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LETTER

Resilience of ecological functions to drought in an oil palm agroecosystem

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Abstract

Oil palm is a major habitat in the tropics. It is highly productive and contributes substantially to the economies of producing countries, but its expansion has caused widespread deforestation, with negative consequences for biodiversity. Such biodiversity losses may have substantial impacts on ecosystem functions within oil palm and resilience of functions to changing rainfall patterns, with impacts on yield. However, although the direct effects of water deficit on yield have been studied, little work has investigated ecosystem processes within plantations or the resilience of functions to changing rainfall. We conducted ecosystem function experiments within mature oil palm at the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme site in Sumatra, Indonesia. We measured rates of leaf litter decomposition, seed removal, mealworm predation, and herbivory at multiple time points spanning the 2015–2016 El Niño - Southern Oscillation (ENSO) event that caused widespread drought within Southeast Asia. We found that mealworm predation, seed removal, and decomposition rates were high, whilst herbivory levels were low, indicating a healthy ecosystem with high levels of pest control and organic matter breakdown. Exclusion tests showed that the presence of invertebrates was associated with higher levels of seed removal and decomposition and the presence of vertebrates with higher predation. All functions were relatively robust to changes in rainfall. Yet, whilst seed removal and herbivory did not alter with rainfall, decomposition and predation showed more complex effects, with levels of both processes increasing with current rainfall levels when rainfall in preceding time periods was low. This suggests that both processes are resilient to change and able to recover following drought. Our results indicate that the ecosystem processes measured within oil palm plantations are healthy and resilient to changing rainfall patterns. This is hopeful and suggests that the crop may be fairly robust to future changes in precipitation.

Introduction

Oil palm has expanded dramatically in recent decades and now forms a major habitat type in the tropics (Phalan *et al* 2013), with over 21 million hectares cultivated worldwide. For example in Indonesia, the world's largest producer, production increased by 68% from 2005–2011 (Murphy, 2014). A significant proportion of this expansion has come at the expense of tropical forests (Turner *et al* 2011, Meijaard *et al* 2018) and has been driven by oil palm's cost-effective production (Woittiez *et al* 2017), wide use, extreme productivity and profitability (Corley, 2009, Wilcove and Koh, 2010). Demand for palm oil is likely to triple by 2050, potentially resulting in a further expansion of 12 million hectares (Corley 2009) and intensified production within the existing land area.

The expansion of oil palm has come at a significant cost to tropical forests and the carbon stocks and biodiversity they contain (Carlson *et al* 2012, Vijay *et al* 2016, Meijaard *et al* 2018). In a multitude of studies comparing forest to oil palm, the majority of taxa show both a reduction in abundance and diversity in oil palm (Fitzherbert *et al* 2008, Foster *et al* 2011). Other studies have highlighted shifts in the functional composition of taxa in oil palm compared to forest (e.g. Luke *et al* (2014), Prabowo *et al* 2016), as well as changes in functional redundancy (Chapman *et al* 2018). For example, studies have reported reduced proportions of predatory (Chung *et al* 2000) and insectivorous species (Najera and Simonetti 2009) in oil palm. Given the link between functional diversity and ecosystem functioning (Flynn *et al* 2008), such an change could influence the long-term level and stability of ecosystem functions in oil palm landscapes. A recent review found that 11 of 14 ecosystem functions assessed in oil palm and forest, showed lower levels in oil palm (Dislich *et al* 2017). Beyond this, there has been little work that assesses the impact of biodiversity loss on ecosystem processes within oil palm landscapes (Savilaakso *et al* 2014).

Despite biodiversity declines, many species are still found within oil palm landscapes (e.g. Turner and Foster 2009, Azhar *et al* 2011). Although these are predominately generalist or widespread species (Fayle *et al* 2010) and therefore not a conservation priority, such species can provide valuable ecosystem services to promote crop production (Rusch *et al* 2016). For example, decomposition (Foster *et al* 2011), soil processing (Ashton-Butt *et al* 2018), and pollination (Li *et al* 2019) all rely on invertebrates within the oil palm landscape, whilst a multitude of vertebrate and invertebrate taxa have been identified as important pest control agents in oil palm (Turner and Hinsch, 2018). In contrast, other species found within plantation landscapes can have negative impacts on oil palm health and production. Such pests can act as defoliators, trunk borers, sap suckers, and fruit eaters (Dislich *et al* 2017), as well as vectors of disease (Gitau *et al* 2009), significantly reducing palm oil yield (Corley and Tinker 2015).

With pests and diseases being among the key reasons for yield gaps in palm oil production (Woittiez *et al* 2017), supporting healthy populations of beneficial species is therefore a priority for plantation management. Increasing yield or maintaining high yield per unit area is also key for biodiversity conservation, as it can reduce pressure for further habitat conversion and spare remaining natural areas (Phalan *et al* 2011). Recent work has demonstrated that experimental enrichment of oil palm with forest trees (Teuscher *et al* 2016), management for a structurally-complex understory (e.g. Najera and Simonetti 2010, Luke *et al* 2019), introduction of alley-cropping systems (Ashraf *et al* 2018), and mulching under palms with organic material (Tao *et al* 2018) can all benefit aspects of biodiversity and ecosystem processes within oil palm landscapes.

The majority of oil palm is cultivated in Southeast Asia (Turner *et al* 2011), where high rainfall generally promotes high productivity in the crop. However, the region experiences occasional droughts (Walsh and Newbery 1999), which together with haze events, can be associated with the El Niño - Southern Oscillation (ENSO) (Khandekar *et al* 2000). Since the widespread expansion of oil palm in Southeast Asia from the 1980 s (Snaddon Willis and Macdonald, 2013), there have been five strong ENSO events, with the most recent being in 2015–16 (Santoso, McPhaden and Cai 2017). In Indonesia, the impact of ENSO on drought conditions varies across the region and with time of year, but strong ENSO events generally lead to a reduction in precipitation and an increased impact of drought over large areas (Setiawan Lee and Rhee 2017). Reduced rainfall and rising temperatures can have a direct impact on oil palm yield (Caliman 1992, Suresh 2013, Woittiez *et al* 2017), with reduced yields being recorded when there is a water deficit between 30 and 6 months before harvest (Caliman and Southworth 1998). In general, a 100 mm water deficit results in a yield loss of around 10% of the potential yield (Corley and Tinker 2003). Warmer temperatures associated with recent ENSO events have also been associated with reduced palm oil production in Peninsular Malaysia, Sabah and Sarawak (Shanmuganathan 2012). However, the exact effects of water deficit on yield are complex and can vary with soil type and regularity of seasonal drought, with impacts being mediated through effects on floral initiation, sex differentiation and abortion rate of fruit bunches.

The impact of such climatic fluctuations on ecosystem processes within oil palm landscapes has not yet been studied, although key taxa supporting ecosystem processes within oil palm are known to be affected by drought. For example, numbers of the beetle *E. kamerunicus*, the major pollinator of oil palm, decrease in low-rainfall conditions (Dhileepan 1994), potentially reducing pollination rates . As oil palm flowers and fruits continuously in optimal areas, maintaining sufficient pollinator numbers to support pollination is therefore critical for annual production (Li *et al* 2019). Some climate models predict that El Niño and associated La Niña events will become more frequent with climate change (Timmermann *et al* 2002, Cai *et al* 2015), so it is possible that these impacts may become more marked in the future.

In this study, we investigate the impacts of long-term (previous three months) and short-term (at the time of sampling) rainfall on four ecosystem processes in mature oil palm plantations, in Sumatra, Indonesia. Data were

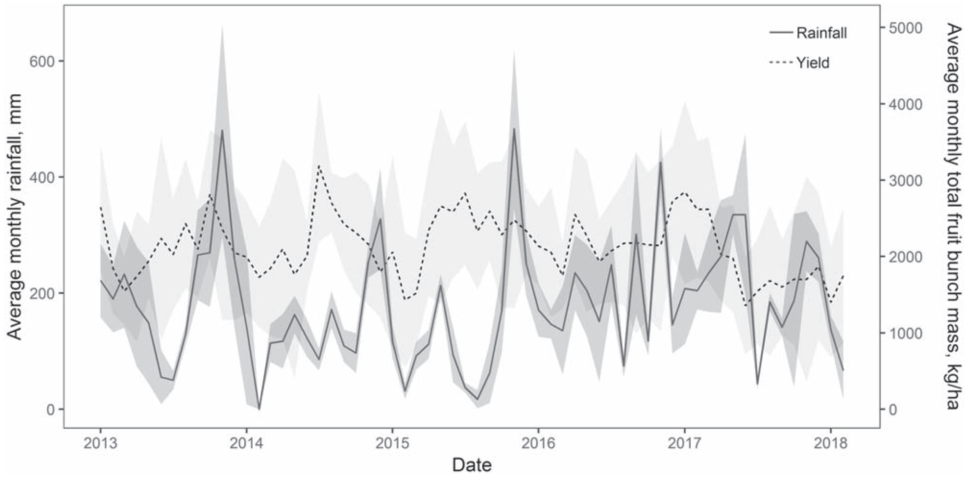

Figure 1. Average monthly rainfall (mm per month) and fruit bunch mass (kilograms per hectare) recorded over the course of the study. Rainfall data were averaged from three weather stations in Ujung Tanjung and two in Kandista Estates. Shaded areas represent standard deviation.

collected over four years and spanned the 2015–16 ENSO event. Processes measured included: decomposition, seed removal, predation, and herbivory. These processes encompass a range of functions that could benefit oil palm production and may be compromised by reduced levels of biodiversity within plantations and variable rainfall. Through a series of manipulative exclusions, we also directly tested the role played by key taxonomic groups in supporting these processes. These included assessing the impact of excluding invertebrates on decomposition levels, the impact of excluding vertebrates and non-flying invertebrates on seed removal levels, and the impact of excluding vertebrates on predation levels. We also recorded yield throughout the study period. However, the effect of low rainfall on yield is known to have a variable but long lag-time, with the exact timing of any lag depending on a number of factors, including soil conditions and impact on the different stages of fruit development (Caliman and Southworth 1998, Corley and Tinker 2003). We therefore only present summary data on yield here, with the aim of this study being a thorough determination of the impacts of drought on ecosystem functions.

Methods

The study was conducted as part of the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme (oilpalmbiodiversity.org; Foster *et al* 2014, Luke *et al* no date), based in Riau Province, Sumatra, Indonesia (0 °55’33.5‘N 101 °11’37.1‘E). Study plots were located within oil palm estates owned and managed by PT Ivo Mas Tunggal, a subsidiary company of Golden Agri Resources (GAR), with technical advice from Sinar Mas Agro Resources and Technology Research Institute (SMARTRI, the research and development centre of GAR). Study plots were on mineral soil, and oil palms in the plots were planted between 1988 and 1993, and were therefore mature at the time of study, with a closed canopy. The surrounding area consisted predominately of oil palm plantations, with only a small amount of other crops, and no extensive forest cover. Rainfall in the area is seasonal and can be influenced by the El Niño-Southern Oscillation (ENSO) (figure 1).

In this paper, we use data from six 50 m by 50 m plots, where management followed standard industry practice. This included the use of herbicides in a 1.5 metre-wide harvesting circle around palms and along access paths, while leaving the rest of the understory unsprayed. The plots were distributed across two oil palm estates (Kandista and Ujung Tanjung), located within the BEFTA Programme area. Plots were flat, between 10–30 m above sea level and distant from settlements and major roads.

Data collection

At each plot, we established three collection points, separated by 50 m from each other and located on the corners of an equilateral triangle based on the plot centre. We collected data on decomposition and seed removal from these points. We also numbered each individual oil palm within the 50 m by 50 m plot and randomly selected three of these at each survey period to measure predation and herbivory. There are therefore three collection points per plot for each ecosystem function variable recorded (18 points in total for each variable). Data were collected from these collection sites across multiple survey periods between 2013 and 2017. Rainfall data were collected over the course of the project (January 2013 - December 2018) from three weather stations in

Ujung Tanjung and two in Kandista. We recorded yield, as fresh fruit bunch weight from all palms within each plot, every month other the study.

Rainfall for the overall study period was high, with a monthly average of 179(SD 104) mm, between December 2012 and January 2018. However, in 2015 ENSO-associated drought reduced the average monthly rainfall to 145 mm. Most notable was a lack of a peak in rainfall in late 2014 and two extended dry periods in 2015, presenting challenges for oil palm cultivation (figure 1). In contrast, monthly rainfall in 2016 was higher than average at 200 mm, associated La Niña. In the area, palms yield continuously, although fresh fruit bunch weight varied, with an average monthly yield of 2129(SD 410) kg/ha in our plots over the course of the study (figure 1).

Litter decomposition

Decomposition was measured seven times from 2013 to 2017 (start points of collection periods: February 2013, February 2014, July 2016, October 2016, February 2017 and May 2017), using mesh bags filled with four grams of mature oil palm frond litter. Fronds were freshly removed from a palm and cut into approximately 2 cm sections, before being oven-dried at 70 °C to a constant weight. We used three different types of mesh bag at each location: 0.1 mm mesh to exclude all invertebrates, 2 mm mesh to exclude medium-sized invertebrates, and 0.1 mm mesh with eight one-cm holes cut into it, to allow access to all invertebrates. Three of each type of bag (9 bags in total) were placed together on the soil surface, under the litter layer at each collection point and collection period. One bag from each bag type were then collected at approximately 10, 30, and 60 days. These were oven-dried as before, gently cleaned of any soil or root contamination and weighed. Two observations gained weight over the course of the study, with a mass of over 4 grams post-treatment (4.005 and 4.190 grams recorded). This was probably due to contamination, so we fixed these at 4 grams.

Seed removal

Seed removal was measured six times between 2013 and 2017 (September 2014, July 2016, October 2016, February 2017, May 2017 and August 2017). The basic unit for seed removal was ten shelled sunflower seeds (successfully used before in other seed studies (e.g. Hargreaves *et al* 2018)), placed on a paper disc of approximately 15 cm diameter, and covered by a polystyrene disposable plate held 10 cm above the soil surface to shelter the seeds from rain. At each sample point, we applied four treatments to exclude vertebrates, non-flying invertebrates, a combination of the two, or neither. These were: a paper disc enclosed within a mesh cage of approximately 35 × 20 x 14 cm, with no holes wider than 1 cm (to exclude vertebrates), a paper disc with a one cm-wide band of grease applied round the edge (to exclude non-flying invertebrates), a paper disc with both grease and a cage (to exclude both non-flying invertebrates and vertebrates), and a paper disc with no grease or cage (a full access control). The number of seeds remaining on each disc after approximately 24 h was recorded.

Predation

Mealworm predation was measured nine times between 2013 and 2017 (twice in February 2014, August 2014, May 2016, July 2016, October 2016, February 2017, May 2017 and August 2017). The basic unit for the predation test was six freshly-killed mealworms (*Tenebrio* sp.), glued onto a fresh section of oil palm frond that had been trimmed so that roughly 10 cm of each of six leaflets remained. We measured predation on the ground, as well as in the canopy at each sample point. We used a throw bag and string to haul two frond pieces into the oil palm canopy. One of these fronds was simply attached to the string, while the other was enclosed within a mesh cage to exclude vertebrates, using the same specifications as cages used for seed removal studies. We also repeated this arrangement on the ground at the base of the oil palm. The number of mealworms remaining after approximately 24 h were counted.

Herbivory

Herbivory, consisting of leaf damage and taking the form of both holes in the middle of the leaf and leaf area removed from the edge of the leaf, was measured 17 times (every 3–4 months) between April 2013 and August 2017. Counting from the youngest fully-opened frond, the 17th frond in the crown of the palm was cut. Frond 17 represents a middle-aged frond (aged between 8.5 and 9 months) in mature palms and is commonly used by the oil palm industry as a standard to measure herbivory and herbivore load. Twenty paired leaflets, spaced evenly along the frond, were cut, placed flat on a white board and photographed (using a Nikon D90 camera). Photography was always carried out by the same person (ADA), from the same angle (bottom left), to reduce sampling bias. Leaf damage was likely to be the result of feeding by lepidopteran larvae, which were commonly observed on the cut fronds.

Photographs were pre-processed to remove noise and converted to binary images in Microsoft Paint (Microsoft Windows version 6.1 (build 7601: Service Pack 1), 2009). The total leaflet area was then measured in

Fiji (Schindelin *et al* 2009, Schneider Rasband and Eliceiri 2012). A second image was prepared in Microsoft Paint, with all herbivory damage 'filled in', such that the leaflets appeared to be intact. Where leaflet tips were missing, a conservative estimate for the leaflet tip was drawn in, based on the length of neighbouring leaflets. This second image was measured in Fiji in the same way and the percent of the leaflet area consumed by herbivores was calculated.

Data analysis

We error-checked 50% of the digitised data against field sheets, finding an acceptable error rate of $<1\%$. We removed 117 of 2301 predation and herbivory observations before analysis, as they were within 10 metres of another experimental manipulation that may have confounded the results. Statistical analyses were performed in R version 3.5.1 (R Core Team, 2018), with R Studio version 1.1.463.

All data were analysed using linear and generalised linear mixed effects models (LMMs and GLMMs), fitted using maximum likelihood, to investigate the effect of rainfall (calculated as mean values from weather stations in each estate) and experimental treatment on the four focal ecosystem functions. As the sampling design was spatially nested and points were sampled multiple times, we included collection point position, nested within plot identity as a random intercept in all analyses unless specifically stated. To determine the significance of explanatory variables, we used a model selection approach together with backwards stepwise elimination. Beginning with the maximal model, where all interactions were included, we removed one term at a time and assessed its significance using likelihood ratio tests (LRTs). We removed non-significant interaction terms, but retained non-significant explanatory variables. Where significance was marginal ($0.05 > P > 0.01$), we used parametric bootstrapping to obtain more robust P-values. This consisted of bootstrapping the likelihood-ratio test between full and reduced models in each scenario, using 1000 iterations. Where factors with more than two levels were significant, we carried out post-hoc analysis using Tukey's HSD to determine significant contrasts between the factor levels. Where there was a significant interaction between rain variables (divided into before and during data collection: see below for specifics for each function measured), we carried out additional post-hoc analyses to test whether the slopes of each rain variable differed significantly from zero, when the other rain variable was held at three constant values (the 5th percentile, the mean, and the 95th percentile).

To analyse the decomposition data, we calculated first-order exponential decay coefficients for each replicate of bag type, collection point, plot, and period, following methods described in Powers *et al* (2009). Our k values, in days^{-1}, were exponential decay coefficients given by the slopes of linear regressions of the natural logarithm of proportion of mass remaining across time. We forced our Y-intercepts at time zero through 1 (100% mass remaining – 4 grams), and all bags with zero mass of litter were set to a proportion of 0.0001 mass remaining, so that we could take their natural logarithm. Our first order decay models fitted the data well, with 275 of 284 regressions having an R^2 value of over 0.8. K values were then log transformed and modelled using a linear mixed effects model (lmer from lme4 package; Bates *et al* (2015)). We analysed the effect of three covariates: average daily rainfall in the 90 days preceding the litter bags being placed in the field as a continuous predictor, average daily rainfall in the 60 days during the experiment as a continuous predictor, and bag type as a three-level factor.

We analysed seed removal and predation data (converted to proportion of seeds or mealworms removed), using generalised linear mixed effect models with beta error structures and logit links (glmmTMB, Brooks *et al* (2017)). Because response variables cannot assume the extremes in a beta distribution (i.e. 0 or 1), we applied the transformation: $(Y^*(N-1) + 0.5)/N$ (Smithson and Verkuilen, 2006)). In the case of seed removal, fixed effects were cage treatment and grease treatment, each as two-level factors, plus rain over the previous 90 days and rain on the day of sampling as continuous variables. In the case of predation, fixed effects were cage treatment and canopy/ground position, each as two-level factors, with mean daily rain over the previous 90 days and rain on day of sampling as continuous variables.

Herbivory, converted to proportion of leaf area removed, was log transformed and analysed using a linear mixed effects model (lmer from lme4 package (Bates *et al* 2015)). The only fixed effect we included was rain over the previous 90 days, as herbivory integrates damage over the full life-span of the leaf. For the herbivory model only, we simplified the nested random effect of collection point position inside plot identity to just plot identity, to avoid a singular fit.

Results

Decomposition

Decomposition varied over the sampling period, and we recorded an average of 45% (SD: 13%) of mass lost after only 60 days (figure 2).

The interaction between rain before and during the study was highly significant (figure 3; LMM LRT: $X_1^2 = 33.19, P < 0.001$), indicating that the response of decomposition to either measure of rainfall depended

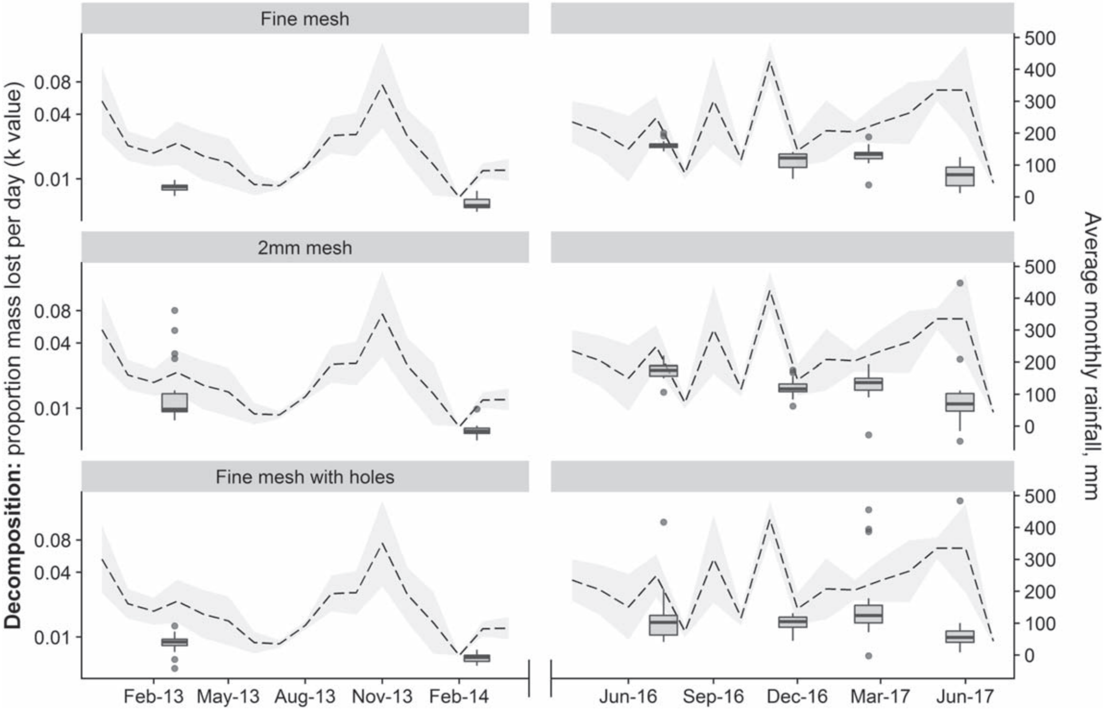

Figure 2. Proportion of litter bag mass loss per day for the three different mesh size treatments (fine mesh, 2 mm mesh, and fine mesh with holes) at the six collection times, and average monthly rainfall over the collection period. Shaded areas represent standard deviation.

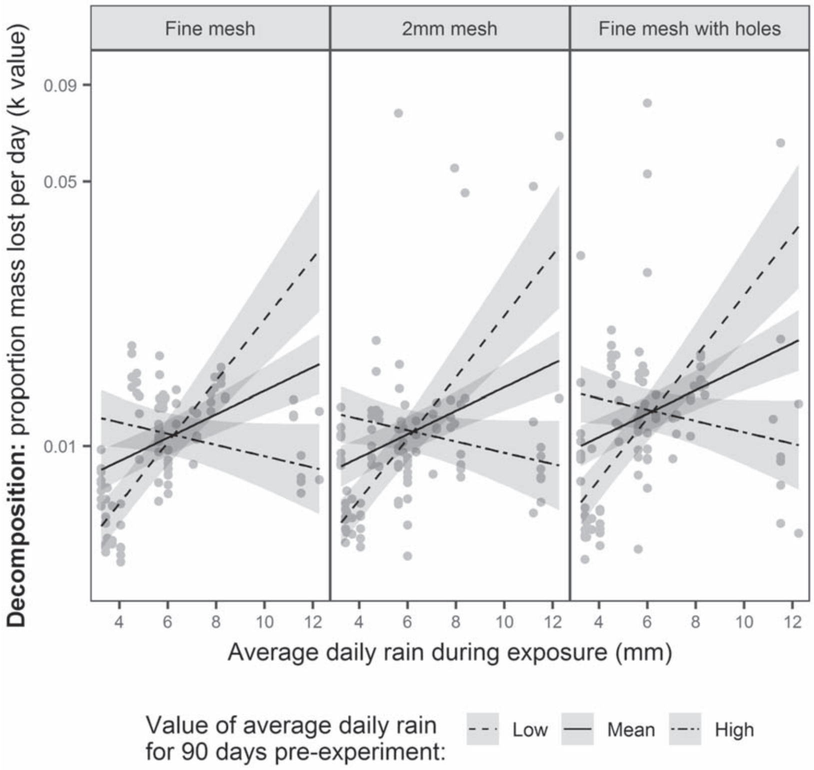

Figure 3. Relationship between the proportion of dry mass loss of litterbags and rainfall during the study, shown at high (95th percentile), mean, and low (5th percentile) values of rainfall 90 days before the study began. Three types of bags were used: fine mesh, 2 mm mesh, and fine mesh with 1 cm holes. Decomposition is shown on a logarithmic scale to help interpretability. Dots represent the raw data. Trend lines are calculated from the model. Grey bands around the trend lines are confidence intervals as derived from the model.

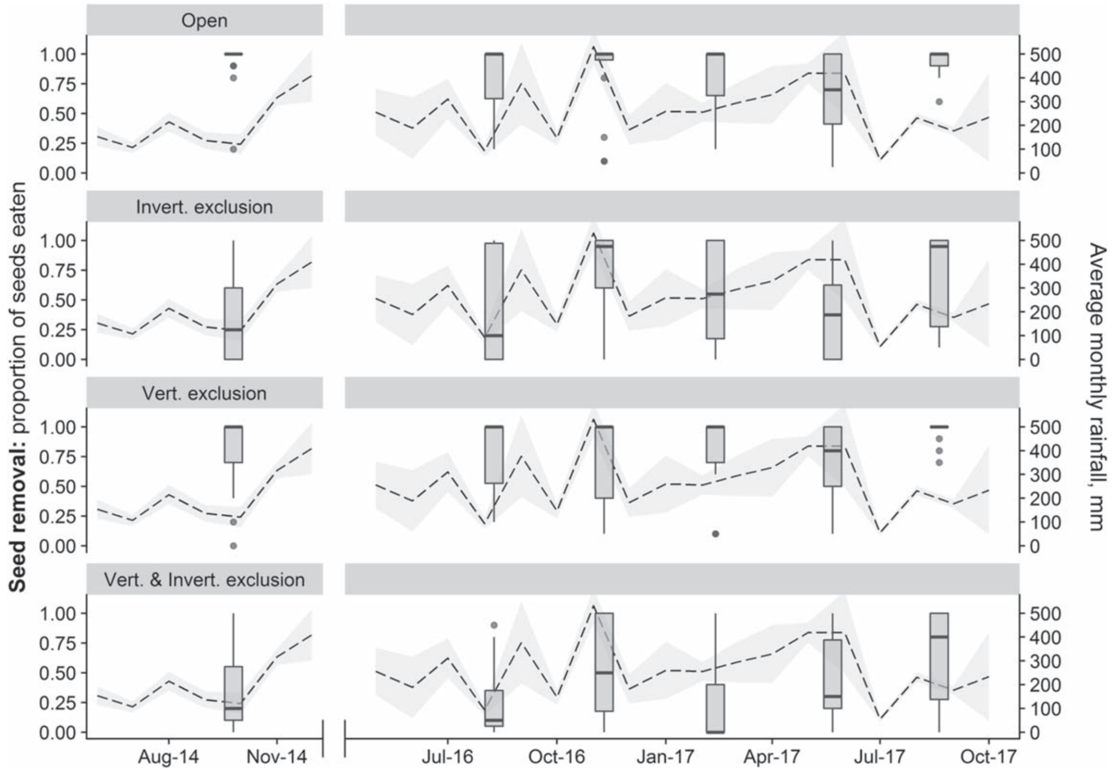

Figure 4. Proportion of seed removal over 24 h across the four different exclusion treatments (open control, invertebrate exclusion, vertebrate exclusion, and both invertebrate and vertebrate exclusion) and average monthly rainfall over the collection period. Shaded areas represent standard deviation.

on the value of the other. In particular, when rainfall was low before the study, decomposition increased sharply if there were higher levels of rainfall during the study. In contrast, when rainfall was high before the study, decomposition was unaffected by rainfall during the study (figure 3; appendix 1 tables A1 and A2)

Litter bag type also significantly influenced decomposition rate (LMM LRT: $X_2^2 = 7.85$, $P_{nsim=1000} = 0.028$), with bags with 1 cm holes decomposing at a significantly higher rate than bags with fine mesh. No other paired comparisons of bag types differed significantly in their rates of decomposition (figure 3; appendix 1 tables A3 and A4).

Seed removal

We recorded an average of 64% (SD: 39%) of seeds being eaten over 24 h over the course of the study, although proportions of seeds removed varied over time and between treatments (figure 4).

Seed predation was not significantly affected by either rainfall during the study period (GLMM LRT: $X_1^2 = 1.61, P = 0.20$), or rainfall over the 90 days before sampling (GLMM LRT: $X_1^2 = 0.20, P = 0.65$). Seed removal was also not affected by the vertebrate exclusion (GLMM LRT: $X_1^2 = 2.04, P = 0.15$), but treatments with walking invertebrates excluded had a significantly lower proportion of seeds removed (GLMM LRT: $X_1^2 = 61.11, P < 0.001$) (figure A1).

Predation

We recorded an average of 74% (SD: 35%) of mealworms being removed over 24 h, with the proportion removed varying across the study period and between treatments (figure 5).

The interaction between rainfall before and rainfall during the study on predation was significant (figure 6; GLMM LRT: $X_1^2 = 9.81, P = 0.0017$). At low to medium values of rainfall before the study, predation increased with level of rainfall during the study. In contrast, at high values of rainfall before the study, the proportion of mealworms eaten did not vary with rainfall during the study (figure 6; appendix 1 tables A5 and A6)

Cage treatment (vertebrate exclusion) also had a significant impact on predation rates, with a higher proportion of mealworms being eaten in the open treatment (figure 6; GLMM LRT: $X_1^2 = 8.35, P = 0.0039$). There was also a significant interaction between height of the mealworms (canopy or ground) and rainfall before the study (figure 6; GLMM LRT: $X_1^2 = 5.51, P = 0.017$), with a lower proportion of mealworms being eaten in

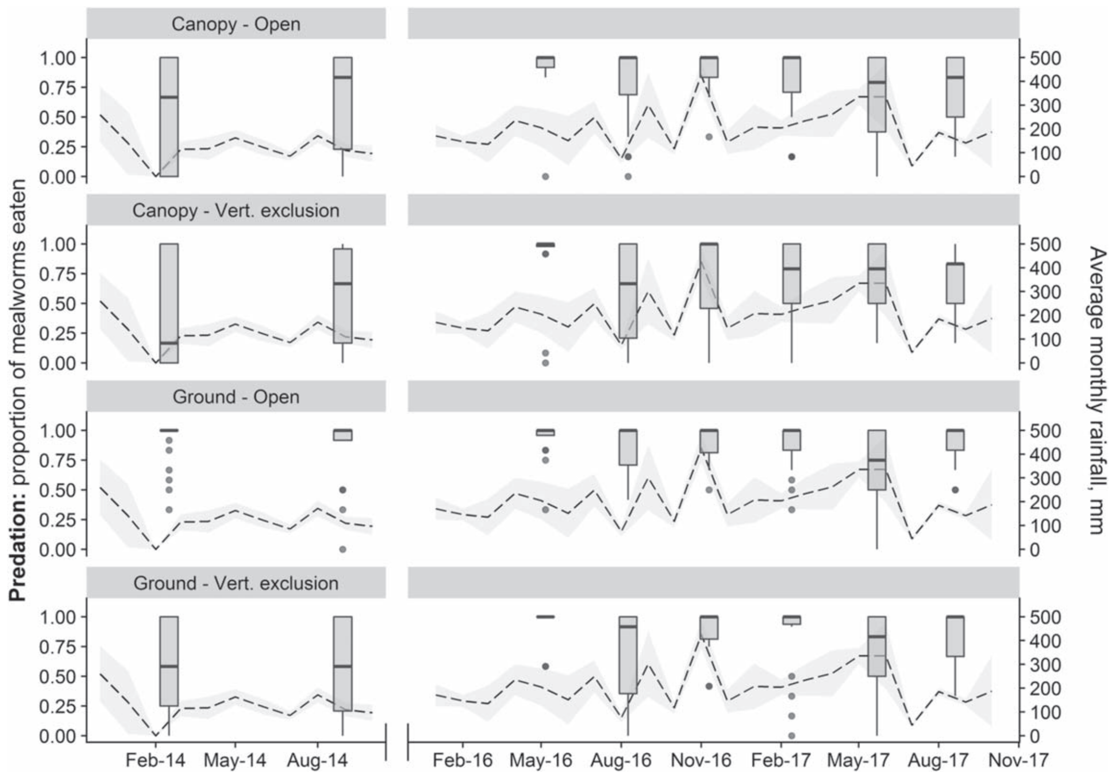

Figure 5. Proportion of mealworms removed in the canopy and ground for both open and vertebrate exclusion treatments and average monthly rainfall over the collection period. Shaded areas represent standard deviation.

the canopy than on the ground at low levels of rainfall before the study, but this difference disappearing as levels of rainfall during the study increased.

Herbivory

We recorded a universally low level of herbivory throughout our study, with an average percentage herbivory of only 1.1% (SD: 1.2%) across sample points, although percentage herbivory varied over the course of the study (figure 7). Herbivory was not significantly related to rainfall in the three months prior to sampling (figure A2; LMM LRT: $X_1^2 = 1.27, P = 0.26$).

Discussion

We recorded high levels of predation and seed removal, with levels of seed removal being higher than that recorded in a comparable tropical forest area (Hargreaves *et al* 2018). Similarly, levels of decomposition were high compared to litterbag experiments in forested and open landscapes (e.g. Beckschäfer *et al* 2015) and to rates of weight loss recorded from empty oil palm fruit bunches, added to plantations as a mulch, from the same study area (Caliman Budi and Saletes 2001). In contrast, herbivory levels were low, with an average of only 1% herbivory per frond. These results indicate that favourable ecosystem services for palm oil production are being maintained within the oil palm landscape. In particular, high predation and low herbivory levels indicate good pest control in the plantation. This is likely to also benefit yield, as previous experimental work on oil palms has found that high levels of leaf damage (of 50%) can result in 45% drop in production (a loss of four tonnes of fresh fruit bunch per hectare) (Wood Corley and Goh 1972). The high level of decomposition and seed removal may also be beneficial for production, potentially supporting nutrient cycling in the system and helping to control the spread of weed species that could compete with the palms. However, it should be noted that all of the plots included in this study are within mature oil palm and were managed with only targeted herbicide applications and intermittent pesticide applications. It is, therefore, possible that our findings may not be applicable to younger or more intensely-managed plantations.

The four ecosystem processes investigated were fairly robust to variation in rainfall. In particular, seed removal and herbivory were unaffected by rainfall levels either before or during the study, while decomposition and predation rates increased with higher levels of rainfall during the study, when rainfall before the study was

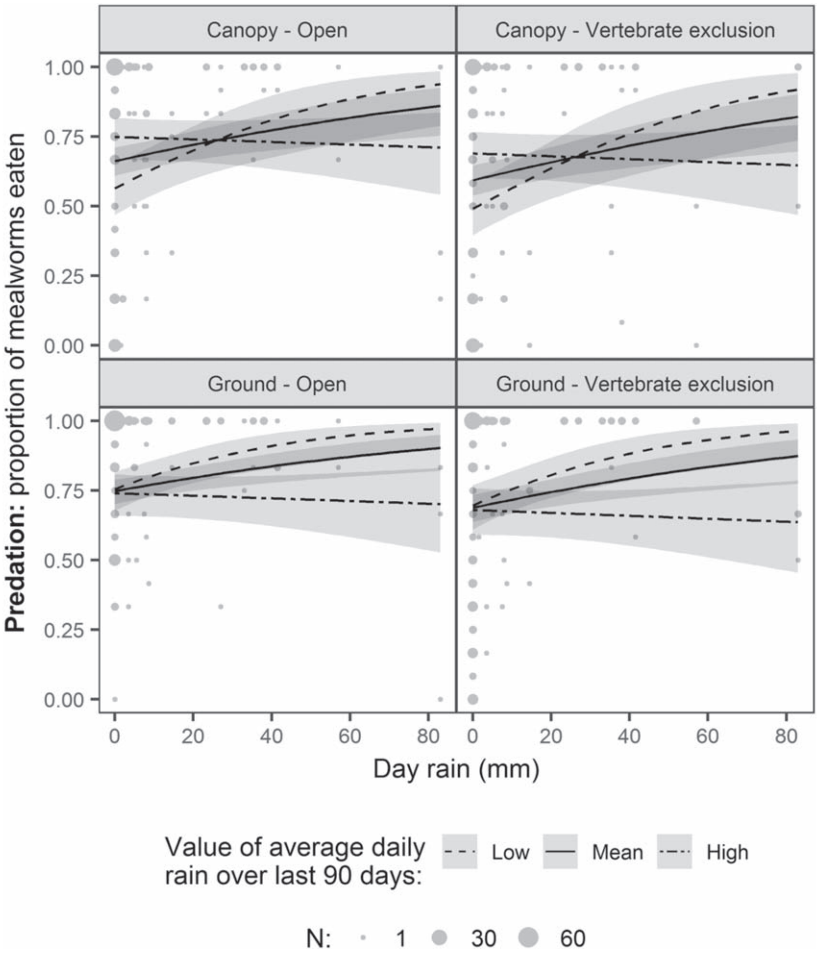

Figure 6. Relationship between rainfall during the sampling period and the proportion of dead mealworm larvae (of six larvae) predated, plotted at high (95th percentile), mean, and low (5th percentile) values of rainfall in the 90 days before the sampling period. Dots represent the raw data, with dot size proportional to the number of data points. Trend lines are calculated from the model. Grey bands around the trend lines are confidence intervals as derived from the model.

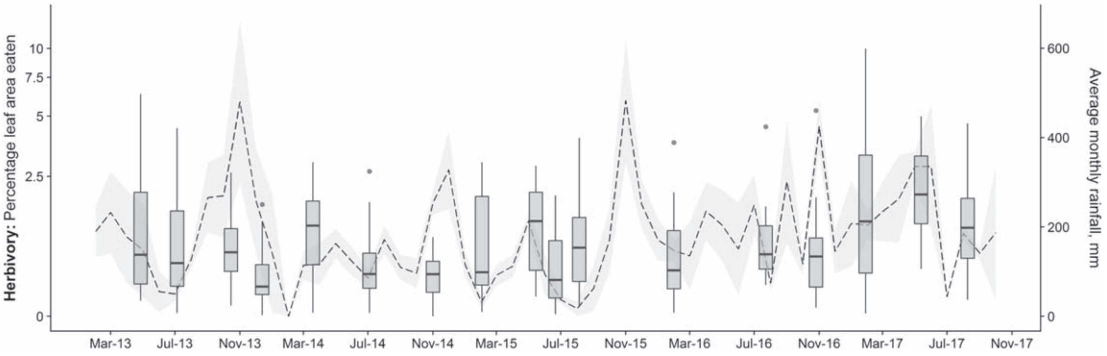

Figure 7. Percentage leaf area eaten over the course of the study period and average monthly rainfall. Shaded areas represent standard deviation.

low. This indicates that the oil palm ecosystem is resilient to periods of drought and can recover following low rainfall, at least when followed by higher rainfall, as is the case in this study (probably associated with La Niña). We cannot say whether the same would be true if periods of low rainfall were more prolonged or not followed by wetter conditions.

The impact of rainfall on rates of decomposition has been shown in previous studies (e.g. Austin and Vitousek, 2000) and may reflect more favourable conditions for microbial communities and microbial action when soil is moister (Riutta *et al* 2012). Similarly, arthropod groups are strongly influenced by seasonal rainfall

(Adis, 1988, Silveira *et al* 2010). In some cases, moister conditions in the leaf litter can benefit soil arthropods (Riutta *et al* 2012), potentially increasing mechanical breakdown of the leaf litter and transport of microbes. The interaction between rainfall before the study and rainfall during the study may be related to the flat and low-lying nature of our study area (all flat and below 30 m above sea level). High levels of rainfall before and during the study period could have resulted in precipitation exceeding evapotranspiration (which generally occurs at approximately 4–5 mm a day in this area; J-P Caliman pers. comm.), producing waterlogged conditions in the plots, reducing oxygen levels and activity levels of decomposers, and potentially reducing arthropod numbers, as has been reported from studies in the Amazonian rainforest (Adis 1988). Another possibility is that drier conditions directly favoured key invertebrate decomposer groups, such as termites. For example, a recent study in rainforest in Sabah, Malaysia, found that termites had a greater impact on decomposition during ENSO-related drought than during normal conditions, possibly because drier soils allowed the termites to move more freely and find leaf-litter (Ashton *et al* 2019).

The interacting impact of rainfall during the study and rainfall before the study on predation is likely to reflect direct impacts of rainfall on predatory groups in the plantation. Due to their open canopy compared to forest, plantations experience high temperature during the daytime and variable temperature over the course of 24 h (Hardwick *et al* 2015). Such extremes of temperature can have negative impacts on invertebrate numbers (Foster *et al* 2011), potentially reducing associated ecosystem processes. However, rainfall can cool these conditions and increase humidity, potentially reducing negative impacts on arthropods (Woon *et al* 2019). This could increase activity and predation levels by predatory invertebrate taxa. In contrast, prolonged rainfall can also depress the abundance of some arthropod groups, including ants (Adis 1988). This might explain the interaction between rainfall level at the time of study and historical rainfall that we recorded, with the positive impact of rainfall during the observation period only being observed when historical conditions had been dry.

Our exclusion experiments demonstrated the important role that both invertebrate and vertebrate groups have on ecosystem processes in oil palm. We recorded lower rates of decomposition and seed removal when invertebrates were excluded, and lower predation when vertebrates were excluded. None of our exclusions had a significant interaction with rainfall levels on the processes measured, indicating that the functional roles of the excluded groups are unaffected by rainfall. The important role that invertebrates play in decomposition and seed removal has been recorded in previous studies. For example, in forest habitats in Sabah, Malaysia, exclusion experiments found significantly reduced decomposition rates and levels of seed removal where invertebrates were excluded (Ewers *et al* 2015). The role of vertebrates in predation within oil palm ecosystems has also been recorded in previous work, with a study in oil palm plantations finding significantly higher levels of pest damage on palms (Koh, 2008) when vertebrates were excluded. The lack of an effect of vertebrate predation on seed removal in our study also reflects the results of the exclusion experiments in Sabah (Ewers *et al* 2015). However, in the case of oil palm, this is surprising, as rodent numbers can be extremely high in plantations (Wood and Chung 2003, Hood *et al* no date) and granivorous birds are relatively common (Prabowo *et al* 2016) and were frequently seen at all our study sites. It is possible that the experimental set-up, such as the use of paper disks, discouraged birds and rats from eating the seeds, or it could be that the high abundance of oil palm fruit in the system represents a more profitable alternative food, reducing seed removal.

We recorded higher levels of predation on the ground than in the canopy during dry but not wet conditions, perhaps reflecting a change in foraging patterns of predators with rainfall. For example, upward movement of invertebrates during the wet season has been recorded in the Amazonian rainforest during the wet season (Adis and Schubart 1984). An alternative explanation is that hotter and more-variable temperature conditions in the canopy (as has been recorded in rainforests (Hardwick *et al* 2015)) during drier periods disproportionately depressed predator activity there, compared to the ground, but that this impact was less marked in wetter conditions, reducing the differences in predation recorded between the two strata.

Conclusion

Overall, we recorded high rates of litter decomposition, high rates of predation and seed removal, but low levels of herbivory in our study. We also recorded variable effects of rainfall on these factors and impacts of both vertebrate and invertebrate groups on levels recorded. Taken together, these results demonstrate a generally healthy and robust range of ecosystem functions in mature oil palm in our study area and a continued impact of both vertebrate and invertebrate groups in spite of changing rainfall patterns. However, rainfall did have an effect on both decomposition and predation. In particular, decomposition and predation rates both increased with higher levels of rainfall during the study, but only when rainfall was low before the study. These results suggest that ecosystem processes in oil palm are generally resilient to changing rainfall levels under current climatic conditions. However, longer-term drought conditions may suppress ecosystem functions, especially if they are not followed by wetter periods, casting uncertainty on the stability and resilience of ecosystems in tomorrow's climate.

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Appendix 1. Details of post-hoc tests

Decomposition

Interaction between average daily rain 90 days pre-experiment and average daily rain during experiment. The interaction between 'rain-pre' and 'rain-during' was significant in the decomposition model, so we carried out post-hoc analyses to determine whether slopes of each rain variable differed significantly from zero, when the other rain variable was held at one of three constant values. The values we held each rainfall variable at were the 5th percentile, the mean and the 95th percentile.

Bag type factor levels

Bag type was significant in the decomposition model, so we carried out post-hoc analyses using Tukey's HSD to determine which contrasts were significantly different.

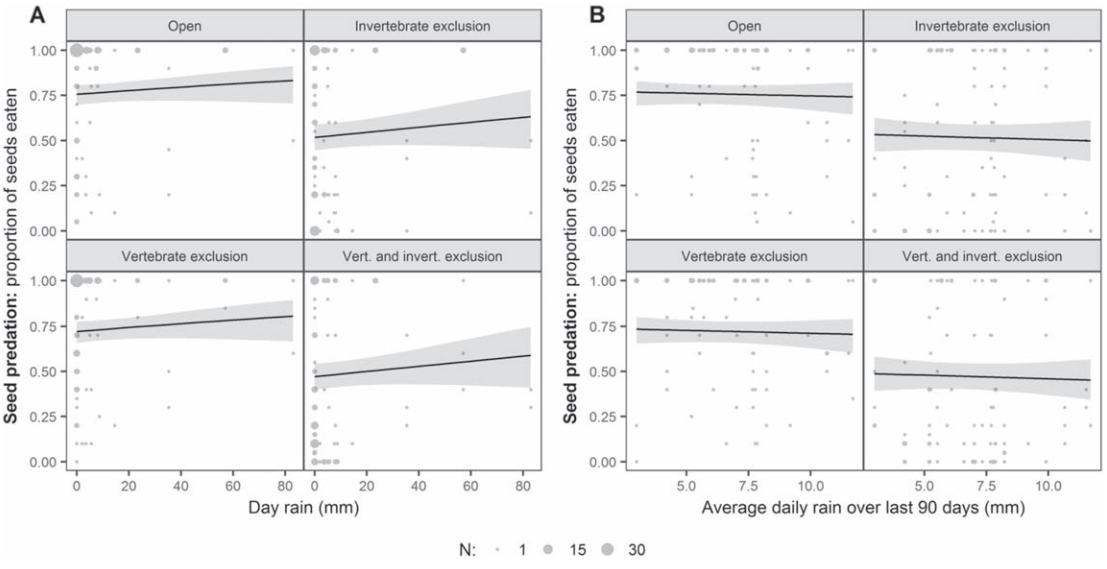

Figure A1. (A) Proportion of sunflower seed kernels (of 10) removed from samples in different exclusion treatments plotted against rainfall on the day of sampling. (B) The same data plotted against rainfall over 90 days prior to the sampling. The dots show the values for the raw data, with dot size proportional to the number of data points. Trend lines are calculated from the model and do not imply a significant relationship. Grey bands around the trend lines are confidence intervals as derived from the model.

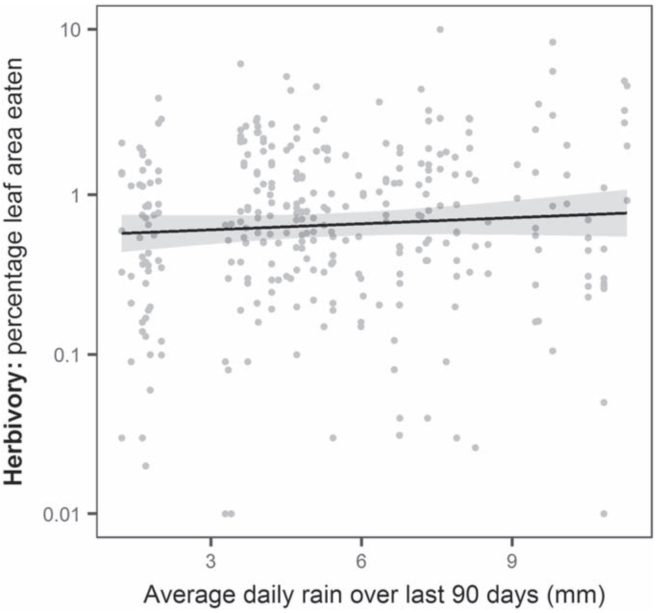

Figure A2. The relationship between the area of palm frond leaflets lost to herbivory and rainfall prior to sampling. Herbivory was not significantly affected by rainfall over the 90-day period prior to sampling. Dots represent the raw data. The trend line was calculated from the model and does not imply a significant relationship. The grey bands around the trend line are the confidence intervals as derived from the model. The data are shown on a logarithmic scale to help interpretability.

Table A1. Trends for rain-during when varying rain-pre.

Rain-pre	Rain-during: trend	SE	df	lower.CL	upper.CL	t.ratio	p.value
3.52 (5th)	0.1862	0.0242	283	0.1386	0.2339	7.689	**<.0001**
6.11 (mean)	0.0711	0.0126	215	0.0462	0.0959	5.641	**<.0001**
8.47 (95th)	−0.0343	0.021	270	−0.0756	0.00707	−1.632	0.1039

Results are averaged over the levels of: bag_type.
Trends are based on the log (transformed) scale.
Confidence level used: 0.95.

Table A2. Trends for rain-pre when varying rain-during.

Rain-during	Rain-pre: trend	SE	df	lower.CL	upper.CL	t.ratio	p.value
3.25 (5th)	0.1325	0.0204	279	0.0924	0.1727	6.499	**<.0001**
5.97 (mean)	0.0115	0.0164	279	−0.0208	0.0439	0.702	0.4834
11.52 (95th)	−0.2352	0.051	276	−0.3357	−0.1348	−4.61	**<.0001**

Results are averaged over the levels of: bag_type.
Trends are based on the log (transformed) scale.
Confidence level used: 0.95.

Table A3. Means.

Bag_type	lsmean	SE	df	lower.CL	upper.CL
Fine_mesh_g	−4.56	0.0603	20.1	−4.68	−4.43
Fine_withholes_g	−4.41	0.0606	20.5	−4.54	−4.28
Two_mm_mesh_g	−4.53	0.0599	19.5	−4.66	−4.41

Degrees-of-freedom method: kenward-roger.
Results are given on the log (not the response) scale.
Confidence level used: 0.95.

Table A4. Contrasts.

Contrast	Estimate	SE	df	t.ratio	p.value
Fine_mesh_g - Fine_withholes_g	−0.145	0.0563	271	−2.581	**0.0279**
Fine_mesh_g - Two_mm_mesh_g	−0.021	0.0558	271	−0.376	0.9252
Fine_withholes_g - Two_mm_mesh_g	0.124	0.0557	271	2.233	0.0676

Results are given on the log (not the response) scale.
P value adjustment: Tukey method for comparing a family of 3 estimates.

Table A5. Trends for rain-during when varying rain-pre.

Day-rain	Rain-pre: trend	SE	df	lower.CL	upper.CL	t.ratio	p.value
0 (5th)	0.0478	0.0321	616	−0.0152	0.11085	1.49	0.1367
7.25 (mean)	0.0186	0.0305	616	−0.0412	0.07838	0.61	0.5423
40.62 (95th)	−0.116	0.0561	616	−0.2261	−0.00592	−2.069	**0.0389**

Results are averaged over the levels of: cage treatment (cage or no cage), canopy treatment (canopy or ground).
Trends are based on the logit (transformed) scale.
Confidence level used: 0.95.

Table A6. Trends for rain-pre when varying rain-pre.

Rain-pre	Day rain: trend	SE	df	lower.CL	upper.CL	t.ratio	p.value
2.7 (5th)	0.02976	0.00891	616	0.01226	0.04725	3.341	**0.0009**
6.65 (mean)	0.01382	0.00437	616	0.00525	0.0224	3.166	**0.0016**
10.66 (5th)	−0.00234	0.0046	616	−0.01136	0.00669	−0.508	0.6113

Results are averaged over the levels of: cage treatment (cage or no cage), canopy treatment (canopy or ground).
Trends are based on the logit (transformed) scale.
Confidence level used: 0.95.

Mealworm predation

Interaction between average daily rain in 90 days pre-experiment and day rain. The interaction between 'rain-pre' and 'day-rain' was significant in the decomposition model, so we carried out post-hoc analyses to determine whether slopes of each rain variable differed significantly from zero, when the other rain variable was held at one of three constant values. The values we held each rainfall variable at were the 5th percentile, the mean and the 95th percentile.

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