The role of ants, birds and bats for ecosystem functions and yield in oil palm plantations

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Abstract

One of the world's most important and rapidly expanding crops, oil palm, is associated with low levels of biodiversity. Changes in predator communities might alter ecosystem services and subsequently sustainable management but these links have received little attention to date. Here, for the first time, we manipulated ant and flying vertebrate (birds and bats) access to oil palms in six smallholder plantations in Sumatra (Indonesia), and measured effects on arthropod communities, related ecosystem functions (herbivory, predation, decomposition and pollination) and crop yield. Arthropod predators increased in response to reductions in ant and bird access, but the overall effect of experimental manipulations on ecosystem functions was minimal. Similarly, effects on yield were not significant. We conclude that ecosystem functions and productivity in oil palm are, under current levels of low pest pressure and large pollinator populations, robust to large reductions of major predators.

Introduction

Conversion of natural forests to agricultural systems results in considerable losses in biodiversity (Newbold et al. 2015), yet the remaining biodiversity can play an important role through supporting ecosystem functions and services, alongside inputs such as fertilisers and labour (Fischer et al. 2006). In tropical agricultural systems, species groups including ants, birds and bats contribute to a number of ecosystem services, in particular predation (biocontrol), soil aeration and nutrient cycling (Folgarait 1998, Vandermeer et al. 2002, Evans et al. 2011), and have been shown to positively affect yield (Evans et al. 2011, Wielgoss et al. 2014, Maas et al. 2015, Maine and Boyles 2015). Currently the most rapidly expanding tropical perennial crop is oil palm, the world's most important oilseed commodity (Phalan et al. 2013). Despite the importance of oil palm, there have been few studies linking biodiversity and function (e.g. Dejean et al. 1997, Koh 2008, Slade et al. 2014) and the majority of these have looked at only one function or service (but see, Gray and Lewis 2014) and no studies as yet have analysed the relationship between biodiversity, functions and yield.

Almost all organisms studied thus far show a steep decrease in species diversity from forest to oil palm (Fitzherbert et al. 2008, Foster et al. 2011, Barnes et al. 2014). In smallholder plantations, bird communities in particular are dominated by generalist omnivorous species, but abundances are relatively high (Azhar et al. 2011, Jambari et al. 2012, Prabowo et al. 2016). More importantly, this biodiversity loss is often non-random, endangering ecosystem functioning (Fitzherbert et al. 2008, Senior et al. 2013). However, certain management practices can promote biodiversity in oil palm plantations (Chung et al. 2000, Nájera and Simonetti 2010, Teuscher et al. 2015). Plantation owners are unlikely to adopt new management practices to increase biodiversity alone. However, if there is a positive relationship between biodiversity and yield or any beneficial ecosystem service, this could influence a plantation owner's willingness to alter management practices.

While ant species richness and abundance in oil palm can equal, exceed or be less than that in lowland rainforest dependent on the study area and strata investigated (e.g. Denmead et al. in review, Room 1975, Fayle et al. 2010, Rubiana et al. 2015), species and functional composition is always drastically altered (Senior et al. 2013, Luke et al. 2014, Rubiana et al. 2015). Therefore, although ants remain dominant and likely play an important part in oil palm plantations, their influence on the community and certain ecosystem functions may be altered which is particularly important in regards to their potential for biocontrol (Way and Khoo 1992, Dejean et al. 1997). Furthermore, birds and bats can reduce the abundance of arthropod communities in agricultural systems, which results in lower herbivory and higher yields (Maas et al. 2015). For instance, birds can lower leaf damage by pests in young, unproductive oil palms (Koh 2008). However, null and negative effects of birds and bats on herbivory and yield have also been reported for other systems (e.g. Gras et al. 2016).

Exclusion studies have become an important method for determining the effects of key taxa on community composition and ecosystem processes. Exclosures manipulating ants, birds and bats can predict their effect on arthropod communities, which contribute to key ecosystem functions strongly related to crop productivity. Studies manipulating these predator groups within one experiment are scarce (but see Gras et al. 2016) but have exhibited important intra-guild interactions that led to non-additive effects (Maas et al. 2015). In the present study, we established a one year long, large-scale full-factorial combination of flying vertebrate (birds and bats) and ant exclosures in young, productive oil palm plantations in Sumatra, Indonesia. We comprehensively assess the influence of ants, birds and bats on arthropod communities and associated ecosystem functions and services, including herbivory, predation, pollination (using pollinators as a proxy), decomposition and oil palm yield. This is the first study to assess the impact of predator exclusions on oil palm yield.

Methods

Study area

The experiment was carried out in the Batanghari Regency of Jambi Province, Sumatra, Indonesia. The climate of the region can be characterised as tropical humid, with more than 2000 mm rainfall per year (Allen et al. 2015) and a long sunshine duration of an average 6h/day. Thus, it is classified as suitable for oil palm production (Corley and Tinker 2016), and attainable yields are above 30,000 kg FFB/ha/year (FFB=fresh fruit bunch) during the most productive phase in the life cycle of the oil palm (Hoffmann et al. 2014). Over the past 20 years oil palm has become one of the most dominant crops in the Province, increasing almost 4-fold from 150,000 ha to 550,000 in the period from 1996 to 2011 (Gatto et al. 2014).

Experimental design

Six smallholder oil palm plantations were selected in the study area for inclusion in this study with a minimum distance between the sites of 1.0 km (mean distance to closest site: 2.4 km; Appendix S1, Figure S1). We chose oil palm sites with trees that were 2–3 years old as this is the age at which harvesting begins in our region, which also allows experimental installation of cages. The plantation management was consistent with plantations in the study area and site conditions were similar (Supplementary methods, Appendix S1, Table S1). Within each plantation we created a full factorial combination of ant and flying vertebrate (bird and bat) exclusion plots, and each plot's location was randomly assigned (Figure 1). This resulted in four experimental plots per site: control, ant exclusion only, flying vertebrate exclusion only and both ant and flying vertebrate exclusion. Each plot was approximately 16 × 16 m large, encompassing four oil palm trees.

Exclusion methodology

Two methods were used to suppress ants in the exclusion plots. A 50 cm high aluminium barrier was established surrounding the plot, buried 20 cm beneath the soil and the top of the barrier was covered in insect glue (Tanglefoot, Contech Enterprises Inc., British Columbia). The glue was regularly checked and replaced when dry. We also carried out toxic baiting five days per week

and targeted poisoning of ant nests during the first month of the experiment and then toxic baiting three times per week for the duration of the experiment. The toxic baiting consisted of placing sugar and tuna as attractants (Klimes et al. 2011) , mixed with the insecticide chlorpyrifos (Dursban[TM] 200EC, Dow AgriSciences, Jakarta, Indonesia) in nine random locations (one in each tree, five on the ground) in each ant suppression plot for a minimum of one hour.

Flying vertebrate (birds and bats) exclusion cages were constructed by assembling a metal structure consisting of nine 5.0–5.5 m high iron poles (2.5 inches diameter). The poles were embedded in concrete foundations, lined with plastic bags to prevent leaching of carbonate to the soil. Fish nets (35 × 35 mm mesh size, transparent nylon) were pulled over the structure and fastened to the ground. The chosen mesh size prevented most birds from entering but also could have excluded some larger arthropods (e.g some large Coleoptera, Odonata and Lepidoptera). Due to the size of the exclosure and the length of the experiment it was not possible to use removable nets that could be manipulated to differentiate between the effects of vertebrates with day or night activity (i.e., birds and bats; Maas et al., 2013). Ant suppression and bird and bat exclusion was continuous for one year, from August 2013 until August 2014 in four out of six plots, and from May 2014 to May 2015 for the other two. In October 2014, we attached red-white flagging tape to all of our cages to prevent further flying vertebrates becoming entangled in our exclusion nets. Prior to this, seven bats and six birds in total had died after becoming entangled. Following installation none were entangled.

Monitoring of manipulated predators

Ants were surveyed monthly in every plot (including controls) to assess their abundance and to monitor the effectiveness of the ant suppression methods. We used two plastic observation plates per plot with two baits of 2 cm^3 of tuna in oil and two sponges saturated with 70% sugar solution attached (Wielgoss et al. 2010). At 15, 30, 45 and 60 minutes after placing the plates on the ground the abundance of each ant species present on the plate was recorded. Specimens were collected from each ant species present and were identified to species or morpho-species level (Fayle et al. 2014). The abundance of each ant species at a given plot each month was defined as the mean of the maximum number of that species on each plate (at any time measurement) used at that plot. The sum of all species abundances at each plot determined the total ant abundance each month, which was then averaged across all months (hereafter, "average ant abundance").

Bird and bat calls were recorded in January (4 sites) and July (6 sites) 2014, and January 2015 (remaining two sites) with automated sound recorders attached to the central oil palm, and fitted with one acoustic and one ultrasound microphone (SM2Bat+ recorder, SMX-II and SMX-US microphones, Wildlife Acoustics Inc., Massachusetts, USA). We recorded sound for 48 hours starting at sunset, and programmed a sampling rate of 44.1 kHz during the day and a sampling rate of 192 kHz at night. Bird and bat recordings were processed using an online sound platform (http://soundefforts.uni-goettingen.de/). Two ornithologists identified bird species in one morning

recording per plot for each month (40 min after sunrise). We classified bird species into feeding guilds based on Thiollay et al. (1995) and data not contained in Thiollay et al. (Thiollay 1995) were retrieved from del Hoyo et al. (2015). The distance to calling birds was estimated by the ornithologist and checked by an additional listener. We excluded calls beyond 35 m, which could potentially come from neighbouring plantations or other vegetation. For bats, night recordings of 40 min per plot for each month (starting from 18:30) were time-expanded by a factor of 4 (from 192 to 48 kHz sampling frequency) to make bat ultrasound calls audible. For insectivorous and omnivorous birds as well as insectivorous (echolocating) bats, we used the total duration of their vocalizations in each plot to measure their activity in minutes, which is an extension of the acoustic activity index (Miller 2001). The activity of birds and bats inside cages was assumed to be zero.

Sampling methods

Soil and tree variables

In each plot we measured four variables which could potentially vary between and within sites and influence our experiment's response variables to be included in our analysis: Soil pH (H_2O), soil texture (clay content), initial oil palm height, and oil palm red/green leaf colour ratios (Appendix S1). We took soil cores in each experimental plot at a depth of 50 cm eight months after experiment start and measured soil pH and texture using standard methods (Appendix S1) to assess soil conditions at our plots. Initial oil palm height (from oil palm base to tip of the meristem) was measured to account for oil palm developmental stage. Finally, the occurrence of red and brown spots on the oil palm leaves was determined by analysis of the red and green components of leaf JPEG photographs taken for herbivory measurements to estimate a red/green leaf area ratio to gauge the proportion of the leaves that had photosynthetic activity (Appendix S1 Figure S2).

Final arthropod collection and identification

The arthropod communities present in the oil palms were sampled intensively after one year of exclusion through three destructive survey methods: insecticide spraying, beating and vacuuming. All methods were completed at one plot before moving to the next. First we laid four 0.9 m x 2.9 m white sheets on the ground at right angles from four points at the base of the trunk of each oil palm. One person then walked around the palms twice spraying an insecticide with knock-down effect (Deltamethrin, Decis ® 2,5 EC, Bayer CropScience, Jakarta, Indonesia) over each palm using a knapsack sprayer. After 15 min all arthropods on the sheets were collected. Next, the beating method was completed by holding a 5 m × 3 m sheet under four different fronds per palm and shaking the frond up and down so arthropods dropped onto the sheet. All arthropods that had dropped onto the sheet were collected. Finally, arthropods in the oil palm leaf axils and flowers were collected by vacuuming the axils for four minutes per palm using a modified vacuum cleaner.

Arthropods were counted and identified to taxonomic groups (Lawson 1959, Johnson and Triplehorn 2004, Mathews et al. 2007) which allowed their assignment to feeding guilds: herbivores, predators, detritivores and omnivores based on literature and morphological characteristics (Appendix S1, Table S2). Fungivores and nectarivores were excluded from the dataset due to low numbers and little relevance for the considered ecosystem functions. For analysis, arthropods were grouped within feeding guild by habitat; individuals from beating and insecticide spraying samples were pooled to represent frond communities and the vacuum samples represent trunk communities. The introduced oil palm pollinator *Elaeidobius kamerunicus* (Coleoptera: Curculionidae) was excluded from the arthropod dataset due to its use as a proxy for pollination in our ecosystem function analysis (see below). Ants collected as part of these samples were excluded from subsequent analyses of predators.

Ecosystem functions

In each of the plots, data on four important ecosystem functions were collected: herbivory, decomposition, predation and pollination.

Herbivory was quantified using photos of two leaflets (pinnae) from four randomly selected fronds per palm (eight leaflets per palm). Percentage leaf loss per photo was calculated using ImageJ software and converted to an average leaf loss per palm. These photos were taken at nine months after exclusion

Leaf-litter decomposition was measured using litter bags (Falconer et al. 1933). Litter bags were 20 cm × 20 cm and made from glass fibre with a 4 × 4 mm mesh size. Each litter bag contained a known dry weight (10.0 g ± 0.05 g) of oil palm leaves. Four litter bags were placed at random points within each plot approximately seven months after the experiment began. After four and a half months the litter bags were collected and the remaining contents were air dried and weighed. Any dirt or vegetation within the bags was removed before weighing. Initial weight minus weight at collection divided by days exposed determined the decomposition rate.

Predation rates were estimated using three different prey sizes. To represent the large prey size we used dummy caterpillars modelled on (similar size and colour) a common species of nettle caterpillar that is known to attack oil palm (*Setothosea asigna*). Although dummy caterpillars may reflect a lower predation rate than the real rate in the field, they can be used to compare relative predation rates between different sites/plots (Howe et al. 2009) and the bite marks can be identified in most cases (providing important additional data), which is not the case with many real bait types. Four dummy caterpillars were glued to a leaflet on four different fronds on each oil palm (four caterpillars/palm) and collected 48 hours later. Each caterpillar was defined as predated (visible marks present in the clay) or not (no marks present) and missing caterpillars were excluded from analysis. This method was carried out four and eight months after exclusion started. To represent a medium and small prey size we used dead crickets (*Acheta domesticus*) and aphids (*Aphidoidea* sp.) respectively. Four individuals were glued onto a piece of card and then one card was glued to four

different fronds on each oil palm (16 individuals/palm for both prey). Cards were checked after two hours for crickets and four hours for aphids, and each individual was defined as predated (visible marks present, or individual missing) or not (no marks present). The cricket predation method was carried out at 12 months, and the aphid predation method at 11 and 12 (first four sites), and five and eight (last two sites) months after exclusion.

We used the abundance of the oil palm pollinator weevil, *E. kamerunicus* (weevil abundance) collected at final arthropod sampling as a proxy for pollination in our ecosystem functions analysis. *E. kamerunicus* was introduced to South East Asia in the 1980s and is now the main pollinator of oil palm in the area (Foster et al. 2011). The introduction resulted in an approximate 20% increase in yield and removed the need for hand pollination (Greathead 1983, Foster et al. 2011).

Oil palm yield

Yield measurements continued throughout the experiment and six months after exclusion ended (total = 18 months), except for one plot where the plantation owner decided to terminate their partnership with the experiment at exclusion end (site EO2, Appendix S1, Figure S3). Plantation keepers harvested fruit bunches following their normal schedule (twice per month). Yield as fresh fruit bunch weight (kg/palm) was calculated as a result of recorded bunch number and mass for each palm. In oil palm, pollinated flowers take 5-6 months until they reach bunch maturity (Verheye 2010), therefore we discarded the first six months of data and used the following 12 months' data in order to reduce carry-over effects from the pre-study period. Also, a few palms had not developed mature bunches by the experiment start, therefore, we computed yield by time by dividing yield by the number of days since the first harvest (FFB (kg/palm)/day) (Appendix S1, Figure S3). Two palms (out of 96) that were never harvested were excluded from the overall analysis. Analysis of all 18 months of yield data (FFB (kg/palm)/day) was also included in the supporting information.

Statistical analysis

Effectiveness of ant suppression

We used linear mixed effects models (LMMs) to determine the effect of ant suppression (independent of bird/bat exclusion) on ant abundance and species richness in the experimental plots with plantation (experiment site) included as a random effect. To meet assumptions of normality, ant abundance was log-transformed prior to analysis. LMMs were conducted using the nlme (Pinheiro et al. 2015) package in R 3.2.0 (R Core Team 2015).

Statistical model construction

We used generalized linear-mixed effect models (GLMMs) to determine the effect of the manipulated predators on the trunk and frond arthropod feeding guild abundances (predator, herbivore, detritivore and omnivore, excluding ants), pollinator (weevil) abundances, oil palm herbivory (% leaf loss), decomposition rate (g/day), predation rates (of dummy caterpillars, crickets, and aphids), oil palm bunches (day^{-1}), bunch mass (kg), and oil palm yield (FFB (kg/palm)/day). Negative binomial distributions were specified for modelling arthropod abundances, binomial distributions were specified for modelling predation rates - where we used the counts of predated and unpredated prey items – and normal distributions were used for all other variables. Experimental treatment consisted of three continuous variables: average ant abundance (determined from monthly baiting plate surveys), bird activity and bat activity (measured in minutes; bird and bat activity in caged plots was set to zero). To account for the different combinations of exclusion we included an interaction term for ants and birds and ants and bats. We used these three continuous variables instead of the factorial treatment to account for the variation in the effectiveness of ant suppression and the known variation in bird and bat activity between sites (Appendix S1, Table S3, Figures S4 and S5). In each model all other theoretically possible measured predictors were also included additively and treatment (plot) was nested within site (plantation) as a random effect. Oil palm initial height, soil pH and soil clay content were included as predictors in all the models where this was theoretically relevant due to preliminary analyses determining there were significant differences between treatments within sites (Appendix S1, Table S4). Due to highly skewed distributions, we log-transformed weevil abundance (after adding one). All numeric predictors were z-transformed to facilitate comparisons of effect sizes and model convergence.

Statistical model selection

We then used a model selection approach to assess which of the variables included were most important in explaining each response variable (i.e., maximized the likelihood of the model). For each response, we constructed a model set – based on the initial full modelwhich included all possible combinations of predictors up to a model including only the intercept – and ranked models within each set using Akaike's Information Criterion for small sample sizes (AICc) (*dredge()* function in R-package MuMIn (Bartoń, 2013)). We then identified the best models as those with ΔAICc < 2 (Burnham and Anderson 2002). We excluded non-converging models from the subsequent analysis. For each of the best models, we generated Pearson standardized residuals graphs to assess the model fit and heteroscedasticity, and calculated Cook's distances at the observation level (*influence* function in package influence.ME (Nieuwenhuis et al. 2012)).

To interpret our results, we used model averaging to combine the best models, (Grueber et al. 2011), and derived relative variable importance by summing up the predicted variable weights (*model.avg()* function in package MuMIn) (Burnham and Anderson 2002). To assess the robustness of each relationship, we then removed influential data points (with a Cook's distance superior to 4 divided by the number of observations) from our dataset which were common to all best models to construct a new "reduced" average model without these influential points (Bollen and Jackman 1990). All analyses were conducted in R 3.2.2 (R Core Team, 2015).

Results

The following results from LMMs are displayed in Figure 2, 3 and 4 and listed in detail in the supplement (Appendix S1, Table S5). If not specified, discussed relationships are significant at least at a *P*-value of <0.05. When relationships are not significant anymore in the reduced average models, they are stated as "not robust".

Effectiveness of ant suppression

The ant suppression treatment resulted in an average reduction in ant abundance and richness of respectively 38% and 4 % (Appendix S1, Figure S4), but only the reduction in abundance was statistically significant (Appendix S1, Table S3). Average ant abundance per plot over the span of the experiment ranged between 8 and 109 individuals.

Arthropod responses to ant, bird and bat treatments and predator arthropods

We collected a total of 8065 invertebrates, 46 % of which were collected from the fronds and 54 % from the trunk (Appendix S1, Table S2). Predators made up the highest percentage of frond arthropods (38%), 94 % of which were spiders, followed by herbivores (24 %), omnivores and (22 %) detritivores (16 %). Omnivores made up the highest percentage of trunk arthropods (40 %), followed by detritivores (33 %), predators (17 %) and herbivores (10 %).

Our manipulated average ant abundance and bird activity had negative effects on trunk and frond predator abundance respectively (Figure 2). However, bat activity did not significantly influence predator abundance (Figure 2). Average ant abundance, bird activity and bat activity had no influence on the abundance of trunk or frond arthropods from the other feeding guilds (omnivores, herbivores and detritivores) except for a positive relationship between bird activity and trunk omnivores. Arthropod predators were also always positively associated with the other arthropod feeding groups (detritivores, herbivores and omnivores) from the corresponding habitat (frond vs. trunk, Appendix S1, Table S5).

Ecosystem function responses to ant, bird and bat treatments and arthropod guilds

Our ant, bird and bat manipulations had no effects on ecosystem functions (Figure 3). Furthermore, there were no robust relationships between herbivory and our other measured variables (Appendix S1, Table S5). We found no robust predictors of cricket and dummy caterpillar predation. Aphid predation however, had a positive relationship with trunk herbivores. Ant abundance from baiting plates did not affect predation rate for any of the prey types. Pollinator weevil abundance was not affected by ant abundance but there is a non-robust positive relationship between bird and bat activity and weevil abundance. Also, weevil abundance was negatively related to oil palm initial height.

Oil palm yield responses to ant, bird and bat treatments and ecosystem functions

Total oil palm yields for the year averaged 36 kg FFB/palm (±28 kg SD). The variables included in our models had no robust effects on yield (FFB (kg/palm)/day) (Figure 4) and the supplementary yield measurement variables (without a 6 month delay after exclusion start) showed similar results (Appendix S1, Table S5). Closer analysis of the yield components (bunch number and mass) revealed a significant, non-robust, negative effect of herbivory on fruit bunch mass, and a non-robust positive effect on fruit bunch number.

Discussion

This is the first exclusion experiment in productive oil palm plantations covering considerable temporal and spatial scales. Our results detail the role of ants, birds and bats for arthropod communities, ecosystem functions and yield in oil palm. We found a strong negative effect of manipulated ant abundance and bird activity on arthropod predators (90% of which were spiders), and a positive effect of birds on trunk omnivores. The measured ecosystem functions, including herbivory, predation, decomposition and pollination, did not respond to variation in ant, bird and bat abundance, even though ants were the main predator of dummy caterpillars (Appendix S1, Figure S6). Only cricket predation rates were strongly affected by arthropod predator, omnivore and herbivore abundances. The economically most important ecosystem service, yield, however, did not respond to our measured predictors. Finally, our statistical results were confirmed by a supplementary analysis (Appendix S1, Figure S7) using structural equation models (cf. Appendix), stressing the robustness of our results.

Birds and ants have strong effects on arthropod predators but not on other arthropod groups

Our study showed that ants and birds both have a strong negative influence on arthropod predators. However, except for a positive influence of birds on omnivores, all other feeding guilds were not influenced by our experimental exclusion. Previous research has shown that many of the predators (ants, birds, and other arthropod predators) in our disturbed sites are likely to be generalists (Fitzherbert et al. 2008) and therefore can exert similar predation pressures on the other arthropod communities. The predators would be complementary through processes such as mesopredator release or similar in the sense that the absence of one predator group is compensated by the increase of the other, resulting in a constant predation pressure. Indeed, the most active birds (Appendix S1, Table S6) all consume arthropods to some degree, and all but one species were omnivores and small insectivores who glean arthropods. The lack of bat effects on arthropods could be due to bats mostly feeding on aerial nocturnal insects, which would not have been optimally sampled with our methods and can disperse freely between experimental cages, diluting the effect of bat predation.

Furthermore, the observed positive association between arthropod predators and all other arthropod groups suggests that arthropod predators are bottom-up controlled by the other arthropod feeding guilds and thus unable to control them. Similarly, the general lack of effects of our manipulated predators (ants, birds and bats) implies that there is little top-down regulation of the arthropod communities

No net effects of ants, birds and bats on ecosystem functions in oil palm plantations

We found no significant effects of ant, bird and bat numbers on any of the ecosystem functions measured. Even local environmental variables and arthropods other than ants had little effect on most measured functions. It is possible that the temporal disconnection of the predator, detritivore, and herbivore arthropod sampling from the measurement of their corresponding functions affected our results. However, we decided measuring functions during the experiment was more relevant for determining the effect of excluded predators on function and yield. In addition, destructive sampling during the experiment would have interfered with the study results and was therefore not possible. Nevertheless, cricket predation did respond strongly to arthropods: predators increased predation, while herbivores decreased it, possibly due to a competition effect, as they are also preyed upon by arthropod predators. This also stresses that multiple types of prey should be used to measure predation rates to avoid overlooking existing trends.

Contrary to previous research (Koh 2008), exclusion of birds and bats did not affect oil palm herbivory. However, the previous research looked at very young (one year old) palms, which are likely more susceptible to damage (Coley 1980). Furthermore, these plants were situated in a relatively old (more than one crop generation) and large oil palm complex (pers. comm. Lian Pin Koh), where pest pressure may be higher and birds potentially play a role in suppressing arthropod pests (De Chenon and Susanto 2006). Our sites were smallholder plantations all bordered by other vegetation types, including forest and jungle rubber. The herbivory we measured on our palms was overall low (0–4.8%, mean ± standard error of 0.9 ± 0.1 %, versus 0-21% herbivory in Koh (2008)). Overall, our findings correspond well to reports by local farmers that defoliating pests are not a major problem in the smallholder oil palm plantations of Jambi Province yet, where the crop has been introduced only one crop cycle ago at the time of writing. In particular, two of the most important defoliating pests of oil palm, the nettle caterpillar (*Setothosea asigna*) and bagworm (*Metisa plana*) are relatively uncommon in the study area (Nurdiansyah et al. unpublished data) and tend to have non-cyclic outbreaks. We only observed a single pest outbreak in our experimental sites, which subsided without control, and insecticide application throughout the entire experiment was zero. However with time, if pest numbers increase and outbreaks become cyclic the role of predators for pest control may become more important.

Ant, bird and bat manipulation did not affect decomposition rates directly or indirectly through changes in detritivore abundance. This suggests that other variables than the variables we measured are important for the decomposition rate of oil palm leaves. Many other factors can contribute to decomposition, such as local climatic variables as well as microbial activity and soil nutrients, both of which were not altered over the course of the experiment (Vossbrinck et al. 1979, Dyer et al. 1990).

The pollination of oil palm in Indonesia relies to a large extent on the weevil *E. kamerunicus* (Foster et al. 2011)*.* While birds can consume *E. kamerunicus* in oil palm plantations (Amit et al. 2015), the lack of predator effects on *E. kamerunicus* found in our study is reassuring, and suggests that measures taken to increase the abundance and diversity of predators of arthropods are unlikely to be accompanied by reduced pollination. However, in the long-term the reliance on a single pollinator species may be a risky strategy given the significant fluctuations of wild and managed pollinators in other agricultural systems (Potts et al. 2010).

Ants, birds and bats and other measured variables do not influence oil palm yield

Oil palm yield was not affected by the variables studied in this research, indicating that our manipulations of biodiversity or even variation in arthropods and ecosystem functions do not affect oil palm productivity.

Most surprisingly we found no direct link between herbivory and yield: as mentioned, herbivory was low at the sites, and in the past other studies have shown leaf herbivory is not always important for yield, rather other types of herbivory can be more important (e.g. flower herbivory (Maas et al. 2013)). The positive relationship between cricket predation and growth found in this study may be an indication of this. Also, yield responses to herbivory may only be observed in the case of pest outbreaks (Kamarudin and Wahid 2010), which are rare in oil palm in Indonesia. However, there is evidence from other crops that as the area cultivated increases there is an increase in pest and disease problems (Clough et al. 2009). Interestingly though, we found a negative effect of herbivory on fruit bunch mass, which was compensated by a positive effect on fruit bunch number. Such an effect, while having a net null effect on yield, may still be detrimental as it incurs higher labour costs for harvesting the more numerous fruit bunches. The lack of any effects on total yield at these sites suggests that other limiting factors play a more important role in yield variation, such as nutrient availability, rainfall and efficiency of light uptake from the canopy (Rafflegeau et al. 2010, Breure 2010). For example, the very low soil pH across sites could indicate a potential phosphorus deficiency. Furthermore, the absence of a biodiversity and yield relationship suggests there is an opportunity for a win-win situation for high biodiversity and yield in oil palm plantations (Clough et al. 2011, Teuscher et al. 2015).

Conclusions

We conclude that ecosystem functions and productivity in oil palm are, under current levels of pest pressure and pollinator populations, robust to large reductions major predators. Although it is widely presumed that biocontrol plays a major role in crop production elsewhere, the lack of relationship we observed between predators and yield proves that expectation to be wrong in this context. However biodiversity conservation should not be compromised if it is not coupled with economically meaningful services (Silvertown 2015); its intrinsic value alone is important.

Acknowledgements

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Figure legends

Figure 1. Experimental design. Full factorial combination of ant and bird and bat exclusion plots at each study site. (a) both bird, bat and ant exclusion, (b) ant exclusion only, (c) control (no exclusion), (d) bird and bat exclusion only. (e) Example of a bird, bat and ant exclusion plot with approximate scales indicating the cage dimensions (Photo courtesy of Eulefilm ©).

Figure 2. The response of arthropod feeding guilds in trunk and frond habitats to average ant abundance, bird activity and bat activity. Significant ($P<0.05$) relationships are indicated with a solid line. Darker shading of points indicates multiple overlapping points.

Figure 3. The response of measured ecosystem functions to average ant abundance, bird activity and bat activity. Significant ($P<0.05$) relationships are indicated with a solid line. Darker shading of points indicates multiple overlapping points.
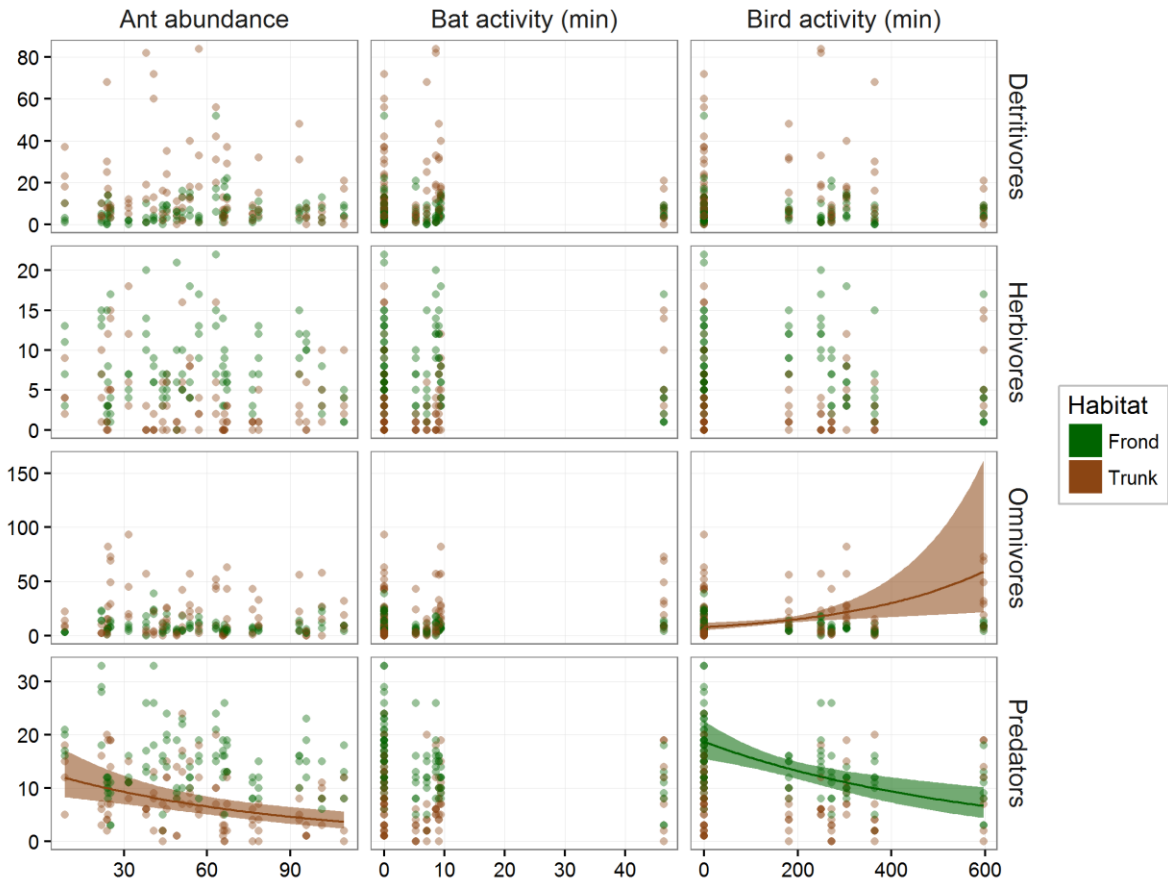
Figure 4. The response of yield (FFB (kg/palm)/day), bunch number (day^{-1}) and mass (g) to average ant abundance, bird activity and bat activity. Significant ($P<0.05$) relationships are indicated with a solid line. Darker shading of points indicates multiple overlapping points.
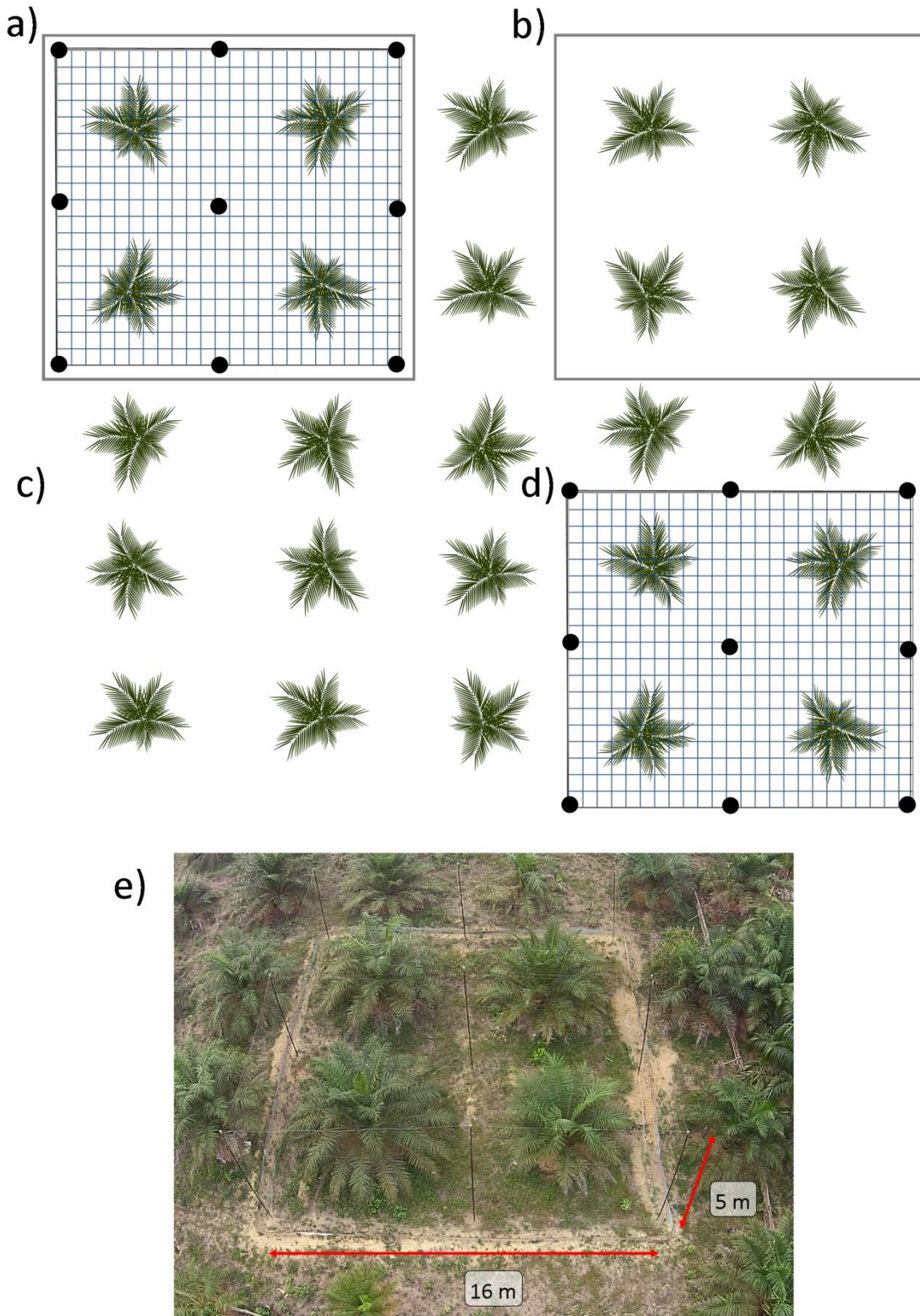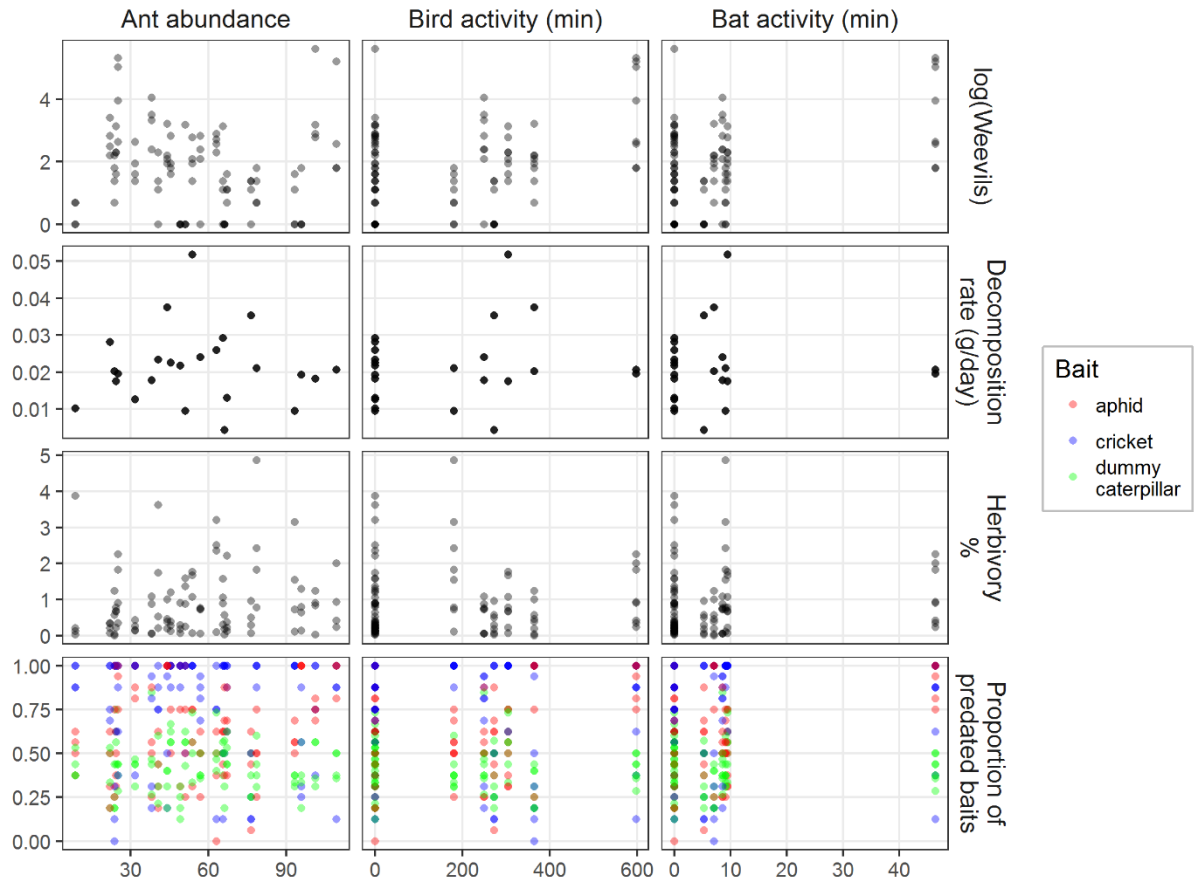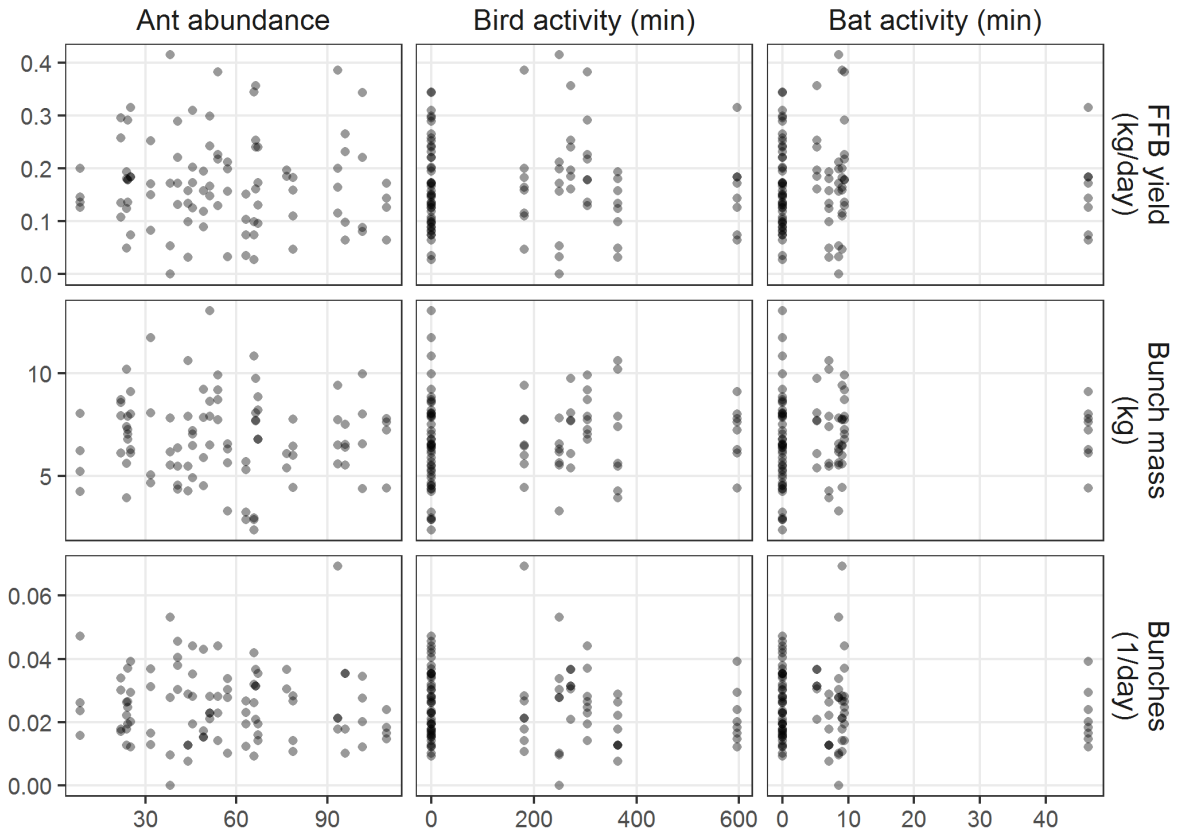
Figure 1.

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