borneo, has mostly replaced secondary forest [3,4], and 33.4% (from 2005–2010) of Sarawak's peatland [5–7]. Between 1990 and 2005, plantation area increased from 1.8 mil. to 4.2 mil. ha in Malaysia, and as of 2015 Malaysia is the second largest producer of oil palm globally, with 5.4 mil. ha of oil palm producing 25 mil. tons of palm and kernel oil annually with a value of RM63.62 bil. [8]. The palm oil market is not yet saturated and increasing diversification of uses and its value as biodiesel portents further increases in the production [9]. It is estimated that by 2050 a further 12 million ha of oil palm will have to be planted to meet demand [10]. Extensive clear-felling and

replacement of primary and secondary forests by oil palm compromise ecosystem function and services [11,12]. These simplified landscapes are more susceptible to harmful non-native invasive species [12], potentially reducing production through increased herbivory or disease and there is a significant effect on biodiversity and ecosystem services [13,14]. Here we examine the effect of landscape-scale oil palm estates, and the potential mitigating effect of remnant forest patches, on insect pollinator assemblages and services essential for healthy natural and production ecosystems and human livelihoods.

Massive clearing of lowland forests by oil palm agriculture in Malaysia and Indonesia has caused the steepest decline of biodiversity for any region [15]. Oil palm plantations filter the native forest fauna, allowing only a narrow spectrum of taxa to persist [12,16–19], resulting in very different species compositions in each habitat [20–22]. Species lost to land conversion tend to be those that: have specialist diets; are reliant on habitat features that are not present in plantations; have small range sizes; and are of high conservation concern [23]. While species commonly found in oil palm plantations are abundant generalists, pests and invasive species that are more common in the wider agricultural landscape [24–27] and few forest species [22].

Insects are the most prominent pollinators worldwide [28]. Bees are the main service provider globally [29] and the dominant pollen vector in tropical forests [30–32]. Devising management strategies to make oil palm a more environmentally friendly and sustainable crop depends on understanding key processes, such as pollination biology, that are affected by oil palm. Conversion to oil palm plantation, from either primary or secondary forests, has resulted in a 70–77% reduction in tropical bird diversity and a 79–83% reduction in butterfly diversity [33]. Only 29% of invertebrate and 22% of vertebrate species were shared between oil palm and natural forests [34], and across all animal taxa, an average of only 15% of species are shared [4]. Groups such as ants [21,35], dung beetles [36], beetles in general [26,36,37], isopods [38], cockroaches [23], mosquitoes [39], moths [24], butterflies [40], lizards [41], primates [20], small mammals [19,42], birds [18,25] and bats [20,43] show changes in abundance but significant declines in diversity [22]. Only bees show increased diversity in oil palm plantations [27]. Commensurate with the latter trends is an increase in the number of harmful non-native species, such as the yellow crazy ant (*Anoplolepis gracilipes*) [44]. It is clear that oil palm plantations present a boundary barrier, varying in effect from soft (a moderately permeable barrier to cross-boundary movement) to hard (impermeable boundary with little penetration into oil palm) depending on the functional traits of the native species, preventing key ecosystem processes, such as gene flow, for the survival of small communities in remnant native vegetation [45,46].

Oil palm relies on insect pollination [47]. In West Africa, where oil palm originates, it has several native pollinators including four species of weevils: *Elaidobius kamerunicus* Faust, *E. subvittatus* Faust, *E. plagiatus* Faust and *E. sigalaris* Faust. (Coleoptera: Curculionidae) [48]. The most effective of the West African pollinators, *E. kamerunicus*, has been introduced to oil palm plantations outside of West Africa [49]. *E. kamerunicus* is crop-specific, feeding on and laying eggs below the anthers of the male inflorescence. The emerging male weevils carry pollen between male and female inflorescences when feeding [47]. Prior to the introduction of *E. kamerunicus*, plantations outside West Africa experienced low fruit sets and were hand pollinated [47]. Since the introduction of *E. kamerunicus* to Malaysia in 1981 the need for assisted pollination has ceased [50] and the crop yield has increased by 20% [49].

Relying on a single pollinator for such a vital ecosystem service is precarious and unsustainable [50,51]. Concern has been expressed about the effectiveness and viability of weevil populations following periodic occurrences of poor pollination and yield loss in certain locations in Malaysia [50,52]. The introduced weevils have proven to be ineffective in dry conditions and in heavy rain [47,50]; their fitness is affected by nematode worms [50,53]; and they display inbreeding depression due to low numbers of breeding pairs at their introduction [50]. To ensure the security of oil palm pollination a more diverse insect pollinator guild offering robust responses to environmental change is required [54–56]. Several native pollinators have been observed pollinating oil palm [57], including *Thrip hawaiensis* (Thysanoptera) and moths

(*Pyroderces* spp.) [48] and other flying insects may also hold the potential to provide pollination services to oil palm as well as other vegetation in plantations. Caudwell, Hunt, Reid, Mensah and Chinchilla [50] reported that in Malaysian plantations, a high abundance of native pollinator species could support adequate pollination and fruit set of oil palm. Accordingly, high conservation value (HCV) forest patches within plantations may provide viable pollination services although this is yet to be confirmed [27,34].

The Roundtable for Sustainable Palm Oil (RSPO) has recommended best practices for palm oil agriculture on an industrial scale [58] that address the maintenance of pollination services, such as banning particularly damaging processes such as fire clearing and replacement of primary forest with oil palm, as well as limiting the use of insecticides. Most of these recommendations have been adopted by palm oil producers [59]. Consequently, more recently established oil palm plantations retain riparian zones [60] and HCV areas [61,62]. The HCV remnant forest patches within oil palm plantations buffer biodiversity and support the persistence of isolated wildlife communities by improving their connectivity [63]. These forest refugia can improve the diversity of insects on oil palm estates [40,64].

Here we examine whether potential insect pollinator assemblages differ between and across the oil palm–forest boundary. We address the ability of forest patches to act as refugia for flying insects that are potential pollinators of surrounding oil palms. The abundance, diversity and richness of flying insect taxa from the orders Blattodea, Coleoptera, Diptera, Hemiptera, Hymenoptera and Lepidoptera were compared between forest and palm oil habitats. We examined the abundance, diversity and richness of bees, as the main pollinators of tropical forests, and the abundance of *E. kamerunicus,* as the main pollinator of palm oil. The functional diversity of two important pollinator groups, flies (Diptera) and bees (Apoidae) was examined, seeking a functional gap filled by thrips that are known to pollinate oil palm. A gradient of declining abundance and diversity of flying insect taxa is expected from the forest into the plantation habitat with increasing distance from the forest–plantation ecotone. Differences among insect orders in the steepness of this gradient may define the strength of the boundary or filtering effect of oil palm.

2. Materials and Methods

2.1. Study Area

Flying insects were sampled in Sarawak, Malaysian Borneo on two neighbouring oil palm plantations, Saremas 1 and Segarmas (3°31′15″ N, 113°45′0″ E; elevation 1288 m), owned and managed by PPB Oil Palm Berhad (Figure 1). The plantations are in the moist aseasonal tropics, with a mean annual temperature of 31 °C and mean annual rainfall of 2605 mm. Both plantations comprise mature fruiting oil palm trees of approximately 10 m to 16 m height, planted at 10 m intervals. Saremas 1 (4614 ha) and Segarmas (3334 ha) were previously secondary forests, cleared from 1990 onwards and planted in 1996 and 1994–1995, respectively. The plantations gained RSPO certification in June 2010. Segarmas plantation contains the Bukit Durang Conservation Area (3°28′31.0″ N 113°50′04.5″ E), an HCV forest patch (Forest Patch 1) of 990 ha, located on a steep hillside that extends into two other palm oil plantations. Saremas 1 plantation contains an HCV forest patch (Forest Patch 2) of 116 ha (3°34′03.8″ N 113°46′04.6″ E). Both forest patches are classified as HCV level 4 (RSPO, 2014) because of their capacity to provide "*basic ecosystem services in a critical situation, including protection of water catchment and control or erosion of vulnerable soils and slopes*". Management activities such as harvesting, pruning, fertilizing and insecticide spraying are common in both oil palm plantations.
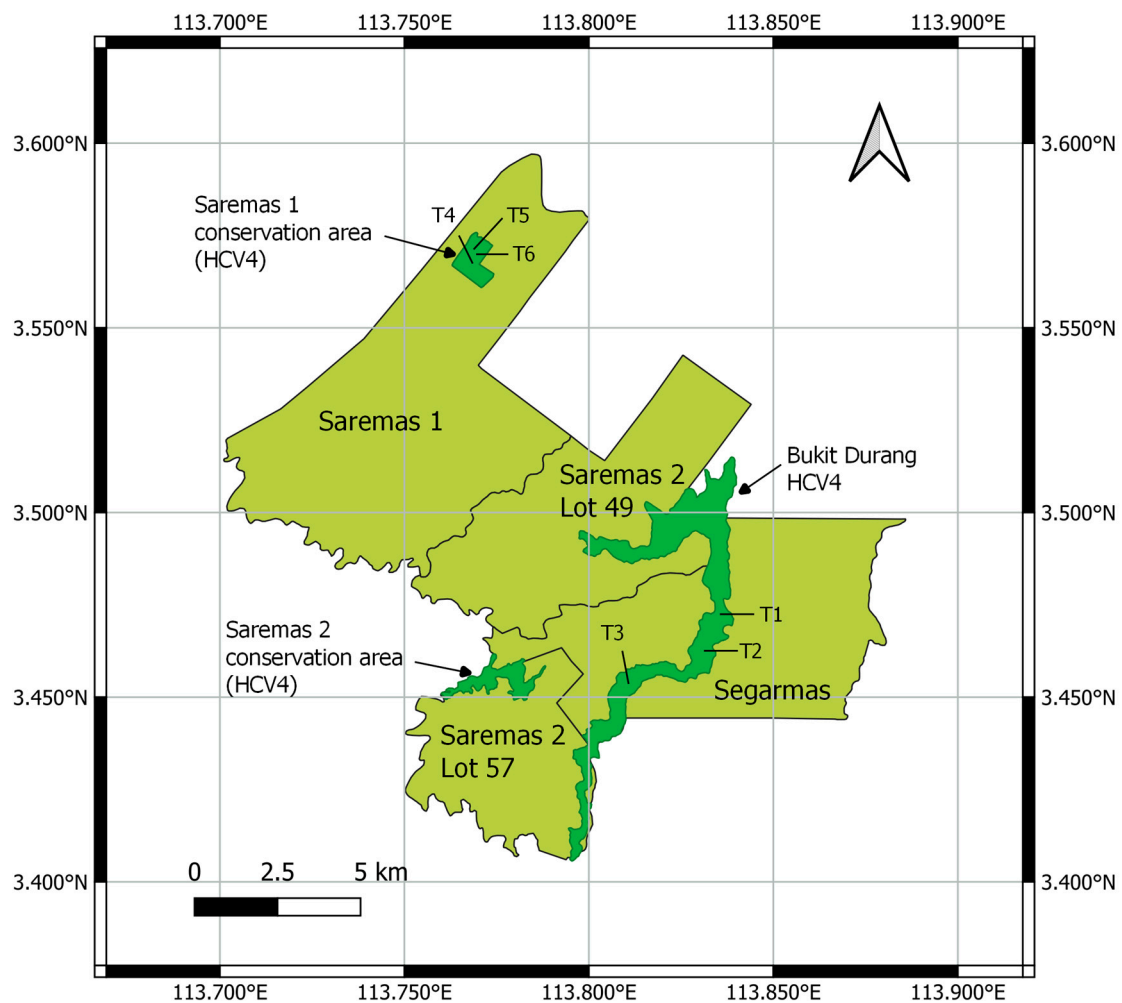
Figure 1. Transect locations. Transects 1, 2 and 3, are situated in the Bukit Durang HCV forest patch. Transects 4, 5 and 6 are situated in the Saremas 1 conservation area. Transect lines are not drawn to scale. Lighter green indicates oil palm estate and darker the HCV forest patches.

2.2. Insect Sampling

Flight interception traps placed along six 600 m transects were used to sample flying insects. Transects crossed the forest–plantation boundary and extended 300 m into each habitat. The six transects were divided evenly between Saremas 1 and Segarmas (Figure 1). Traps were positioned in each habitat along each transect, at 50 m, 150 m and 300 m from the forest–plantation boundary, totalling 6 traps per transect.

A handheld Global Positioning System (GPS) was used to measure the length of the transects and determine the location of the traps. Each flight interception trap comprised a 2 m × 1 m fine black net pulled taught between two trees with a trough positioned below to catch insects flying into the net [65,66]. The trough was filled with 4.5 litres of water, and approximately 20 mL of dish soap was added to elevate water surface tension, along with 0.2 litres of spirit alcohol to preserve the insects until samples were collected [66]. Samples were collected every second day. The liquid mixture in each trough was renewed after each sample collection. Sampling took place over 40 days during June and July of 2015 (18 trap days). Insects were sorted by order and then into morphospecies based on defining characteristics using methods described in Oliver and Beattie [67]. An individual from each morphospecies was kept as a reference specimen and photographed. The reference collection was preserved at −10 °C.

2.3. Habitat Complexity and Physiognomy

To quantify the differences in habitat physiognomy between plantation and forest the percentage cover of leaf litter, dead wood, vines, and vegetation between 0 and 0.5 m, between 0.5 m and 1 m, and between 1 m and 2 m, were estimated within 10 m × 10 m quadrats (0.01 ha) centred on each trap. Measurements were focussed on understory vegetation between 0–2 m to match the height of the traps. Trees (DBH > 15 cm), poles (5 cm < DBH < 15 cm) and saplings (DBH < 5 cm) were counted, and their density was estimated in a larger 20 m × 20 m quadrat (0.04 ha), also centred on a trap.

2.4. Bee and Fly Functional Diversity

Functional richness (FR) of bees was compared between oil palm and forest habitat types using a single trait—body size. Body size influences a wide range of physiological, behavioural and ecological traits [68]. Furthermore, there is evidence that plant morphology affects body size and that different body sizes fill different pollination niches in some taxa [69]. Single-trait analysis was chosen over multi-trait analysis because of the nature of identification in this study. Bee body size was measured as the distance between wing bases, intertegular (IT) span, as this measures the thorax that contains the flight muscles, and is correlated with dry bodyweight: IT span = $0.77(mass)^{0.405}$ R^2 = 0.96; mass in mg and IT in mm; [70]. Fly body size was measured as the width of the thorax at its widest point. Each species' maximum and minimum body size represented their range in functional space. FR was compared using individuals' functional range (FR_{is}) following Schleuter, Daufresne, Massol and Argillier [71].

2.5. Data Analysis

Morphospecies individuals were analysed at the level of trap (6 traps × 6 transects) and repeated samples (18 samples) from each trap station were pooled. All statistical analyses of morphospecies abundance and diversity were completed in R statistical software (ver. 4.2.2.) [72]. Species diversity and evenness were compared between habitat types using Shannon–Wiener diversity indices and Pielou's evenness index using the "vegan" package [73]. Species richness and sampling saturation was estimated using rarefied species accumulation curves (specaccum function in "vegan") and by averaging three popular abundance-based extrapolation methods (Chao1, Jack1, Bootstrap) using the specpool function. As sampling effort was the same between and within habitats, for comparison the absolute species richness is analysed and displayed in graphics. Differences in morphospecies composition between habitats were examined by non-metric multidimensional scaling ordination using the metaMDS function in the vegan package. Bray–Curtis dissimilarity was used as it is non-Euclidean and better suited to detecting underlying ecological gradients using ranked data [74]. Solutions were scaled so that one unit change equates to a halving of community similarity. Differences in composition between habitats were also examined by permutational multivariate analysis of variance PerMANOVA; [75], using the ADONIS2 function and Bray–Curtis distance.

The effect of distance from the ecotone on flying insect diversity and abundance was examined for each order using a general linear mixed model (GLMM). Distance of the trap station from the ecotone and forest patch was included as fixed effect and the transect within a forest patch as a random effect. Second-order or higher linear functions were fitted to the models to better illustrate the relationship between insect abundance and distance from the ecotone. Difference in abundance of *E. kamerunicus* and differences in the abundance and diversity of bees were examined between habitats. Bee data were extracted from the Hymenoptera data set. The abundance and diversity of bees and *E. kamerunicus* were compared between habitats using the Kruskal–Wallis test as data did not fit the assumptions of parametric analysis.

Finally, functional diversity between communities was compared using the individual trait variance of species within each community. The FR_{is} score was the union of all species

trait ranges (R_{ts}) in a particular community, standardised by the trait ranges of every species that appears in all communities [71]:

$$R_{ts} = \max_{i \in s}[x_{its}] - \min_{i \in s}[x_{its}] = \int 1_{st}(x)dx$$

$$FR_{Is} = \frac{\bigcup_{s \in Sc} R_{ts}}{\bigcup_{s \in \cup Sc} R_{ts}} = \frac{\int \max_{s \in Sc}[1_{st}(x)]dx}{\int \max_{s \in \cup Sc}[1_{st}(x)]dx}$$

where *t* stands for trait value, *s* for species, *i*∈*s* for individual *i* belonging to species *s* and $1_{st}(x)$ is the indicator function for trait *t* in species *s.*

3. Results

3.1. Habitat Complexity and Physiognomy

Trees occurred at a greater density in forests than in plantation habitats (Figure 2a). There were no pole-sized trees recorded in the plantation habitat. Saplings occurred at a greater density in forests than in plantation habitats where they were absent (Figure 2a).
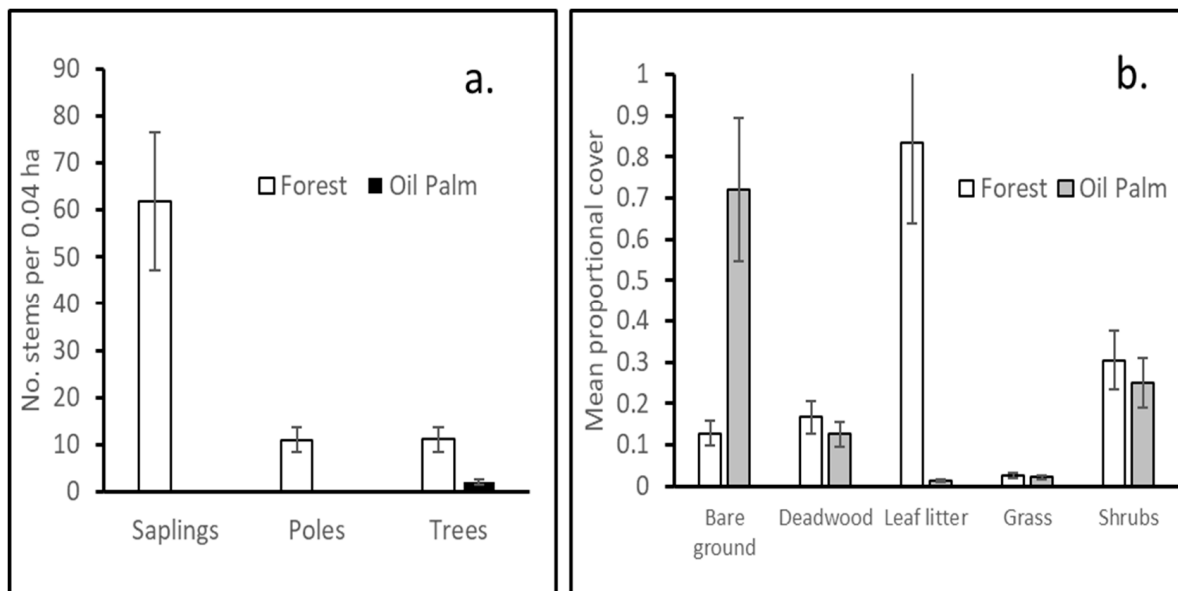

Figure 2. Tree, pole and sapling density (**a**) and proportional cover of bare ground, deadwood, leaf litter, grass and shrubs (**b**) in forest and plantation.

The percentage of canopy cover was 78% in forests and 60% in plantations. Although the two habitats have similar ground cover, the plantation understory was dominated by mosses and ferns and was more open with very low flowering shrub and leaf litter cover (Figures 2b and 3).

3.2. Comparison of Insect Abundance, Diversity and Richness between Habitats

A total of 8917 individuals and 682 species were sampled. More species were recorded in the forest (557) than in the palm oil plantations (471). Rarefied species accumulation curves indicate that all orders in each habitat appear to be reaching their asymptotes (Figure S1) and >74% of species were sampled. Of these, 211 (31%) were unique to the forest habitat, 125 (18%) were unique to the plantation habitat and 346 (51%) species were recorded in both habitat types. Of the six insect orders sampled, the greatest species abundance and richness were recorded for the Coleoptera, with a total of 3587 individuals from 267 morphospecies (Figure 4).

Figure 3. Schematic lateral section through an oil palm plantation (**a**) and a remnant forest patch (**b**). Each section is 50 m in width and 50 m in height and is based on density estimates using 10 m^2 and 20 m^2 quadrats. In the plantation, the understory is dominated by mosses and ferns and is much more open with very little, if any, flowering plant diversity.
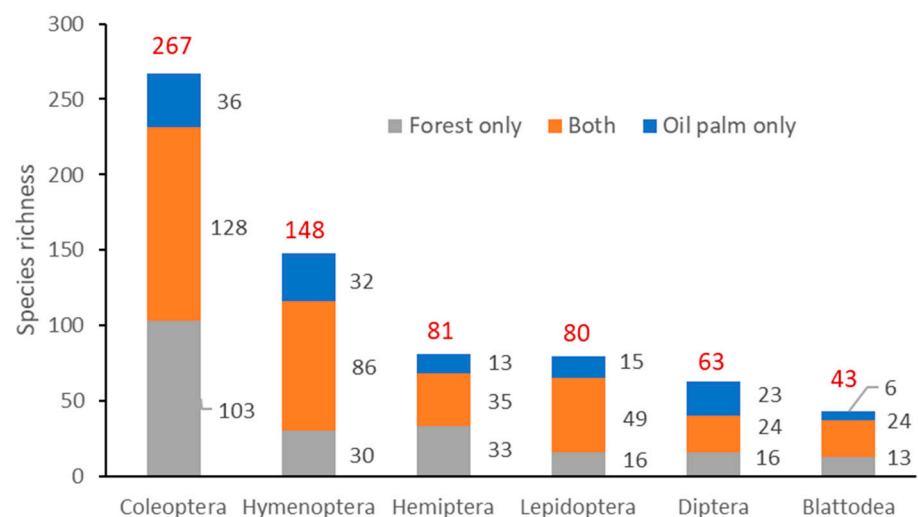

Figure 4. Morphospecies richness by order in forest habitat only, in both forest and plantation habitat and in oil palm plantation only. Morphospecies richness for each order given above each bar in red and alongside for each category.

In the other orders, 782 individuals of Blattodea representing 43 morphospecies; 773 Diptera of 63 morphospecies; 519 Hemiptera of 81 morphospecies; 2524 Hymenoptera of 148 morphospecies, of which 94 were ants, 37 were wasps and 17 were bees; and 732 Lepidoptera comprising 80 morphospecies, of which 3 were butterflies and 75 were moths.

All orders were dominated by a few hyper-abundant species. For example, one species accounted for 17.5% (628 individuals) of total Coleoptera abundance; one species accounted for 30.9% (782 individuals) of all Hymenopterans recorded; and a species of fly represented 37.4% (289 individuals) of the dipterans captured. Diptera and Hymenoptera were significantly more abundant in the plantation habitat (Table 1). Of the 48 species of Diptera sampled in the plantation habitat, three species accounted for 71% of all individuals. Similarly, of the 119 species of Hymenoptera in the plantation habitat, three accounted for 48% of all individuals sampled.

Table 1. Order-level differences in abundance between forest and plantation habitats. Significantly different abundances in bold type.

Order	Adj.R^2	df	MSE	F Value	*p* Value
Blattodea	−0.030	1/33	0.5	0.002	0.963
Coleoptera	−0.005	1/33	0.3	0.8	0.371
Diptera	**0.682**	**1/33**	**0.291**	**73.8**	**<0.005**
Hemiptera Patch 1	0.000	1/15	0.1	1.0	0.334
Hemiptera Patch 2	**0.506**	**1/15**	**0.3**	**18.4**	**0.001**
Hymenoptera	**0.111**	**1/33**	**0.3**	**5.3**	**0.029**
Lepidoptera	0.021	1/33	0.5	1.7	0.195

3.3. Comparison of Community Assemblages between Oil Palm and Forest

In general, species richness and diversity were greatest in the forest for all orders, and community structure was more even (Table 2). Diptera abundance and species richness were greatest in oil palm, and Hymenoptera and Lepidoptera species richness were the same or near identical. Community assemblages differed significantly between forest and plantation (Figure 5; ADONIS2 $F_{1,22}$ = 4.91, *p* < 0.0001), and for some orders between HCV forests and between oil palm estates (Figure 6). For example, Coleoptera forest communities differed significantly from those in oil palm ($F_{1,22}$ = 5.61, *p* < 0.0001), and Saremas 1 communities differed from those in Segarmas (Figure 6). The composition of Blattodea, Hemiptera, Diptera and Hymenoptera communities were significantly different between the two habitat types (Blattodea: $F_{1,22}$ = 3.71, *p* < 0.0001; Hemiptera: $F_{1,22}$ = 2.74, *p* < 0.0003; Diptera: $F_{1,22}$ = 5.86, *p* < 0.0001; Hymenoptera: $F_{1,22}$ = 2.74, *p* < 0.0001), but were not grouped between sites (Figure 6). Lepidoptera communities differed significantly between habitat groups ($F_{3,20}$ = 2.26, *p* < 0.0001), and between Saramas 1 and Segarmas and Bukit Durang and the HCV4 forests (Figure 6).

3.4. Species Richness Gradients across the Forest—Plantation Ecotone

All orders were more species-rich within the forest ecotone (Figure 7). Coleoptera and Hemiptera were more species-rich in the plantation than in the adjacent forest, while the Diptera declined in species richness from forest to oil palm (Figure 7).

For the remaining orders, there was no appreciable difference in species richness between forest and oil palm (Figure 7). These order level patterns of species richness may be mistaken for suggesting that oil palm plantation does not present a hard boundary to insects. However, the striking differences in community composition and turnover between forest and oil palm plantation (see above; Figure 6) emphasises that plantation does significantly filter the insect community.

Coleoptera communities are significantly filtered by oil palm with a significantly different but richer community in plantations. Diptera communities show opposite trends to the Coleoptera with fewer ($F_{1,33}$ = 6.02, *p* < 0.02) and different species in oil palm habitat (Figure 7). Similar differences in community assemblage composition and turnover between habitats (see above) occur in other orders.

Table 2. Insect diversity, richness and abundance for forest and plantation. Data are provided separately for each forest patch and the adjacent plantation. Diversity is according to Chao 1 diversity index; richness according to rarefied species richness, which was calculated based on the lowest number of individuals sampled; and abundance is the number of individuals sampled. H′ is the Shannon–Weiner index, and SR is species richness.

Order	Diversity Index	Forest		Plantation	
		Patch 1	**Patch 2**	**Patch 1**	**Patch 2**
Blattodea	Chao 1	38	62	30	59
	Exp (H′)	14	14	10	12
	Simpson's index	0.908	0.895	0.808	0.848
	Rarefied SR	21	28	22	20
	Observed SR	25	31	22	28
	Abundance	219	154	178	231
Coleoptera	Chao 1	239	279	184	171
	Exp (H′)	57	63	22	36
	Simpson's index	0.966	0.961	0.825	0.944
	Rarefied SR	131	153	115	100
	Observed SR	159	171	131	103
	Abundance	1029	900	913	745
Diptera	Chao 1	52	57	100	38
	Exp (H′)	14	18	8	8
	Simpson's index	0.848	0.925	0.775	0.739
	Rarefied SR	22	24	14	16
	Observed SR	31	25	37	31
	Abundance	100	54	312	307
Hemiptera	Chao 1	76	84	40	58
	Exp (H′)	27	21	20	25
	Simpson's index	0.952	0.847	0.931	0.948
	Rarefied SR	31	29	31	27
	Observed SR	37	55	29	33
	Abundance	86	273	93	67
Hymenoptera	Chao 1	125	96	147	110
	Exp (H′)	25	21	19	24
	Simpson's index	0.878	0.847	0.861	0.900
	Rarefied SR	81	72	69	68
	Observed SR	94	73	89	85
	Abundance	567	409	840	708
Lepidoptera	Chao 1	63	78	54	60
	Exp (H′)	28	33	22	24
	Simpson's index	0.946	0.956	0.934	0.924
	Rarefied SR	41	41	34	29
	Observed SR	42	52	39	51
	Abundance	103	158	186	285
	Total species	391	404	349	320

3.5. Changes in Abundance across the Forest—Plantation Ecotone

The abundance of individuals in each order broadly followed the trends observed for species richness (Figure 8). There were significantly fewer Diptera and Lepidoptera individuals, and significantly more Hemiptera individuals, in oil palm plantations than in forests. Coleoptera, Blattodea and Hymenoptera did not differ in abundance between habitats (Figure 8).
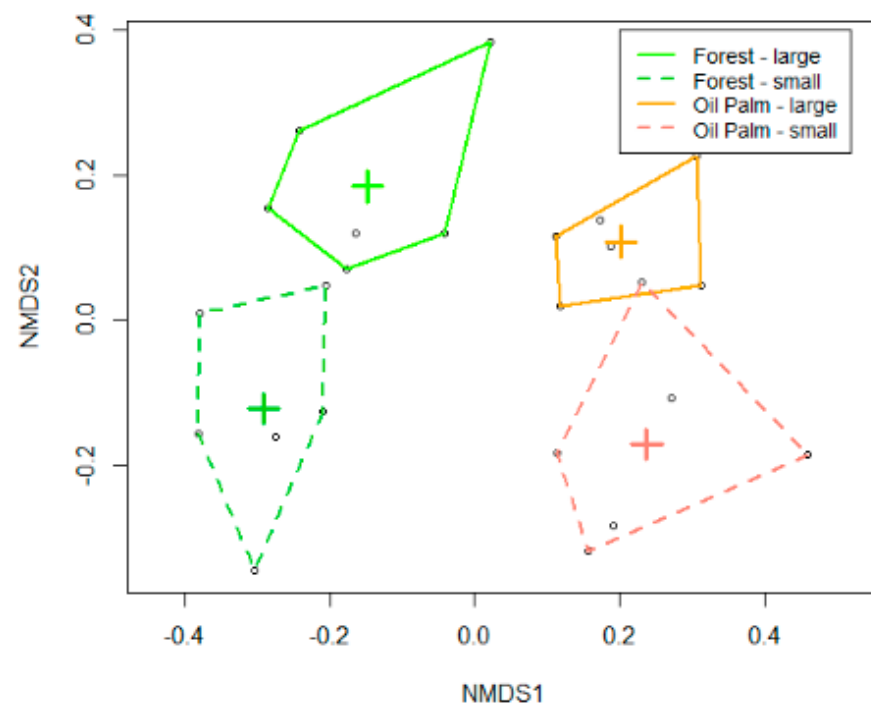
Figure 5. Non-metric multidimensional scaling (MDS) ordination of species assemblages comprising all orders examined in this study. Assemblages are grouped separately for the two forest fragments and their adjacent oil palm plantations.
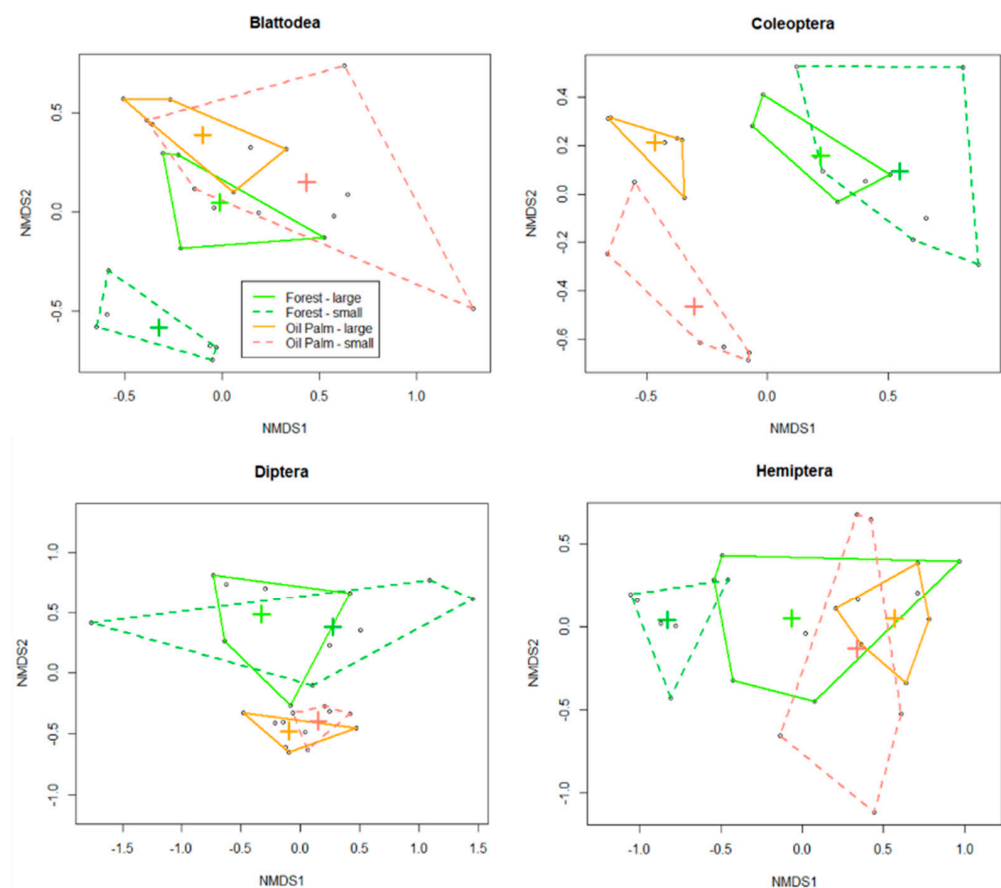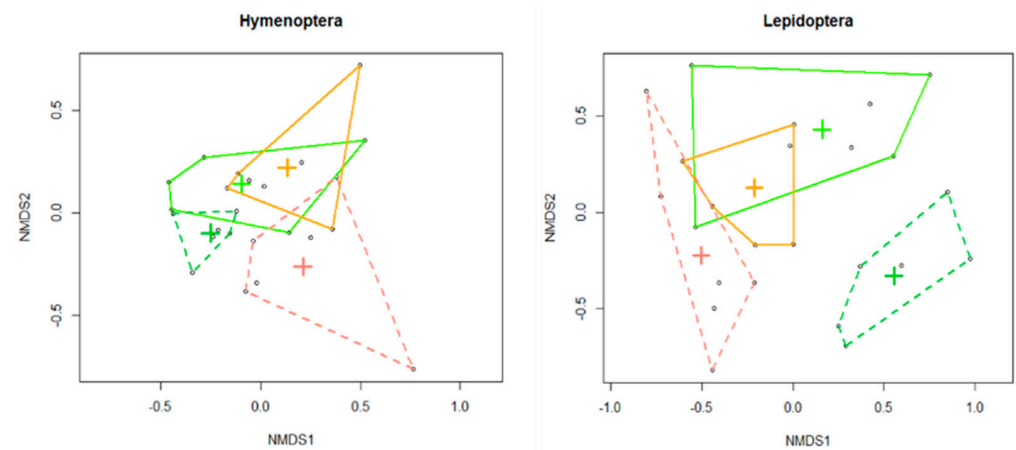

Figure 6. *Cont*.

Figure 6. Non-metric multidimensional scaling (MDS) ordination of order level species assemblages between habitats (see legend in Blattodea) at transect scale.
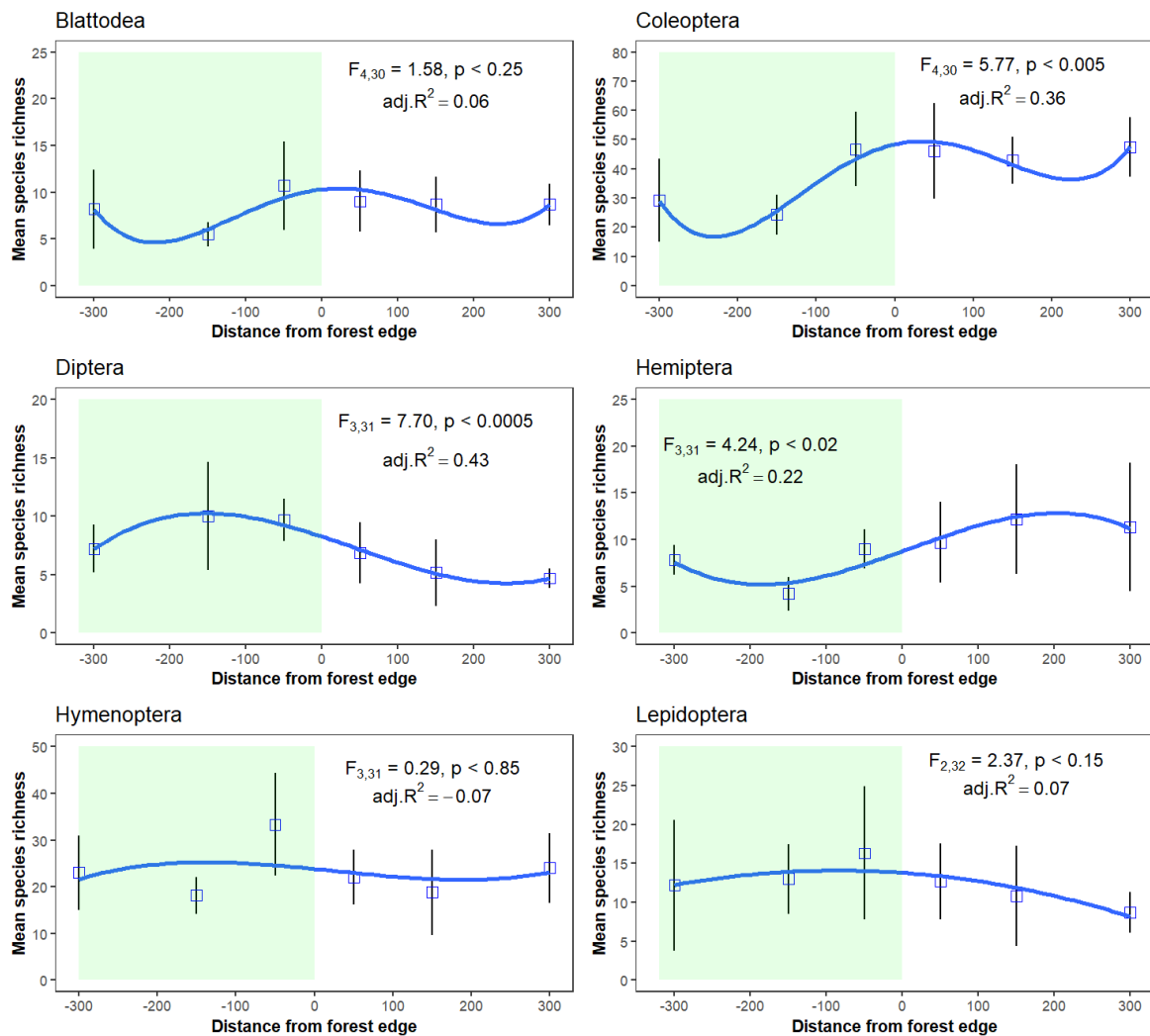

Figure 7. Species richness across the ecotone from forest (green) to plantation (white). Fitted lines are second- or third-order linear functions. Data points are the mean species richness (n = 6 transects) and their 95% confidence limits. The fit of the models is given by the F-test and adjusted R^2.
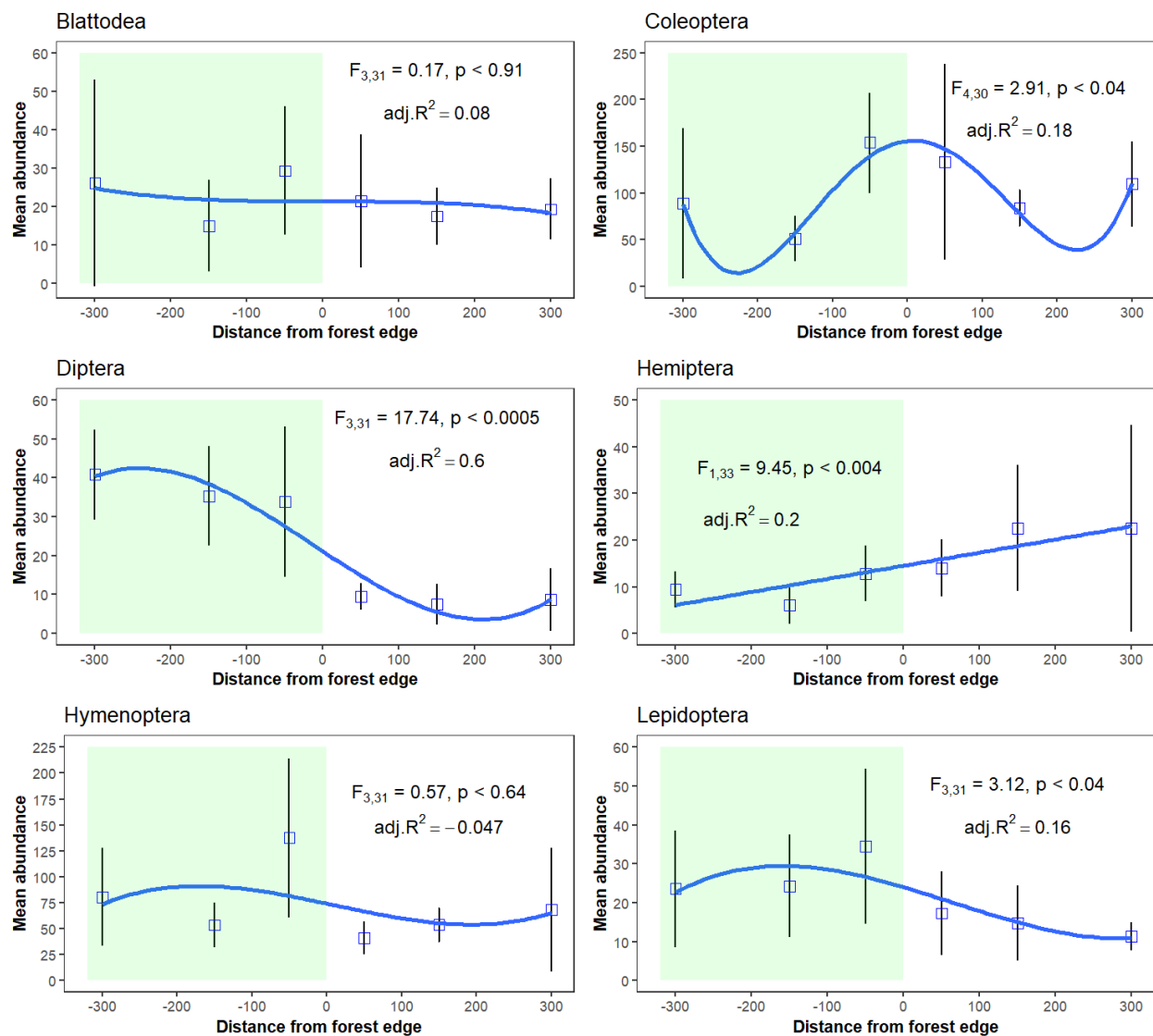
Figure 8. Mean abundance (number of individuals trapped) across the ecotone from forest (green) to plantation (white) for each order. Fitted lines are first-, second- or third-order linear functions. Data points are the mean abundance (n = 6 transects) and their 95% confidence limits. The fit of the models is given by the F-test and adjusted R^2.

3.6. Potential Native Pollinators of Oil Palm

Thrips (Thysanoptera) are native pollinators of oil palm [76]. Significantly fewer thrip individuals (n = 30, 27.3%) were found in forest patches than in oil palm plantations (n = 80, 72.7%; t = −2.63, df = 22, p = 0.015). Thrip abundance did not increase with proximity to the forest ecotone (R^2 = 0.044, $F_{1,4}$ = 2.02, p = 0.170) as observed in many orders.

A few of the introduced oil palm pollinating weevils, *Elaiedobius kamerunicus* were collected in the traps (n = 22). Most of these individuals were found in the oil palm plantation (86.4%, n = 19; χ^2 = 7.94, df = 1, p = 0.005; Figure 9).

Ninety-two bee individuals were sampled from seventeen species. Six species were unique to the plantation habitat and four species to the forest habitat, while seven species were found in both habitats. Bee abundance did not differ significantly between habitats (χ^2 = 2.13, df = 1, p = 0.145; Figure 9, Table S1).
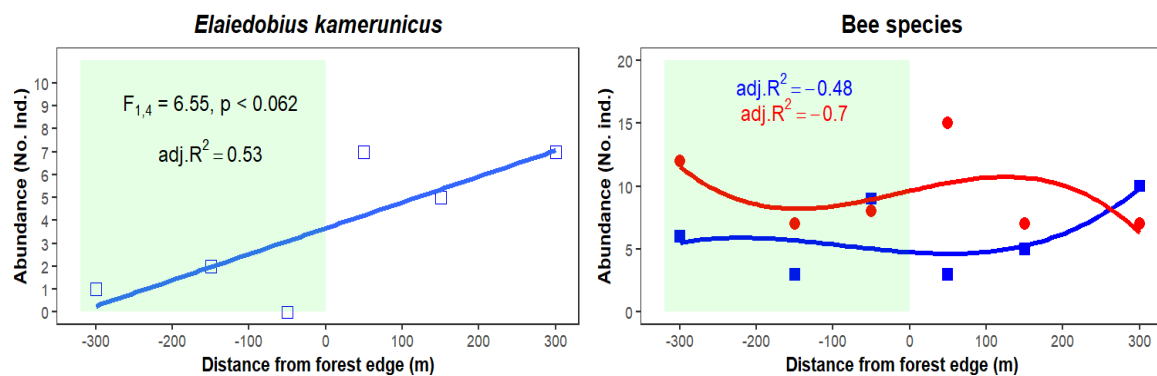
Figure 9. Abundance of *Elaiedobius kamerunicus,* the introduced palm oil weevil, and all bee species across the ecotone from forest (green) to plantation (white). Bukit Durang and adjacent plantation (■) and the small HCV 4 forest and adjacent plantation (●) are plotted separately for bees and the pooled data for both forest patches (□) for *E. kamerunicus.*

3.7. Functional Diversity of Potential Bee and Fly Pollinator Species

Bee functional diversity (17 species) across all habitats was lower (FR_{is} = 2) than fly functional diversity (28 species; FR_{is} = 3.620). Bee functional diversity was greater in oil palm (FR_{is} = 0.950) than in the HCV forest patches (HCV4 FR_{is} = 0.895; Bukit Durang FR_{is} = 0.860) (Figure S2). Diptera displayed the opposite relationship with assemblages in HCV forests presenting greater functional diversity (HCV4 FR_{is} = 0.980; Bukit Durang FR_{is} = 1.000) than oil palm (FR_{is} = 0.765) (Figure S3). Both bee and fly assemblages had a high proportion of functionally redundant species (Diptera 57%, n = 16 species; Bee 58%, n = 10 species). Both assemblages were dominated by species with a broad range of functional traits. For instance, fly species-14 presented 21% and bee species-2 presented 28% of the total trait range. The bee community also included two species with an extreme trait value but a low variation, increasing the trait range by 70%.

4. Discussion

4.1. Comparing Forest and Plantation Insect Assemblages

In spite of the potential of native species as pollinators of oil palm, Edwards, Edwards [61] found that their net effect on oil palm yield was neutral. They urged a more nuanced assessment of the effects of forest remnants and their biodiversity on oil palm yields, and that the benefits of retaining forest remnants are dependent on their size and number. At current levels, the retention of remnants is not beneficial to the environment as a whole, with HCVs supporting only fractionally more diversity than the oil palm itself [62,77]. The reduced assemblages of dung beetles [78], termites [79] and birds [18,80] in remnant forests have low functional diversity, affecting ecosystem services. Nevertheless, retaining old growth forests on the boundary of plantations does significantly increase biodiversity [81], and the current opinion is that conservation efforts are best focused on conserving larger remaining primary and secondary forests.

In this study, both species diversity and richness were lower in oil palms than in forests. The difference between habitats (Figure 5) was consistent with other studies [34] with on average 28.1% (s.e. = 4.3%) of species among the orders being unique to oil palm (Table 1, Figure 4) and 71.9 ± 4.3% of species found in both forest and oil palm. Only the Hemiptera were less species-rich in the forest than in oil palm habitats. Coleoptera species richness was greater than expected in oil palm when compared to primary and logged forest and oil palm [26].

A similarity in species diversity among habitats is usually ascribed, in part, to the influence of habitat patch size and isolation [82]. It is likely that species lost when forest is converted to oil palm are replaced by disturbance-tolerant generalist species [24–26]. Our results support species replacement rather than retention, with plantation communities in all orders differing in assemblage composition from their respective forest assemblages

(Figure 6). Both retention of important forest species [45] and replacement of forest species in oil palm [78] have been observed. However, in the Coleoptera, species replacement was less than expected from continuous forest adjacent to the plantation [64,77]. This suggests that while they experience large losses of diversity, forest fragments are able to retain some hardy forest species [78,83], and that a select number of generalists dominated the community, with several species in oil palm reaching exceptionally high abundances, reducing species evenness and increasing total abundances in oil palm (Table 1).

4.2. Plantation Boundary Effect on Insect Assemblages

The oil palm plantation boundary is an environmental filter and affects flying insects in two ways. First, it filters species by habitat so that in most orders the composition of assemblages was different in plantation from forest (Figure 6). Second, species richness and abundance are expected to decline with distance into the plantation. In this study, species richness and abundance trends did not decline as expected (Figures 7 and 8). These trends are likely confounded by species replacement in oil palm by generalist species [83] and perhaps by the relatively short distance surveyed (300 m) into the plantation. Thus, the oil palm boundary represents a hard boundary for habitat specialists and a soft boundary for generalist species. In general, a decline in species richness and abundance with distance into oil palm is explained by high levels of functional redundancy among generalist species, and secondly by an assumed increase in competition among functionally similar species with increasing simplification of the oil palm habitat with distance from the forest–plantation ecotone (Figures 2 and 3). The latter trends were most notable for native Coleoptera (Figures 7 and 8), although the introduced weevil increased in abundance further into the plantation (Figure 9). Consistent with the observed richness across the forest–oil palm habitat gradient [64], Lepidoptera were more diverse at the habitat boundary (Figure 7). However, while Lepidoptera typical of tropical forests have been observed in plantation habitats, species that are common in oil palm have not been observed in forest [40]. *Pyroderces* species of moth known to occur in forests, and are possible pollinators of oil palm, were not identified in this study. Boundary filtering of the oil palm weevil and thrips was not observed. There was a strong distance effect on the richness and abundance of Diptera in oil palm plantations (Figure 7). Despite the abundance of Diptera and Hymenoptera in the plantation environment, there was at best a weak forest edge effect with few "oil palm" species penetrating into the forest, consistent with the findings of Lucey and Hill [40].

4.3. Potential Native Oil Palm Pollinators

Neither thrips nor *E. kamerunicus* increased in abundance with proximity to forests (Figure 9) and appear to be oil palm-dependent species [57]. Both were significantly more abundant in oil palm than in forest. This concurs with previous studies that show that native oil palm pollinators are not found in close proximity to forest [57] and palm oil yield does not decline in proximity to forest [61]. In fact, the forest provides a reservoir for parasites and predators of native oil palm pollinators affecting yield [84]. Other tropical crops such as coffee show the opposite yield trends [85,86]. However, coffee plantations are a mix of crop and non-crop plants, rather than a monoculture, and are more hospitable to forest species [87]. Trends in the diversity of Lepidoptera in oil palm suggest that moths may be potential pollinators too. However, potential oil palm pollinator moths of the genus *Pyroderces* could not be identified in the field. Their abundance and effect on yields should be investigated. Coleoptera richness across the distance gradient did not predict *E. kamerunicus* abundance patterns in this study.

4.4. Functional Diversity of Potential Pollinator Taxa

The diversity of bees in an oil palm plantation on Peninsula Malaysia (17 species) [27] was similar to the 11 species sampled in oil palm in this study. However, diversity indices do not reflect the ecological importance of species. We examined the proposition that bee

species are differentiated according to their functional traits and capability. We intuitively expected bee functional diversity to be greatest in the complex forest habitat but found that it was greatest in oil palm. This accords with Liow, Sodhi's [27] finding that bee diversity was greatest in oil palm landscapes. The smaller of the two forest patches sustained higher functional diversity than the larger Bukit Durang area. Bukit Durang is a long and thin forest (Figure 3) with greater edge effects on bee diversity [88] than Saremas 1 HCV 4. A reduction in core habitat is known to result in the loss of specialist forest species and forest size and shape may limit species diversity and their functional diversity.

Diptera functional diversity was commensurate with trends in the literature with higher functional diversity in forest patches [78–80]. Saremas 1 HCV4 had far fewer species than the oil palm, but the absent species were functionally redundant. In contrast, species absent from oil palm included two functionally extreme species that were not replaced by disturbance-tolerant species. We conclude that the functional diversity of bees and flies in oil palm is not limiting the potential for these orders to be native pollinators of oil palm.

4.5. Do Forest Refugia Benefit Oil Palm?

Forest patches within the oil palm landscape provide essential ecological services to palm oil plantations. This study shows that native pollinator species that reside in forest refugia have the potential to supplement pollination by the introduced oil palm weevil [89]. Retaining more native forest vegetation on palm oil estates can provide pollination services but also provide benefits to soil and water retention and quality, as well as improving and sustaining biodiversity. Riperian habitat, when large enough, can effectively combat soil erosion and protect waterways [60]. The latter is essential for proper environmental certification of palm oil products. Furthermore, forest refugia are necessary to support connectivity and the maintenance of metapopulations of wildlife that would otherwise undergo area- and isolation-dependent extirpation. This study demonstrates that forest refugia may be important species pools or sources for generalist and highly mobile insects [23,90]. Insect community assemblages are known to differ between forest and oil palm [23] and these differences were also observed in this study. Clearly, some insect taxa perceive the oil palm boundary as a hard boundary (hence the differences in assemblage structure and composition), for others such as Coleoptera and Lepidoptera, it is a soft boundary. Butterflies are able to migrate long distances with relatively high accuracy [91]. Previous research on bird diversity and abundance in wildlife-friendly oil palm estates found that while the retention of forest fragments is desirable [81], protecting contiguous forests on or adjacent to estates is preferred [77]. An analysis of the complexity of the food web and community structure [92–94] on oil palms estates with different amounts of forest refugia is needed to establish what level of forest cover and connectivity is best in planning and restoring oil palm estates [22,33].

5. Conclusions

Several key findings relating to environmentally responsible management of oil palm landscapes can be derived from this study.

1. While insect diversity in oil palms is generally lower than in forests, the differences in richness reported in other studies were not observed. In this study, this may be due to sampling insects in oil palms in relative proximity (within 300 m) to forests. Nevertheless, the value of retaining forest fragments within oil palm-dominated landscapes is indicated by the high proportion of species (72%, 346 species) recorded in both habitat types.
2. Insect assemblage composition differed between forest and oil palm and to a lesser extent between the forests examined in this study. Clearly, not all forests are the same and community dynamics may differ among fragments dependent on their area and isolation characteristics and history. Optimizing the retention of forest fragments with different characteristics and history on oil palm landscapes is recommended, but the larger and less linear (except for riparian forests) the better.

3. While species richness was slightly less and potentially different (see Point 2) in oil palm from forests, species evenness in oil palm was low and dominated by a few species, especially among the Coleoptera, Hymenoptera and Diptera. These dominant species are likely generalists [24–26], capable of persisting in oil palm and should be more closely investigated for their potential as native pollinators of oil palm.

4. Identifying orders and related species, such as Lepidoptera, for whom oil palm presents a softer and more permeable boundary is an essential step in managing oil palm for both environmental and economic viability. Retaining riparian forests is important for retaining native species, especially moths in the genus *Pyroderces*, that may have the potential to pollinate oil palm [81,95].

5. The abundance of the oil palm weevils (*Elaeodobius kamerunicus*) was low compared to the native dominants, but similar to levels displayed by native thrips that may be pollinators of oil palm. In addition, the weevil was more abundant further into oil palm. Previous studies show no decline in oil palm yield with proximity to the boundary, suggesting that either the low abundance of the weevil is sufficient for the economic viability of oil palm, or that native species assume the role of pollinators near forest fragments. It is likely a combination of the latter, but further species-focused research is required [96,97], especially thrip species [76,98] and moths in the genus *Pyroderces* [95,99].

6. The functional diversity of well-known pollinator guilds—bees and flies—was similar in forest and oil palm, suggesting that potential pollinators may yet exist among native orders of insects. Ongoing reviews of potential pollinators are advised, as the functional diversity of potential native pollinators suggests sufficient phenotypic plasticity to adapt to pollinating oil palms.

7. The estate management policy of planting non-native flowering plants along roadsides, and its effect on potential insect pollinator diversity in oil palm, needs to be reviewed for its effectiveness. Management of the moss- and fern-dominated understorey in oil palm to increase the abundance of flowering plants is recommended.

8. Finally, conserving and including forest fragments in an oil palm-dominated landscape has mainly positive benefits for the environment and oil palm productivity. Some have argued that these benefits are outweighed by the benefits of focusing on protecting remaining continuous forests through a large-scale land-sparing approach [4,22,77,100]. However, where oil palm establishment has occurred or is inevitable, as much native forest habitat should be included on estates as possible, especially well-buffered (wide) riparian forests [45,60].

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