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Understory vegetation in oil palm plantations benefits soil biodiversity and decomposition rates

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Abstract

Oil palm is the most productive vegetable oil crop per unit area and is crucial to the economy of developing countries such as Malaysia and Indonesia. However, it is also highly controversial due to the impact it has on biodiversity. Inputs of herbicides to control understory vegetation in plantations are high, which is likely to harm native biodiversity, but may be unnecessary in protecting oil palm yield. In this study we investigate the effects of understory manipulation using herbicides on soil fauna, litter decomposition rates and soil abiotic variables: pH, soil organic carbon, soil water content, nitrogen, carbon/nitrogen ratio, potassium and phosphorous. Understory vegetation was manipulated in three treatments: enhanced understory complexity (no herbicides, developed understory), normal understory complexity (intermediate herbicide use with some manual removal) and reduced understory complexity (heavy herbicide use, no understory vegetation). Two years after treatment, soil macrofauna diversity was higher in the enhanced than the normal and reduced understory treatment. Furthermore, both macrofauna abundance and litter decomposition was higher in the enhanced than the reduced understory treatment. By contrast, soil fertility did not change between treatments, perhaps indicating there is little competition between oil palms and understory vegetation. The reduction of herbicide use should be encouraged in oil palm plantations, this will not only reduce plantation costs, but improve soil biodiversity and ecosystem functioning.

Introduction

Oil palm is the most productive vegetable oil crop per unit area (Zimmer, 2010) and is a crucial part of the economy in developing countries such as Indonesia and Malaysia (Koh & Wilcove, 2007). However, with over 21 million ha of plantations covering the tropics (FAOSTAT, 2016) oil palm cultivation is also one of the most controversial land uses. This is primarily due to the negative impacts on biodiversity and climate change caused by forest conversion to plantations (Carlson et al., 2013; Savilaakso et al., 2014). Therefore, improving the management of oil palm plantations to protect existing biodiversity and ecosystem functions is vital for agricultural sustainability and biodiversity conservation (Foster et al., 2011). Furthermore, it is in the interest of plantation managers to develop and apply sustainable practices, as this can lead to economic gain (Woittiez et al., 2017) and there is considerable market demand for palm oil to be certified as sustainable by the Round Table on Sustainable Palm Oil (RSPO) (Tayleur et al., 2018). Oil palm has the potential to implement relatively long-term sustainable management practices as it is a perennial crop with a ~25 year commercial lifespan. One of the core management criteria for plantations to be certified as sustainable by the RSPO is to improve soil sustainability (Roundtable on Sustainable Palm Oil, 2013).

Soil biodiversity plays a large part in the ecosystem functions that help maintain soil sustainability (Bardgett & van der Putten, 2014). Soil biota are important for many vital ecosystem functions such as: nutrient cycling; carbon sequestration; and nutrient uptake by plants. However, soil biodiversity is threatened by land use change and agricultural intensification (Franco et al., 2016; Tsiafouli et al., 2015) which can reduce ecosystem functioning (Bardgett & van der Putten, 2014; de Vries et al., 2013). For example, reductions in decomposer functional diversity has been shown to reduce decomposition rates and carbon and nutrient cycling (Handa et al., 2014), which are important ecosystem functions for soil formation and fertility (Nielsen et al., 2011).

While there has been a recent upsurge in research investigating the effects of oil palm plantation management on aboveground biodiversity and ecosystem function (Nurdiansyah et al., 2016; Syafiq et al., 2016; Teuscher et al., 2016), belowground biodiversity and soil functioning has been severely neglected (Bessou et al., 2017). Recent studies have found large declines in soil fertility and, in particular, soil organic carbon (SOC) in oil palm plantations after forest conversion, with continued declines as plantations age (Ashton-Butt et al., in review.; Guillaume et al., 2018; Matysek et al., 2018). There are also changes to belowground biodiversity after forest conversion to oil palm; with termites and litter feeding ants showing severe declines (Luke et al., 2014); and soil microbial communities have been found to alter in community composition and functional gene diversity (McGuire et al., 2015; Tripathi et al., 2016). However, the effect of these changes in biodiversity on ecosystem functioning is little known (Dislich et al., 2016). Recent research has found that the application of organic matter to the soil can improve soil quality and related biotic functions (Carron et al., 2016; Tao et al., 2016, 2018) and different zones around the palm hold varying amounts of soil fauna and nutrients as a result of standard management regimes (Carron *et al.*, 2015).

Soil communities and their functioning are largely impacted by the diversity and abundance of plant communities (Eisenhauer et al., 2011; Thakur & Eisenhauer, 2015). Oil palm plantations can have a reasonably diverse plant understory (Foster et al., 2011). However, these plants are often seen as weeds thought to compete with oil palms for nutrients by some plantation managers and although understory vegetation management varies widely between different plantations, complete removal by herbicides and weeding is common (Tohiran et al., 2017). A typical plantation uses up to 90% of its pesticide budget on herbicides such as paraquat, glufosinate ammonium and glyphosphate (Page & Lord, 2006; Wibawa et al., 2010). This extensive use of herbicides can pollute water sources and pose a threat to natural ecosystems and human health (Comte et al., 2012; Schiesari & Grillitsch, 2011). Herbicides are also economically costly, especially to small-scale farmers (Lee et al., 2014). Furthermore, the use of pesticides in agriculture has been linked with mass biodiversity declines around the world (Beketov et al., 2013; Geiger et al., 2010) without consistent benefits to agricultural yield (Lechenet et al., 2017). In oil palm plantations, reduction in herbicide use and a greater coverage of understory vegetation has been shown to improve avian biodiversity (Nájera & Simonetti, 2010; Tohiran et al., 2017). Furthermore, a greater developed understory benefits aboveground invertebrate communities, by providing additional habitat and food resources (Ashraf et al., 2018; Chung et al., 2000; Spear et al., 2018). However, it is not known how the understory vegetation in oil palm plantations influences belowground invertebrate communities and related ecosystem functions.

In this study, we investigate the effect of experimentally manipulating understory vegetation in oil palm plantations on soil macrofauna abundance, diversity and community composition, and litter decomposition rates and soil abiotic properties in oil palm plantations. We hypothesised that macrofauna abundance and diversity would be positively affected by the amount of understory vegetation and that this would have correspondingly positive effects on soil processes. Our findings will have important implications for the sustainable management of oil palm plantations.

Methods

Study area

Fieldwork took place in Sumatra, Indonesia, as part of the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme. The BEFTA Vegetation Project is a large-scale, long-term ecological experiment testing the influence of different understory vegetation management strategies on oil palm biodiversity, ecosystem functioning and yield (Foster et al. 2014). The project is located in oil palm estates owned and managed by Pt Ivo Mas Tunggal, a subsidiary of Golden Agro Resources (GAR) and with technical advice from Sinar Mas Agro Resources and Technology Research Institute (SMARTRI, the research and development centre of GAR). The estates are located in the Siak regency of Riau Province, Sumatra (0°55′56″ N, 101°11′62″ E) (see Foster *et al.*, (2014)). This area receives an average rainfall of 2400 mm/yr, with the natural landscape characterized by wet lowland forest on sedimentary soils. The soil type is ferralitic with gibbsite and kaolinite (Ferric Acrisol according to the FAO classification). Our study area was logged in the 1970s and the resulting logged forest was converted to oil palm from 1985–1995. The plantations included in this study were on average 25 years old (between 29 and 23 years old). The majority of the area around these estates is used to cultivate oil palm. There is no natural forest and few other crops are grown.

Standard fertiliser treatment of oil palm in our study site includes: 1.75 kg tree^{-1} yr^{-1} urea (46% N); 0.5 kg tree^{-1} yr^{-1} triple super phosphate (45% P_2O_5, 15% Ca); 2.5 kg tree^{-1} yr^{-1} muriate of potash (61% K_2O, 46% Cl); and 0.5 kg tree^{-1} yr^{-1} Kieserite (16% Mg, S: 22%).

Understory treatments:

Eighteen study plots were established in October 2012. Oil palms on all plots were planted between 1987 and 1993, and so were mature at the time of the study. Plots were 150 m x 150 m and are located on flat ground between 10 and 30 m above sea level and without adjacent human habitation. The plantations have a typical zonation of soil and vegetation management leading to 3 distinct zones, weeded circle, harvesting path and windrow (Fig 1). The plots were arranged adjacently in triplets, with one plot in each triplet randomly assigned one of three understory vegetation management treatments (Fig. 2). Treatments were implemented in February 2014, and involved the following management:

1) Normal understory complexity: standard company practice, consisting of intermediate understory vegetation management using herbicides and some manual removal. The weeded circle (a circular zone around the palm) and harvesting paths were sprayed, and woody vegetation (shrubs and trees) was removed manually.

2) Reduced understory complexity: all understory vegetation was removed using herbicides.

3) Enhanced understory complexity: understory vegetation was allowed to grow with limited interference except for minimal manual clearance in the weeded circle and harvesting paths.

The herbicides used in the establishment of the plots were Glyphosate (Rollup 480 SL), Paraquat Dichloride (Rolixone 276 SL), metsulfuron- methyl (Erkafuron 20 WG) and Fluroxypyr (Starane 290 EC).

Vegetation sampling

Ground vegetation surveys were conducted (between April and June 2016, two years after the treatments were established)within each of the 6 replicate treatment blocks,at two sampling points (two palms) (12 palms from each treatment), totalling 36 points. At each sampling point, a 1 m x 1 m quadrate was placed randomly, 4 times, within both the weeded circle and windrow zones and the ground cover and bare ground estimated from an average of two observers. In addition, within each quadrat plants were identified to species level and abundance of each species recorded.

Soil macrofauna sampling

Soil macrofauna was sampled at the same points as the vegetation surveys, with samples being taken from both the circle and the windrow, as these have been shown to hold different soil macrofauna abundance and composition (Carron *et al.*, 2015). The harvesting path was not sampled, as this is known to contain a very low abundance of soil macrofauna (Carron *et al.*, 2015). We used a standard Tropical Biology and Fertility Institute soil monolith method to sample invertebrates (Bignell et al., 2008), which involved excavating a 25 cm x 25 cm quadrat to a depth of 20 cm. All macrofauna, characterised as fauna visible to the naked eye (Kevan, 1968), were removed from soil samples in the field by hand-searching. Worms were placed immediately into formalin and all other arthropods were stored in 70% ethanol for later identification. Invertebrates were sorted to order, with the exception of termites and ants, which were separated from Blattodea and Hymenoptera, owing to their abundance and distinct ecology, and Diplopoda and Chilopoda, which were identified to class.

Soil abiotic sampling

Soil abiotic samples were taken from the same sample locations as the vegetation and soil macrofauna surveys. Soil was collected from the weeded circle and windrow from 0-15cm depth using a soil Dutch auger. At each sampling point, three samples were taken and bulked from each of the weeded circle and windrow. The weeded circle and windrow have been found to have different soil nutrient contents in previous studies (Carron *et al.,* 2015; Tao *et al.*, 2016) and thus were kept separate.

The following soil chemical properties were measured: soil pH, soil organic carbon content (SOC), total nitrogen (N) content, carbon/nitrogen ratio (C/N ratio), total phosphorous content (P) and total potassium content (K). The soil pH was determined using a pH meter with a soil to water ratio of 1:1. The SOC concentration was measured by loss-on-ignition, using the Walkley–Black method (Nelson & Sommers, 1982). The total soil P concentration was analysed using the hydrogen chloride extraction method. The total N was determined by the Kjeldahl method (McGill & Figueiredo, 1993). In addition to the chemical properties, soil aggregate stability (the ability of soil particles to resist disintegration) was measured on 3-5 mm aggregates according to the method proposed by Le Bissonais (1996) and soil water content were measured by the oven drying method.

Litter decomposition rates

We used litter decomposition bags, made of fine mesh, to calculate litter mass loss over time. Bags (10 cm x 10 cm) were filled with 4 g of freshly-cut oil palm fronds that had been dried to a constant weight in the oven. Bags were subject to two treatments: closed bag with no holes, excluding invertebrates, and open bags that had eight 1cm holes cut into them, allowing access to invertebrates.

Closed bags represent decomposition from microbes only and open bags decomposition from microbes and invertebrates. Both closed and open bags were stapled together and placed in each weeded circle and windrow at all sampling points (a total of 144 bags). Bags were left in the field for 30 days after which they were collected, dried at 70°C to a constant weight and weighed to measure mass loss.

Statistical analysis

All statistical analysis was performed in R 3.4.4 (R Core Team, 2018). We used linear mixed effects models (LMM) in R package 'lme4' (Bates et al., 2014) to examine the effect of understory treatment on order richness and general linear mixed effects models (GLMM) to examine the effect on soil macrofauna abundance (as count data should not be modelled using a Gaussian distribution). We used a negative-binomial distribution to fit the GLMM to account for overdispersion. Understory treatment and sampling zone (weeded circle or windrow) were fitted as categorical fixed effects. Interaction effects were explored between sampling zone and understory treatment for both LMMs and GLMMs and were introduced into the GLMM based on model selection by the AICc value (Brewer et al., 2016). Sampling zone (weeded circle or windrow) was nested within the oil palm sampled and fitted as random effects. Model estimates for GLMMs were presented as incidence rate ratios (Tripepi et al., 2007) as these are more intuitive than the negative binomially transformed model estimates.

A separate linear mixed effects model with plant species richness and vegetation cover was fitted with understory treatment and sampling location (windrow or weeded circle) as interacting categorical fixed effects to examine the effect of understory treatment on plant species richness and plant cover.

To determine whether understory treatment affected soil macrofauna community composition, we fitted multivariate generalized linear models to the macrofauna abundance data using R package 'mvabund' (functions 'manyglm' and 'anova.manyglm') (Wang et al., 2012). We used this model-based method to analyse community composition because, unlike distance-based methods (e.g. PRIMER), multivariate generalized linear models can account for the confounding mean–variance relationships that often exist in ecological count data by modelling multivariate abundance data with a negative binomial distribution (Warton et al., 2016). Model terms were tested for significance with a likelihood ratio test and a Monte Carlo resampling scheme with 999 iterations. Tests were simultaneously performed for univariate (single-order) responses to treatment, adjusting these univariate p-values to correct for multiple testing (Wang *et al.*, 2012).

To explore the effect of understory treatment on soil abiotic properties, LMMs were used with the same model structure as macrofauna order richness. C/N ratio, aggregate stability and pH fitted a normal distribution, however, soil variables: C, N, P, K and water content were log-transformed to correct for a non-normal distribution.

To determine the effect of understory treatment on decomposition rates we used a LMM. The model included understory treatment, sampling zone (weeded circle or windrow) and decomposition bag treatment as categorical fixed effects. Interaction effects were explored during model selection between the fixed effects, but were not included based on AICc values (Brewer et al., 2016). Sampling zone (windrow or weeded circle) was nested within the oil palm sampled and fitted as random effects. The model was: *decomposition rate~ understory treatment + sampling zone + bag treatment (1| oil palm/sample number)*. Significance of all LMMs and GLMMs were explored via p-values computed by Kenward-Rodger approximation (Luke 2017).

Results

Vegetation

Vegetation cover did not differ between normal and enhanced understory treatments (estimate = -9.23, P = 0.306), but was higher than the reduced treatment for both weeded circle and windrow (Table 1 and Fig. 2). Forty-five plant species were identified in the plantations. *Asystasia micrantha* was the most abundant species followed by *Nephrolepis biserrata*, *Peperomia pellucida* and *Asplenium longissimum.* Plant species richness did not differ between normal and enhanced understory treatments, but was higher than the reduced treatment for both weeded circle and windrow (estimate = -2, P = 0.003) (Fig 3). Sampling zone had an interaction effect within treatment; the windrow of the enhanced understory treatment had a lower species richness than the weeded circle (estimate = -1.31, *P* = 0.035), whereas there was no difference between plant species richness of the weeded circle and windrow in the normal and reduced treatment.

Macrofauna richness and abundance

For the macrofauna survey, we sampled 6417 individuals from 34 orders and taxonomic groups. Ants were the most abundant group found followed by: Dermaptera, Lumbricidae, Aranae, Isopoda, Diplopoda, Chilopoda, Blattodea, Diplura, Coleoptera and Diptera. Order richness was higher in the enhanced understory treatment compared to the normal (estimate = -1.51, $P < 0.05$) and reduced understory treatments (estimate = -2.46, $P < 0.001$) (Table 1 and Fig. 3). Order richness was also higher in the windrow (estimate = +3.11, $P < 0.001$) than the weeded circle in all treatments (Fig. 4). Macrofauna abundance was higher in the weeded circle (but not the windrow) in areas with an enhanced understory than both areas with normal (IRR = 0.22, $P < 0.005$) and reduced understory (IRR = 0.3, $P < 0.01$) (Fig. 4). In addition, abundance was higher in the windrow than the weeded circle of the normal (IRR = 4.64, $P < 0.005$); and reduced understory treatments (IRR = 3.37, $P < 0.01$). However, in the enhanced understory treatment, the windrow had a lower macrofauna abundance than the weeded circle, although, this was marginally non-significant (IRR = 0.53, $P = 0.053$).

Macrofauna Composition

Understory treatment had an effect on macrofauna composition (LR = 144.4, $P < 0.001$). The normal (LR = 52.69, $P < 0.001$) and reduced understory treatment (LR = 115.49, $P < 0.001$) differed in soil macrofauna composition from the enhanced treatment. The reduced understory treatment exhibited a larger difference in macrofauna composition from the enhanced treatment than the normal understory treatment. Zone of oil palm sampled (weeded circle or windrow) also had an interaction effect with treatment on macrofauna composition in the enhanced (LR = 69, $P < 0.001$), normal (LR = 38.93, $P < 0.01$), and reduced (LR = 115.49, $P < 0.001$) understory treatments. Ant (LR = 13.32, $P = 0.02$) Coleoptera (LR = 12.55, $P = 0.038$), Dermaptera (LR = 13.93, $P = 0.012$), Diplopoda (LR = 11.93, $P = 0.048$), Isopoda (LR = 13.8, $P = 0.013$) abundances were all affected by treatment, with lower abundances present in the reduced understory treatment than the enhanced or normal treatments (Fig. 5).

Abiotic variables

Understory treatment had no effect on SOC, N, P, K, SWC, C/N ratio, aggregate stability or pH (Fig. 6 and Table 2). The zone of the oil palm sampled also had no effect on these variables apart from C/N ratio, where the windrow had a slightly higher C/N ratio than the weeded circle (model estimate = +2.65, $P = 0.018$) and total phosphorous where the windrow had a slightly lower total phosphorous level in the soil than the weeded circle (model estimate = -0.40, $P = 0.045$)

Decomposition

Decomposition rate was higher in the enhanced treatment compared to the reduced understory treatment (estimate = -0.0068 g/day, $P = 0.003$) (Table 3 and Fig. 7) and in the normal treatment compared to the reduced treatment (estimate = -0.0054 g/day, $P = 0.028$). Decomposition rate was marginally lower in the normal understory treatment compared to the enhanced understory treatment, although this was not statistically significant (estimate = -0.0014 g/day, $P = 0.548$). Bag treatment also had an effect on decomposition: open bags experienced a higher decomposition rate than closed bags (estimate= 0.0031 g/day, P=0.042). Sampling zone also had a large effect on decomposition with bags in the windrow experiencing a higher decomposition rate than those in the weeded circle (estimate=0.0074 g/day, P<0.001).

Discussion

Our findings show that diversity and abundance of soil macrofauna along with belowground ecosystem functioning can be improved in oil palm plantations by reducing herbicide applications and enhancing understory vegetation. Furthermore, soil nutrient levels were the same in the enhanced understory treatment compared to the other treatments, adding to evidence that understory vegetation is unlikely to compete for nutrients with oil palms.

Soil macrofauna

Soil macrofauna order richness and abundance were higher in enhanced understory plots than the reduced plots and order richness (but not abundance) was higher in plots with an enhanced understory compared to normal understory plots. Increased plant diversity (characteristic of the enhanced understory plots) has been found to benefit soil biota in other systems (Scherber *et al.*, 2010; Eisenhauer *et al.*, 2011, 2012) and increased understory complexity can increase aboveground invertebrate abundance and food web complexity in oil palm plantations by providing greater resources (Spear et al., 2018). Furthermore, oil palm plantations suffer from hotter and drier microclimates than the natural habitat in the region (Luskin & Potts, 2011), which native soil invertebrates can be sensitive to (Fayle et al., 2010). An increased understory is likely to ameliorate this microclimate by preventing exposure of the soil to direct sunlight and by increasing water infiltration, thus benefitting soil invertebrates (Ashraf et al., 2018; Belsky et al., 1993). Soil macrofauna composition was different in the three understory treatments; taxa that include litter feeding organisms: Dermaptera; Diplopoda; Coleoptera; and Isopoda, all increased in abundance in the enhanced compared to the reduced understory treatment. This is likely due to the greater biomass and diversity of decaying vegetation and root matter provided by the understory plants (Wardle et al., 2004). These fauna are considered ecosystem engineers and are key in breaking down leaf litter and creating a wider availability of resources for microbial decomposers (Brussaard, 2012). Furthermore, the reported positive effects of the understory on soil biodiversity may be conservative in our study; benefits of plant diversity on soil biota can have a significant time delay (Eisenhauer et al., 2012). The enhanced understory treatment had only been installed for two years at the time of sampling, therefore, increased positive effects on the soil macrofauna community and associated ecosystem functions can be expected over time. This is extremely pertinent in oil palm plantations, as they have a long commercial lifespan of more than 25 years. This study was conducted in mature plantations; enhanced understory vegetation could be even more important in young plantations where soil erosion and microclimate is more severe, as there is a reduced canopy cover and less organic matter available from decaying fronds (Guillaume et al., 2015; Luskin & Potts, 2011).

Soil abiotic properties

Our results show there was no impact of either treatment on soil fertility. This indicates that the changes in soil macrofauna community were caused by the direct impacts of vegetation. Furthermore, it suggests that the understory vegetation has little impact on nutrient availability for the oil palm, as there was no difference in nutrient levels between the treatments. If enhanced understory vegetation is maintained for an extended period of time, positive effects on soil fertility could be seen as undergrowth is likely to prevent soil erosion, loss of SOM and leaching of other nutrients (Li et al., 2007; Lieskovský & Kenderessy, 2014).

Decomposition

Litter decomposition rates were substantially lower in reduced understory than in the normal and enhanced understory plots. Decomposition influences carbon storage and underlies soil formation (Swan & Kominoski, 2012). It is also a good indicator of the sensitivity of ecosystem processes to change in species richness (Hooper et al., 2012). The slowed rate of decomposition with reduced understory vegetation corresponds to the loss of macrofauna diversity and abundance (particularly litter feeders) in the reduced understory treatment. Bags that were closed to invertebrates also showed slower decomposition rates in all treatments. This is likely to be explained by a reduction in microbial litter decomposition. This could be a result of reduced macrofauna litter decomposition resulting in a lower availability of pre-digested material for microbes (Brussaard, 2012) and/or that the enhanced understory provides a more favourable microhabitat and microclimate for microbial fauna, due to the increased soil cover and greater plant diversity. This could increase both microbial diversity and function (Eisenhauer, 2016). These findings have important impacts on soil sustainability and recovery after forest conversion to oil palm plantations and after replanting events, when soils lose large amounts of SOC (Guillaume et al., 2015; Matysek et al., 2018). Increased understory could help ameliorate these negative effects by biologically enhancing SOC sequestration, providing physical protection from soil erosion and drying and providing a more amenable microclimate.

Conclusions

This study shows that a reduction in herbicide usage and the resulting improvement in understory vegetation diversity and coverage can be a key tool in improving within-plantation belowground biodiversity and ecosystem functioning. Furthermore, we stress that the reduced understory management scheme, that many oil palm plantations employ, has negative impacts on biodiversity and ecosystem functioning. Reducing herbicide application can also benefit plantation owners by lowering operating costs and reducing health risks to plantation workers that are exposed to herbicides, sometimes without being equipped with the necessary protective equipment.

The improved soil quality realised by increasing understory vegetation in oil palm plantations could improve yield (Balasundram et al., 2006). It is thought that understory plants could compete for nutrients and water with oil palms and cause difficulty in harvesting fallen fruit, thus negatively impacting upon yield (Tohiran et al., 2017). However, we found no evidence for nutrient competition in this study. The impacts on yield are a priority for future research and are being addressed in the larger BEFTA project. However, as environmental conditions can take some time to effect yield, these findings are not published here. Further research into the long-term effects of understory management in oil palm plantations may also realise further benefits to soil sustainability. To support soil biodiversity and ecosystem functioning, increasing understory vegetation should be encouraged by certification schemes, such as the Round Table of Sustainable Palm Oil and other advisors of oil palm agriculture best practice.

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Figure Legends

Figure 1. Diagram representing different management zones. The oil palms are the filled circles. The weeded circle is a circular zone with a radius of 1.8 m directly around the palm trunk, which is normally kept "clean" by chemical weed control to facilitate the collection of fruit bunches. The windrow is the zone where the palm fronds pruned during harvest (approximately 18 fronds palm^{-1} year $^{-1}$) are placed on the ground forming a U-shaped windrow around the palm. The harvesting path is a zone cleared for access in the alternate rows, with the windrows in-between.

Figure 2. Photographs of the three understory treatments: Reduced complexity; Normal complexity; and Enhanced complexity (from left to right). Photographs courtesy of Edgar Turner.

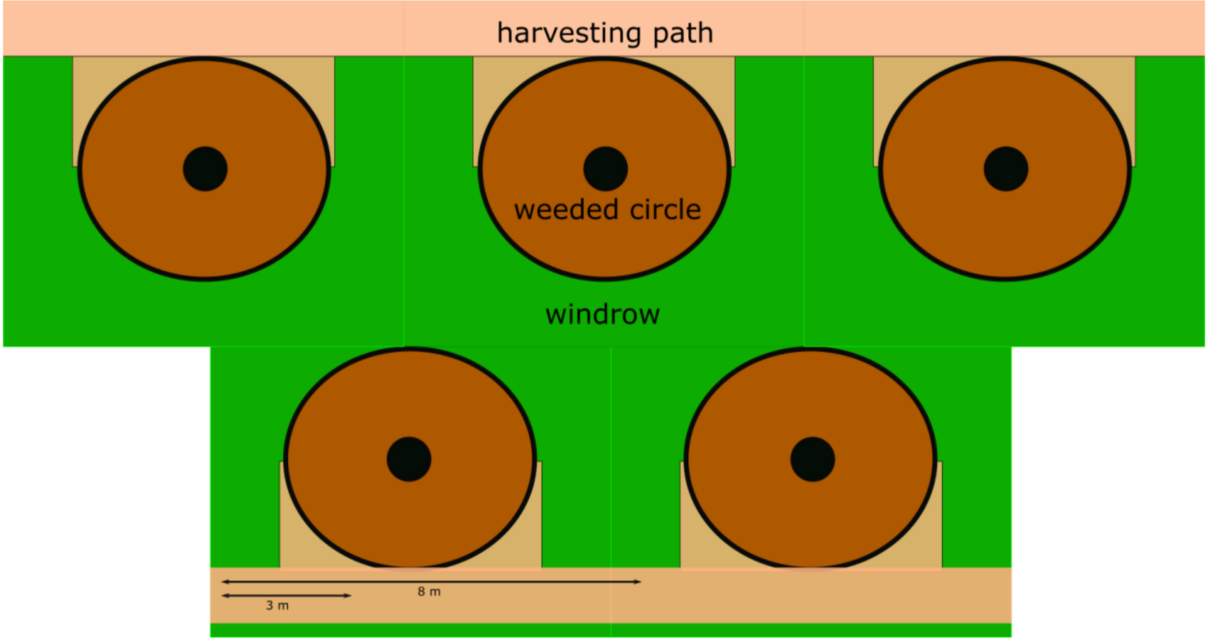
Figure 3. Plant species richness and vegetation cover of the weeded circle and windrow of the Enhanced, Normal and Reduced understory treatments. Filled circles indicate treatment means and bars standard errors.

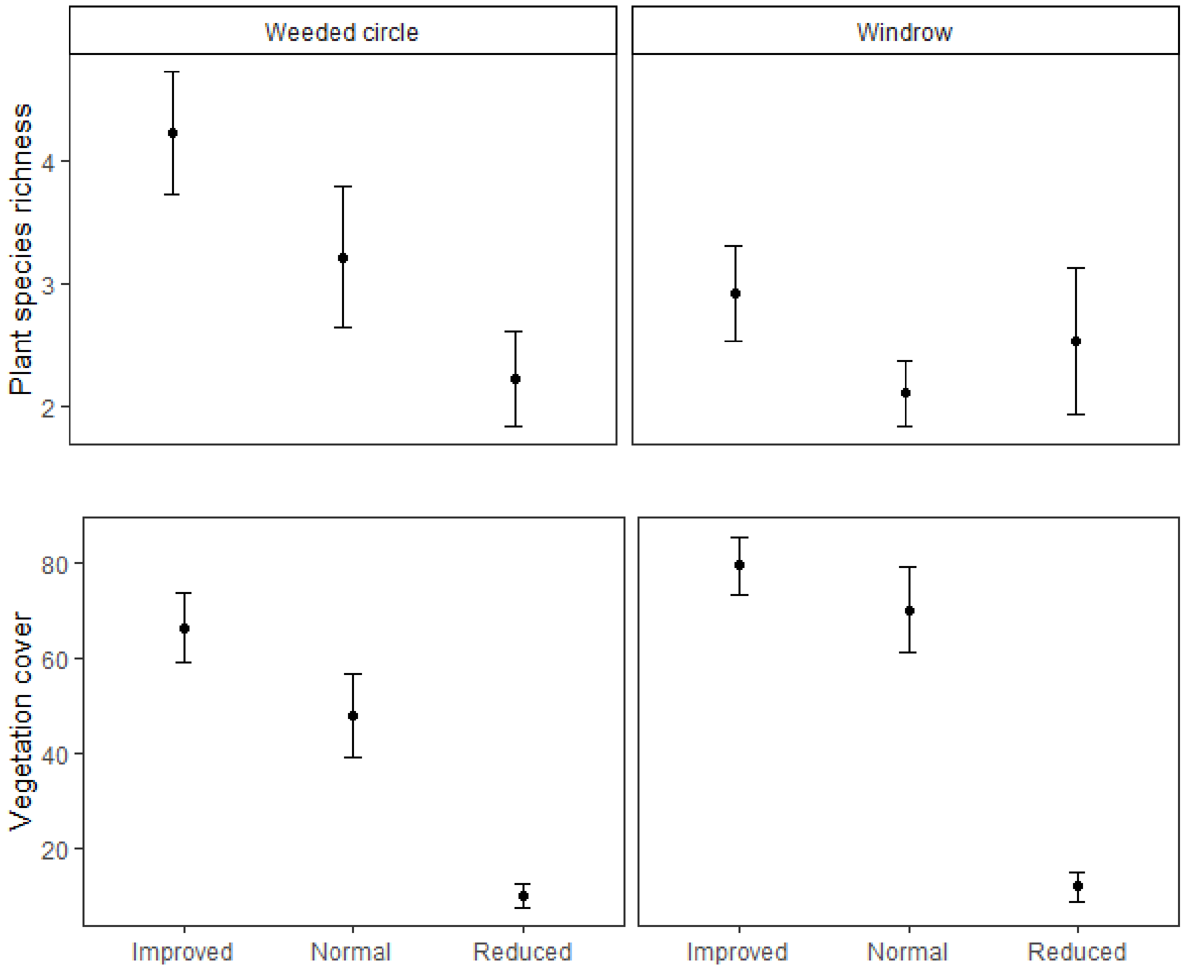
Figure 4. Soil macrofauna abundance and order richness in the weeded circle and windrow of the Enhanced, Normal and Reduced understory treatments. Filled circles indicate treatment means and bars standard errors.

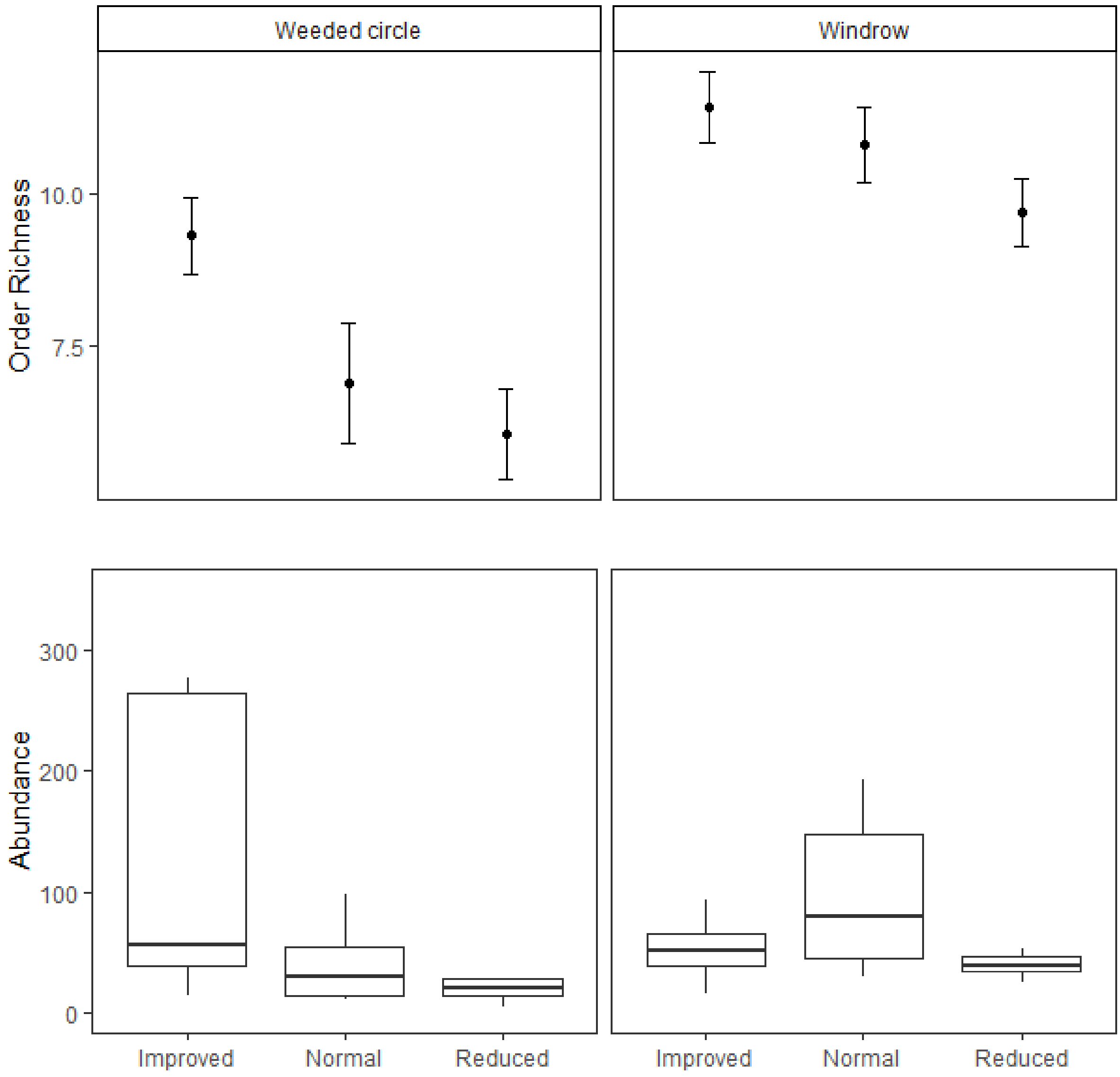
Figure 5. Abundance of the 11 most abundant orders found in the Enhanced, Normal and Reduced understory treatment.

Figure 6. Soil abiotic properties of the Enhanced, Normal and Reduced understory treatments. Box-and-whisker plots present data with a non-normal distribution. Filled circles indicate treatment means and bars standard errors for normally distributed data.

Figure 67 Decomposition rate of litter bags in the Enhanced, Normal and Reduced understory treatment. Filled circles indicate treatment means and bars standard errors.




Weeded circle
Windrow
Plant species richness
4
3
2
Vegetation cover
80
60
40
20
Improved
Normal
Reduced
Improved
Normal
Reduced


Weeded circle
Windrow
Order Richness
10.0
7.5
Abundance
300
200
100
0
Improved
Normal
Reduced
Improved
Normal
Reduced

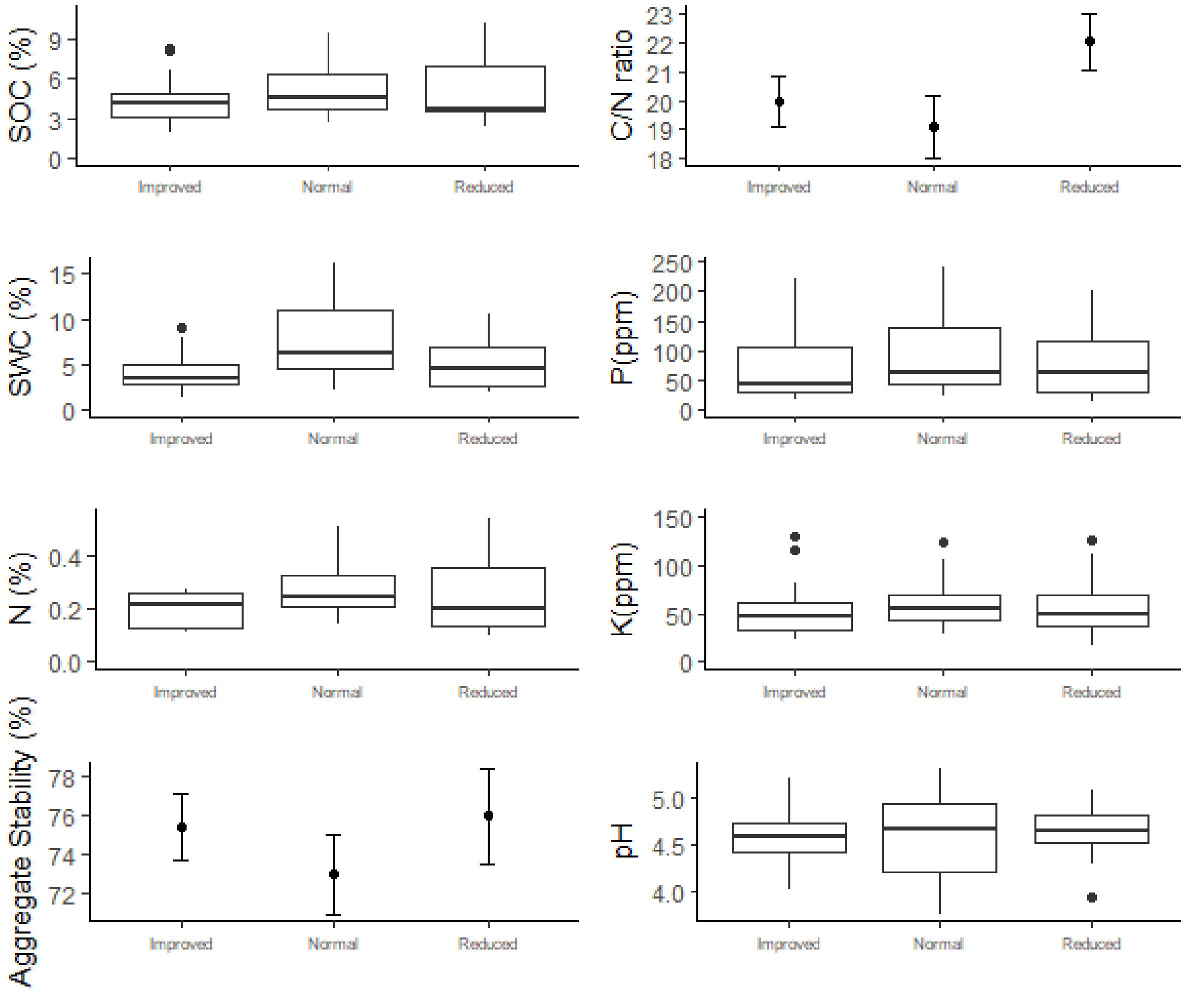

SOC (%)
0
3
6
9
Improved
Normal
Reduced
C/N ratio
18
19
20
21
22
23
Improved
Normal
Reduced
SWC (%)
0
5
10
15
Improved
Normal
Reduced
P(ppm)
0
50
100
150
200
250
Improved
Normal
Reduced
N (%)
0.0
0.2
0.4
Improved
Normal
Reduced
K(ppm)
0
50
100
150
Improved
Normal
Reduced
Aggregate Stability (%)
72
74
76
78
Improved
Normal
Reduced
pH
4.0
4.5
5.0
Improved
Normal
Reduced

Table1. *Model outputs of LMMs and GLMM comparing macrofauna order richness, abundance, vegetation cover and vegetation richness between Enhanced, Normal and Reduced treatment. Table A is the model output with the windrow as the intercept, table B is the model output with the weeded circle as the intercept; Enhanced treatment is the intercept for both table A and B. * denotes an interaction effect.*

(A)	**Order Richness**			**Macrofauna Abundance**			**Vegetation cover**			**Vegetation richness**		
Predictors	*Estimates*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Enhanced treatment	11.90	10.85 – 12.95	**<0.001**	70.62	41.54 – 120.04	**<0.001**	79.23	67.93 – 90.53	**<0.001**	2.92	2.04 – 3.81	**<0.001**
Normal treatment	-1.51	-2.92 – -0.10	**0.036**	1.33	0.59 – 3.02	0.495	-9.23	-26.90 – 8.43	0.306	-0.81	-2.19 – 0.57	0.249
Reduced treatment	-2.46	-3.74 – -1.18	**<0.001**	0.72	0.34 – 1.50	0.377	-67.15	-83.13 – -51.18	**<0.001**	-0.38	-1.63 – 0.87	0.546
Weeded circle	-3.11	-4.18 – -2.05	**<0.001**	1.87	0.99 – 3.54	0.053	-12.92	-26.21 – 0.36	0.057	1.31	0.14 – 2.47	**0.028**
Normal*weeded circle				0.22	0.08 – 0.56	**0.002**	-9.30	-30.07 – 11.47	0.380	-0.20	-2.01 – 1.62	0.832
Reduced*weeded circle				0.30	0.12 – 0.72	**0.007**	11.00	-7.79 – 29.79	0.251	-1.62	-3.26 – 0.03	0.054

(B)	**Order Richness**			**Macrofauna Abundance**			**Vegetation cover**			**Vegetation richness**		
Predictors	*Estimates*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Enhanced treatment	8.79	7.74 – 9.84	**<0.001**	132.24	76.07 – 229.90	**<0.001**	66.31	55.01 – 77.61	**<0.001**	4.23	3.35 – 5.11	**<0.001**
Normal treatment	-1.51	-2.92 – -0.10	**0.036**	0.29	0.12 – 0.66	**0.003**	-18.53	-36.19 – -0.87	**0.040**	-1.01	-2.39 – 0.37	0.153
Reduced treatment	-2.46	-3.74 – -1.18	**<0.001**	0.21	0.10 – 0.46	**<0.001**	-56.15	-72.13 – -40.18	**<0.001**	-2.00	-3.25 – -0.75	**0.002**
Windrow	3.11	2.05 – 4.18	**<0.001**	0.53	0.28 – 1.01	0.053	12.92	-0.36 – 26.21	0.057	-1.31	-2.47 – -0.14	**0.028**
Normal*windrow				4.64	1.78 – 12.08	**0.002**	9.30	-11.47 – 30.07	0.380	0.20	-1.62 – 2.01	0.832
Reduced*windrow				3.37	1.39 – 8.15	**0.007**	-11.00	-29.79 – 7.79	0.251	1.62	-0.03 – 3.26	0.054

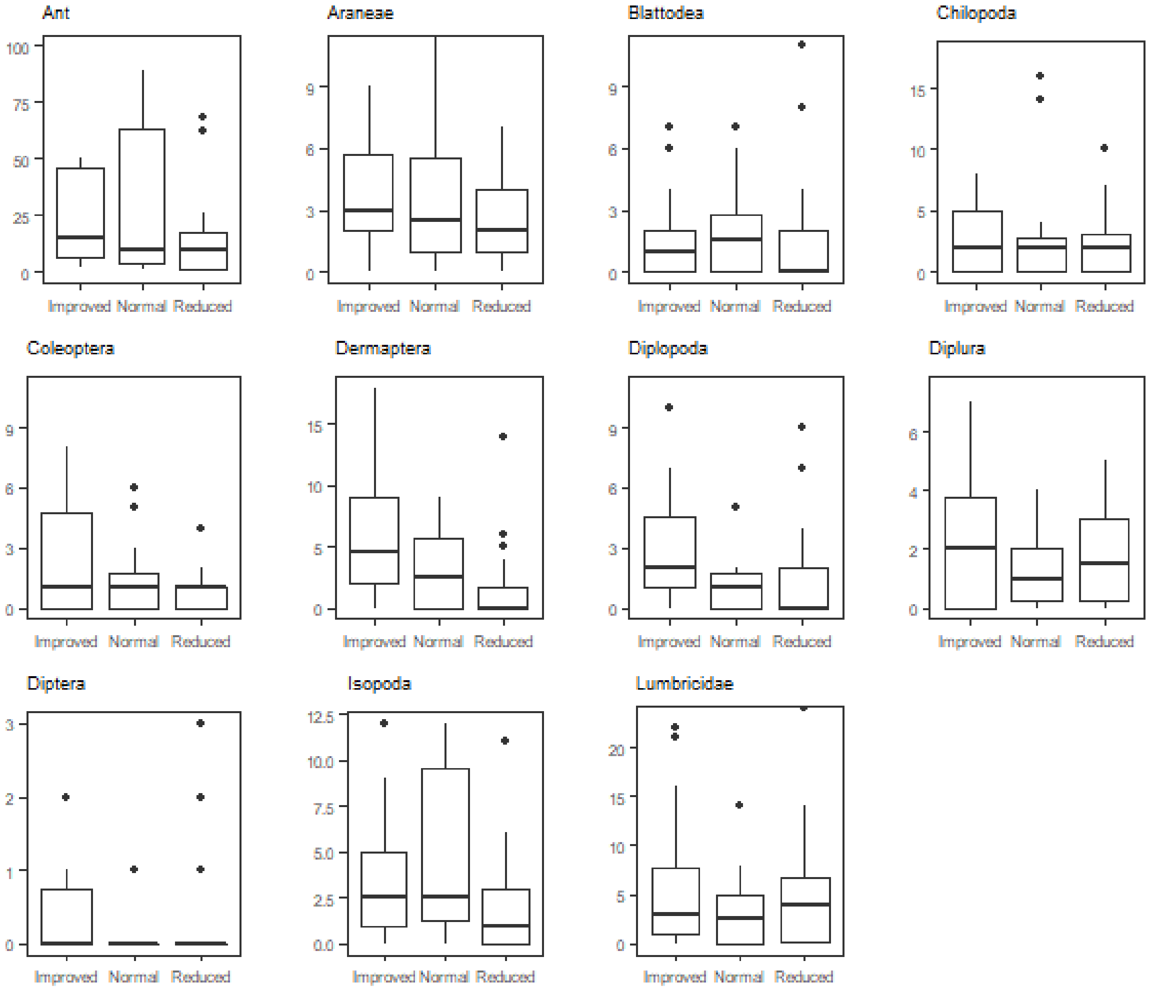
Table 2. *Model outputs of LMMs soil abiotic variables between Enhanced, Normal and Reduced treatment with the weeded circle as the model intercept.*

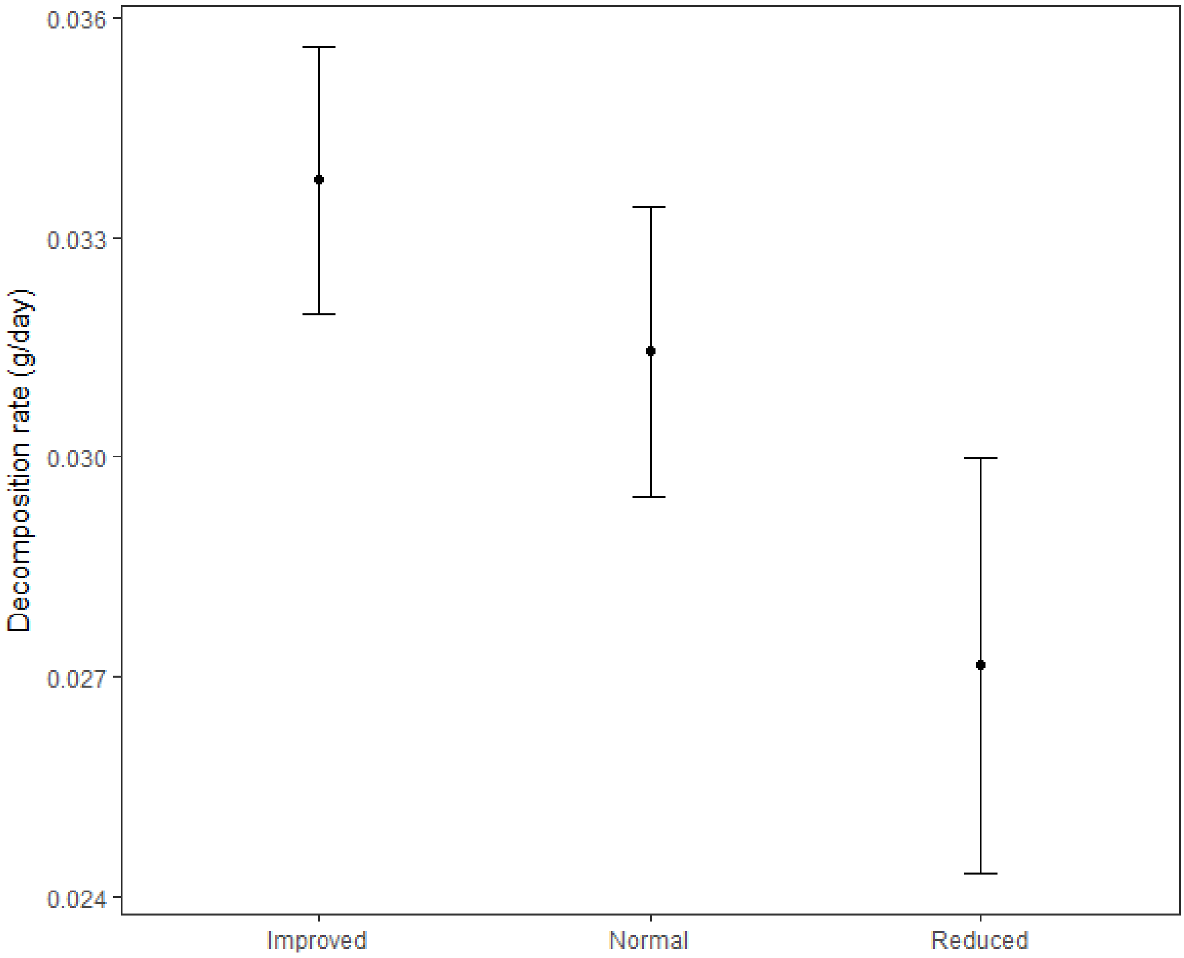
	water			**N**			**C**			**K**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Enhanced treatment	1.39	1.03 – 1.74	**<0.001**	-1.56	-1.82 – -1.29	**<0.001**	1.34	1.10 – 1.57	**<0.001**	3.96	3.69 – 4.22	**<0.001**
Normal treatment	0.47	-0.02 – 0.96	0.058	0.34	-0.02 – 0.70	0.066	0.27	-0.05 – 0.59	0.093	0.11	-0.22 – 0.45	0.502
Reduced treatment	0.16	-0.34 – 0.65	0.541	0.07	-0.30 – 0.44	0.699	0.17	-0.15 – 0.50	0.296	-0.01	-0.35 – 0.33	0.948
Windrow	-0.03	-0.27 – 0.21	0.791	-0.07	-0.26 – 0.13	0.485	0.08	-0.06 – 0.23	0.272	-0.07	-0.34 – 0.20	0.618

	P			**stability**			**C N**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Enhanced treatment	4.22	3.82 – 4.62	**<0.001**	76.11	71.45 – 80.77	**<0.001**	18.63	16.56 – 20.71	**<0.001**
Normal treatment	0.28	-0.23 – 0.79	0.280	-2.46	-8.60 – 3.68	0.432	-0.93	-3.56 – 1.69	0.485
Reduced treatment	0.09	-0.42 – 0.61	0.728	0.55	-5.69 – 6.79	0.863	2.09	-0.57 – 4.75	0.123
Windrow	-0.40	-0.79 – -0.01	**0.045**	-1.44	-5.46 – 2.58	0.483	2.65	0.58 – 4.73	**0.012**

Table 3. *Model outputs of LMM comparing litter decomposition rates between Enhanced, Normal and Reduced treatment with the weeded circle as the intercept.*

	Decomposition rate g/day		
Predictors	*Estimates*	*CI*	*p*
Enhanced treatment	0.0271	0.0234 – 0.0309	**<0.001**
Normal treatment	-0.0014	-0.0061 – 0.0033	0.548
Reduced treatment	-0.0068	-0.0113 – -0.0024	**0.003**
Windrow	0.0074	0.0042 – 0.0105	**<0.001**
Open to invertebrates	0.0031	0.0001 – 0.0061	**0.042**


Ant
100
75
50
25
0
Improved Normal Reduced
Araneae
9
6
3
0
Improved Normal Reduced
Blattodea
9
6
3
0
Improved Normal Reduced
Chilopoda
15
10
5
0
Improved Normal Reduced
Coleoptera
9
6
3
0
Improved Normal Reduced
Dermaptera
15
10
5
0
Improved Normal Reduced
Diplopoda
9
6
3
0
Improved Normal Reduced
Diplura
6
4
2
0
Improved Normal Reduced
Diptera
3
2
1
0
Improved Normal Reduced
Isopoda
12.5
10.0
7.5
5.0
2.5
0.0
Improved Normal Reduced
Lumbricidae
20
15
10
5
0
Improved Normal Reduced


Decomposition rate (g/day)
0.036
0.033
0.030
0.027
0.024
Improved
Normal
Reduced