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

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23

24 Abstract

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

41 Introduction

42 Oil palm is the most productive vegetable oil crop per unit area (Zimmer, 2010) and is a crucial part
43 of the economy in developing countries such as Indonesia and Malaysia (Koh & Wilcove, 2007).
44 However, with over 21 million ha of plantations covering the tropics (FAOSTAT, 2016) oil palm
45 cultivation is also one of the most controversial land uses. This is primarily due to the negative
46 impacts on biodiversity and climate change caused by forest conversion to plantations (Carlson et al.,
47 2013; Savilaakso et al., 2014). Therefore, improving the management of oil palm plantations to
48 protect existing biodiversity and ecosystem functions is vital for agricultural sustainability and
49 biodiversity conservation (Foster et al., 2011). Furthermore, it is in the interest of plantation managers

50 to develop and apply sustainable practices, as this can lead to economic gain (Woittiez et al., 2017)
51 and there is considerable market demand for palm oil to be certified as sustainable by the Round
52 Table on Sustainable Palm Oil (RSPO) (Tayleur et al., 2018). Oil palm has the potential to implement
53 relatively long-term sustainable management practices as it is a perennial crop with a ~25 year
54 commercial lifespan. One of the core management criteria for plantations to be certified as sustainable
55 by the RSPO is to improve soil sustainability (Roundtable on Sustainable Palm Oil, 2013).

56 Soil biodiversity plays a large part in the ecosystem functions that help maintain soil sustainability
57 (Bardgett & van der Putten, 2014). Soil biota are important for many vital ecosystem functions such
58 as: nutrient cycling; carbon sequestration; and nutrient uptake by plants. However, soil biodiversity is
59 threatened by land use change and agricultural intensification (Franco et al., 2016; Tsiafouli et al.,
60 2015) which can reduce ecosystem functioning (Bardgett & van der Putten, 2014; de Vries et al.,
61 2013). For example, reductions in decomposer functional diversity has been shown to reduce
62 decomposition rates and carbon and nutrient cycling (Handa et al., 2014), which are important
63 ecosystem functions for soil formation and fertility (Nielsen et al., 2011).

64 While there has been a recent upsurge in research investigating the effects of oil palm plantation
65 management on aboveground biodiversity and ecosystem function (Nurdiansyah et al., 2016; Syafiq
66 et al., 2016; Teuscher et al., 2016), belowground biodiversity and soil functioning has been severely
67 neglected (Bessou et al., 2017). Recent studies have found large declines in soil fertility and, in
68 particular, soil organic carbon (SOC) in oil palm plantations after forest conversion, with continued
69 declines as plantations age (Ashton-Butt et al., in review.; Guillaume et al., 2018; Matysek et al.,
70 2018). There are also changes to belowground biodiversity after forest conversion to oil palm; with
71 termites and litter feeding ants showing severe declines (Luke et al., 2014); and soil microbial
72 communities have been found to alter in community composition and functional gene diversity
73 (McGuire et al., 2015; Tripathi et al., 2016). However, the effect of these changes in biodiversity on
74 ecosystem functioning is little known (Dislich et al., 2016). Recent research has found that the
75 application of organic matter to the soil can improve soil quality and related biotic functions (Carron

76 et al., 2016; Tao et al., 2016, 2018) and different zones around the palm hold varying amounts of soil
77 fauna and nutrients as a result of standard management regimes (Carron *et al.*, 2015).

78 Soil communities and their functioning are largely impacted by the diversity and abundance of plant
79 communities (Eisenhauer et al., 2011; Thakur & Eisenhauer, 2015). Oil palm plantations can have a
80 reasonably diverse plant understory (Foster et al., 2011). However, these plants are often seen as
81 weeds thought to compete with oil palms for nutrients by some plantation managers and although
82 understory vegetation management varies widely between different plantations, complete removal by
83 herbicides and weeding is common (Tohiran et al., 2017). A typical plantation uses up to 90% of its
84 pesticide budget on herbicides such as paraquat, glufosinate ammonium and glyphosphate (Page &
85 Lord, 2006; Wibawa et al., 2010). This extensive use of herbicides can pollute water sources and pose
86 a threat to natural ecosystems and human health (Comte et al., 2012; Schiesari & Grillitsch, 2011).
87 Herbicides are also economically costly, especially to small-scale farmers (Lee et al., 2014).

88 Furthermore, the use of pesticides in agriculture has been linked with mass biodiversity declines
89 around the world (Beketov et al., 2013; Geiger et al., 2010) without consistent benefits to agricultural
90 yield (Lechenet et al., 2017). In oil palm plantations, reduction in herbicide use and a greater coverage
91 of understory vegetation has been shown to improve avian biodiversity (Nájera & Simonetti, 2010;
92 Tohiran et al., 2017). Furthermore, a greater developed understory benefits aboveground invertebrate
93 communities, by providing additional habitat and food resources (Ashraf et al., 2018; Chung et al.,
94 2000; Spear et al., 2018). However, it is not known how the understory vegetation in oil palm
95 plantations influences belowground invertebrate communities and related ecosystem functions.

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

102 Methods

103 *Study area*

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

118 Standard fertiliser treatment of oil palm in our study site includes: 1.75 kg tree⁻¹ yr⁻¹ urea (46% N);
119 0.5 kg tree⁻¹ yr⁻¹ triple super phosphate (45% P₂O₅, 15% Ca); 2.5 kg tree⁻¹ yr⁻¹ muriate of potash
120 (61% K₂O, 46% Cl); and 0.5 kg tree⁻¹ yr⁻¹ Kieserite (16% Mg, S: 22%).

121 *Understory treatments:*

122 Eighteen study plots were established in October 2012. Oil palms on all plots were planted between
123 1987 and 1993, and so were mature at the time of the study. Plots were 150 m x 150 m and are located
124 on flat ground between 10 and 30 m above sea level and without adjacent human habitation. The
125 plantations have a typical zonation of soil and vegetation management leading to 3 distinct zones,
126 weeded circle, harvesting path and windrow (Fig 1). The plots were arranged adjacently in triplets,
127 with one plot in each triplet randomly assigned one of three understory vegetation management

128 treatments (Fig. 2). Treatments were implemented in February 2014, and involved the following
129 management:

- 130 1) Normal understory complexity: standard company practice, consisting of intermediate
131 understory vegetation management using herbicides and some manual removal. The weeded
132 circle (a circular zone around the palm) and harvesting paths were sprayed, and woody
133 vegetation (shrubs and trees) was removed manually.
- 134 2) Reduced understory complexity: all understory vegetation was removed using herbicides.
- 135 3) Enhanced understory complexity: understory vegetation was allowed to grow with limited
136 interference except for minimal manual clearance in the weeded circle and harvesting paths.

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

140 ***Vegetation sampling***

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

147 ***Soil macrofauna sampling***

148 Soil macrofauna was sampled at the same points as the vegetation surveys, with samples being taken
149 from both the circle and the windrow, as these have been shown to hold different soil macrofauna
150 abundance and composition (Carron *et al.*, 2015). The harvesting path was not sampled, as this is
151 known to contain a very low abundance of soil macrofauna (Carron *et al.*, 2015). We used a standard
152 Tropical Biology and Fertility Institute soil monolith method to sample invertebrates (Bignell *et al.*,

153 2008), which involved excavating a 25 cm x 25 cm quadrat to a depth of 20 cm. All macrofauna,
154 characterised as fauna visible to the naked eye (Kevan, 1968), were removed from soil samples in the
155 field by hand-searching. Worms were placed immediately into formalin and all other arthropods were
156 stored in 70% ethanol for later identification. Invertebrates were sorted to order, with the exception of
157 termites and ants, which were separated from Blattodea and Hymenoptera, owing to their abundance
158 and distinct ecology, and Diplopoda and Chilopoda, which were identified to class.

159 *Soil abiotic sampling*

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

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

174 *Litter decomposition rates*

175 We used litter decomposition bags, made of fine mesh, to calculate litter mass loss over time. Bags
176 (10 cm x 10 cm) were filled with 4 g of freshly-cut oil palm fronds that had been dried to a constant
177 weight in the oven. Bags were subject to two treatments: closed bag with no holes, excluding
178 invertebrates, and open bags that had eight 1cm holes cut into them, allowing access to invertebrates.

179 Closed bags represent decomposition from microbes only and open bags decomposition from
180 microbes and invertebrates. Both closed and open bags were stapled together and placed in each
181 weeded circle and windrow at all sampling points (a total of 144 bags). Bags were left in the field for
182 30 days after which they were collected, dried at 70°C to a constant weight and weighed to measure
183 mass loss.

184 **Statistical analysis**

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

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

200 To determine whether understory treatment affected soil macrofauna community composition, we
201 fitted multivariate generalized linear models to the macrofauna abundance data using R package
202 ‘mvabund’ (functions ‘manyglm’ and ‘anova.manyglm’) (Wang et al., 2012). We used this model-
203 based method to analyse community composition because, unlike distance-based methods (e.g.
204 PRIMER), multivariate generalized linear models can account for the confounding mean–variance

205 relationships that often exist in ecological count data by modelling multivariate abundance data with a
206 negative binomial distribution (Warton et al., 2016). Model terms were tested for significance with a
207 likelihood ratio test and a Monte Carlo resampling scheme with 999 iterations. Tests were
208 simultaneously performed for univariate (single-order) responses to treatment, adjusting these
209 univariate p-values to correct for multiple testing (Wang *et al.*, 2012).

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

214 To determine the effect of understory treatment on decomposition rates we used a LMM. The model
215 included understory treatment, sampling zone (weeded circle or windrow) and decomposition bag
216 treatment as categorical fixed effects. Interaction effects were explored during model selection
217 between the fixed effects, but were not included based on AICc values (Brewer et al., 2016).

218 Sampling zone (windrow or weeded circle) was nested within the oil palm sampled and fitted as
219 random effects. The model was: *decomposition rate* ~ *understory treatment* + *sampling zone* + *bag*
220 *treatment* (1/ oil palm/sample number). Significance of all LMMs and GLMMs were explored via p-
221 values computed by Kenward-Rodger approximation (Luke 2017).

222 Results

223 *Vegetation*

224 Vegetation cover did not differ between normal and enhanced understory treatments (estimate = -9.23,
225 $P = 0.306$), but was higher than the reduced treatment for both weeded circle and windrow (Table 1
226 and Fig. 2). Forty-five plant species were identified in the plantations. *Asystasia micrantha* was the
227 most abundant species followed by *Nephrolepis biserrata*, *Peperomia pellucida* and *Asplenium*
228 *longissimum*. Plant species richness did not differ between normal and enhanced understory
229 treatments, but was higher than the reduced treatment for both weeded circle and windrow (estimate =
230 -2, $P = 0.003$) (Fig 3). Sampling zone had an interaction effect within treatment; the windrow of the

231 enhanced understory treatment had a lower species richness than the weeded circle (estimate = -1.31,
232 $P = 0.035$), whereas there was no difference between plant species richness of the weeded circle and
233 windrow in the normal and reduced treatment.

234 ***Macrofauna richness and abundance***

235 For the macrofauna survey, we sampled 6417 individuals from 34 orders and taxonomic groups. Ants
236 were the most abundant group found followed by: Dermaptera, Lumbricidae, Aranae, Isopoda,
237 Diplopoda, Chilopoda, Blattodea, Diplura, Coleoptera and Diptera. Order richness was higher in the
238 enhanced understory treatment compared to the normal (estimate = -1.51, $P < 0.05$) and reduced
239 understory treatments (estimate = -2.46, $P < 0.001$) (Table 1 and Fig. 3). Order richness was also
240 higher in the windrow (estimate = +3.11, $P < 0.001$) than the weeded circle in all treatments (Fig. 4).
241 Macrofauna abundance was higher in the weeded circle (but not the windrow) in areas with an
242 enhanced understory than both areas with normal (IRR = 0.22, $P < 0.005$) and reduced understory
243 (IRR = 0.3, $P < 0.01$) (Fig. 4). In addition, abundance was higher in the windrow than the weeded
244 circle of the normal (IRR = 4.64, $P < 0.005$); and reduced understory treatments (IRR = 3.37, $P <$
245 0.01). However, in the enhanced understory treatment, the windrow had a lower macrofauna
246 abundance than the weeded circle, although, this was marginally non-significant (IRR = 0.53, $P =$
247 0.053).

248 ***Macrofauna Composition***

249 Understory treatment had an effect on macrofauna composition (LR = 144.4, $P < 0.001$). The normal
250 (LR = 52.69, $P < 0.001$) and reduced understory treatment (LR = 115.49, $P < 0.001$) differed in soil
251 macrofauna composition from the enhanced treatment. The reduced understory treatment exhibited a
252 larger difference in macrofauna composition from the enhanced treatment than the normal understory
253 treatment. Zone of oil palm sampled (weeded circle or windrow) also had an interaction effect with
254 treatment on macrofauna composition in the enhanced (LR = 69, $P < 0.001$), normal (LR = 38.93, $P <$
255 0.01), and reduced (LR = 115.49, $P < 0.001$) understory treatments. Ant (LR = 13.32, $P = 0.02$)
256 Coleoptera (LR = 12.55, $P = 0.038$), Dermaptera (LR = 13.93, $P = 0.012$), Diplopoda (LR = 11.93, P
257 = 0.048), Isopoda (LR = 13.8, $P = 0.013$) abundances were all affected by treatment, with lower

258 abundances present in the reduced understory treatment than the enhanced or normal treatments (Fig.
259 5).

260 *Abiotic variables*

261 Understory treatment had no effect on SOC, N, P, K, SWC, C/N ratio, aggregate stability or pH (Fig.
262 6 and Table 2). The zone of the oil palm sampled also had no effect on these variables apart from C/N
263 ratio, where the windrow had a slightly higher C/N ratio than the weeded circle (model estimate =
264 +2.65, $P = 0.018$) and total phosphorous where the windrow had a slightly lower total phosphorous
265 level in the soil than the weeded circle (model estimate = -0.40, $P = 0.045$)

266 *Decomposition*

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

276 **Discussion**

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

282 ***Soil macrofauna***

283 Soil macrofauna order richness and abundance were higher in enhanced understory plots than the
284 reduced plots and order richness (but not abundance) was higher in plots with an enhanced understory
285 compared to normal understory plots. Increased plant diversity (characteristic of the enhanced
286 understory plots) has been found to benefit soil biota in other systems (Scherber *et al.*, 2010;
287 Eisenhauer *et al.*, 2011, 2012) and increased understory complexity can increase aboveground
288 invertebrate abundance and food web complexity in oil palm plantations by providing greater
289 resources (Spear *et al.*, 2018). Furthermore, oil palm plantations suffer from hotter and drier
290 microclimates than the natural habitat in the region (Luskin & Potts, 2011), which native soil
291 invertebrates can be sensitive to (Fayle *et al.*, 2010). An increased understory is likely to ameliorate
292 this microclimate by preventing exposure of the soil to direct sunlight and by increasing water
293 infiltration, thus benefitting soil invertebrates (Ashraf *et al.*, 2018; Belsky *et al.*, 1993). Soil
294 macrofauna composition was different in the three understory treatments; taxa that include litter
295 feeding organisms: Dermaptera; Diplopoda; Coleoptera; and Isopoda, all increased in abundance in
296 the enhanced compared to the reduced understory treatment. This is likely due to the greater biomass
297 and diversity of decaying vegetation and root matter provided by the understory plants (Wardle *et al.*,
298 2004). These fauna are considered ecosystem engineers and are key in breaking down leaf litter and
299 creating a wider availability of resources for microbial decomposers (Brussaard, 2012). Furthermore,
300 the reported positive effects of the understory on soil biodiversity may be conservative in our study;
301 benefits of plant diversity on soil biota can have a significant time delay (Eisenhauer *et al.*, 2012). The
302 enhanced understory treatment had only been installed for two years at the time of sampling,
303 therefore, increased positive effects on the soil macrofauna community and associated ecosystem
304 functions can be expected over time. This is extremely pertinent in oil palm plantations, as they have a
305 long commercial lifespan of more than 25 years. This study was conducted in mature plantations;
306 enhanced understory vegetation could be even more important in young plantations where soil erosion
307 and microclimate is more severe, as there is a reduced canopy cover and less organic matter available
308 from decaying fronds (Guillaume *et al.*, 2015; Luskin & Potts, 2011).

309 ***Soil abiotic properties***

310 Our results show there was no impact of either treatment on soil fertility. This indicates that the
311 changes in soil macrofauna community were caused by the direct impacts of vegetation. Furthermore,
312 it suggests that the understory vegetation has little impact on nutrient availability for the oil palm, as
313 there was no difference in nutrient levels between the treatments. If enhanced understory vegetation is
314 maintained for an extended period of time, positive effects on soil fertility could be seen as
315 undergrowth is likely to prevent soil erosion, loss of SOM and leaching of other nutrients (Li et al.,
316 2007; Lieskovský & Kenderessy, 2014).

317 ***Decomposition***

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

334 **Conclusions**

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

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

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590 Figure Legends

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

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

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

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

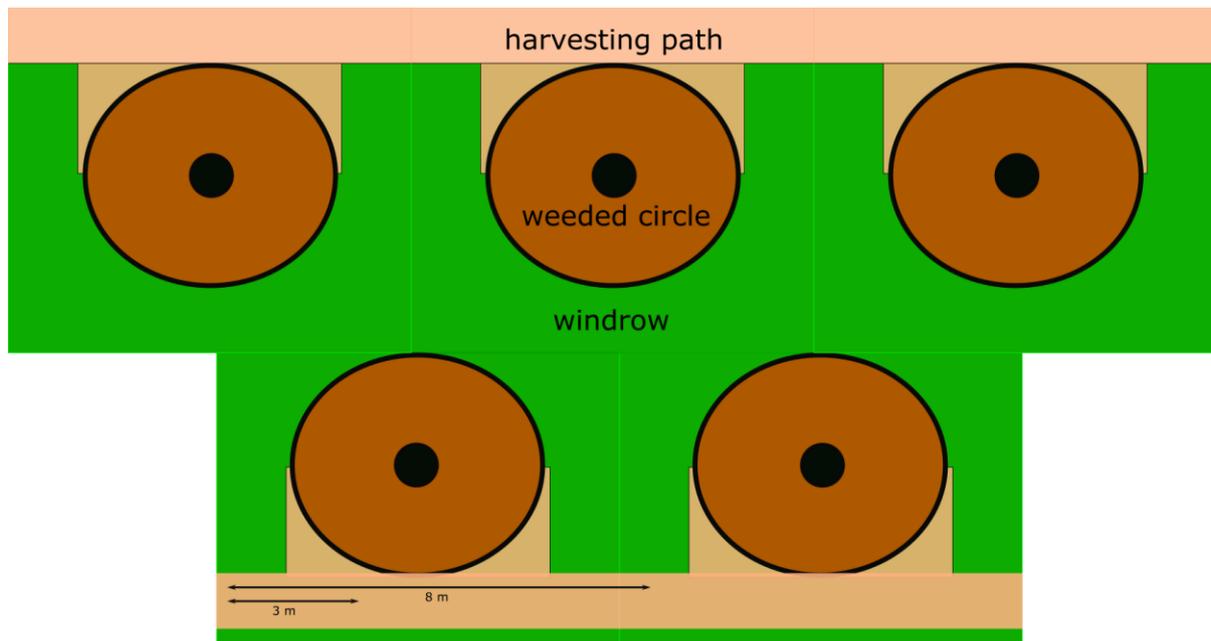
605 Figure 5. Abundance of the 11 most abundant orders found in the Enhanced, Normal and Reduced
606 understory treatment.

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

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

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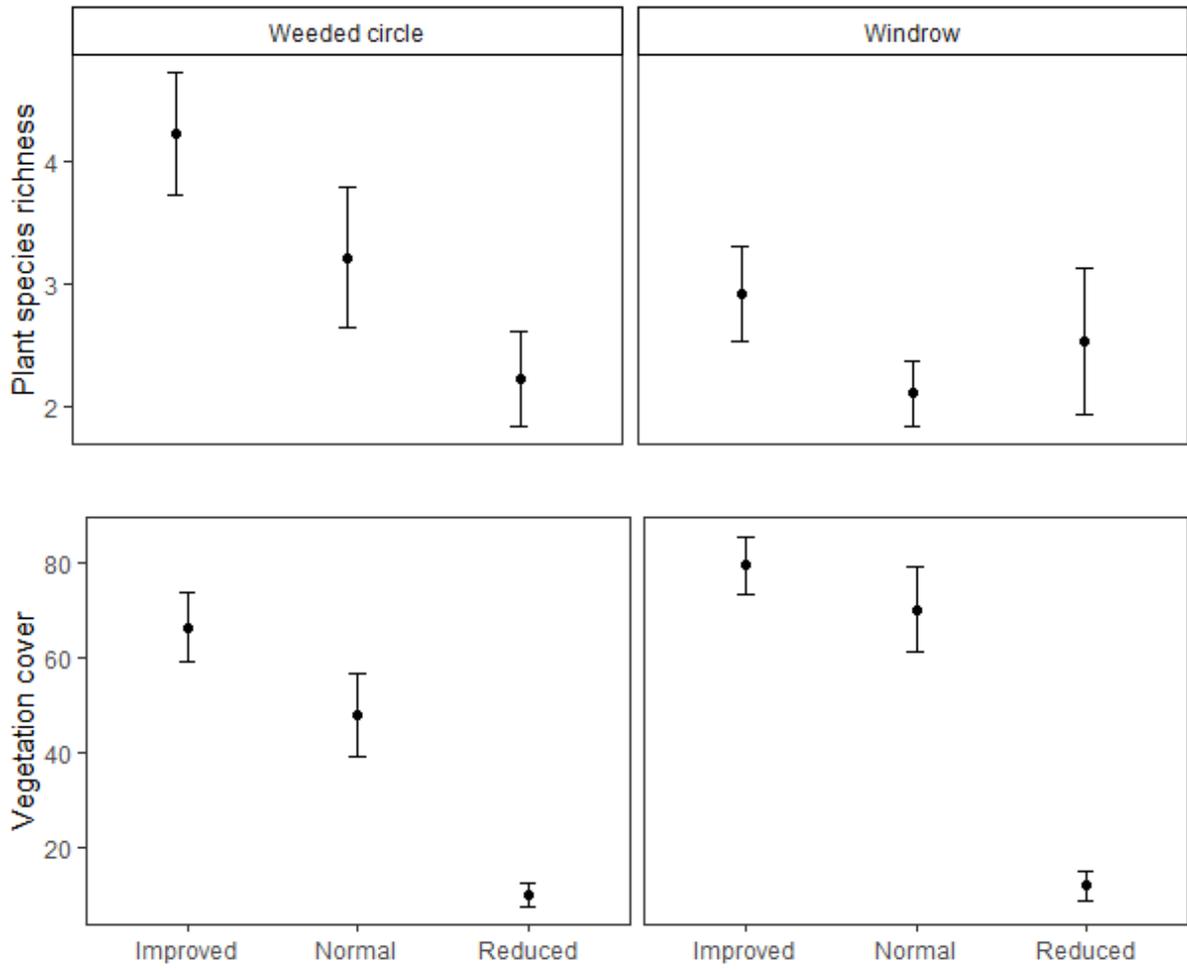
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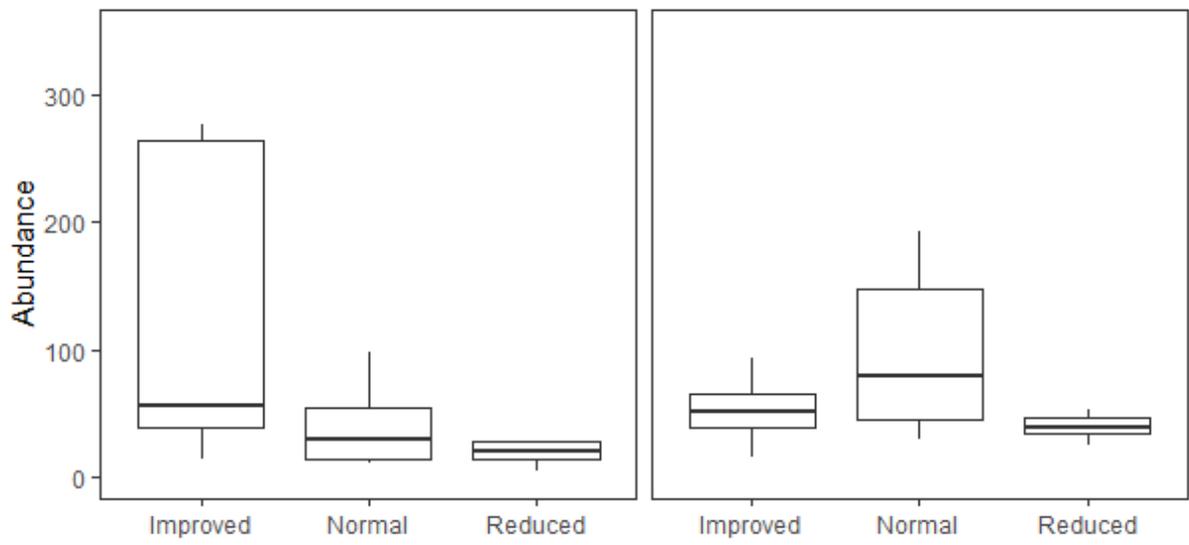
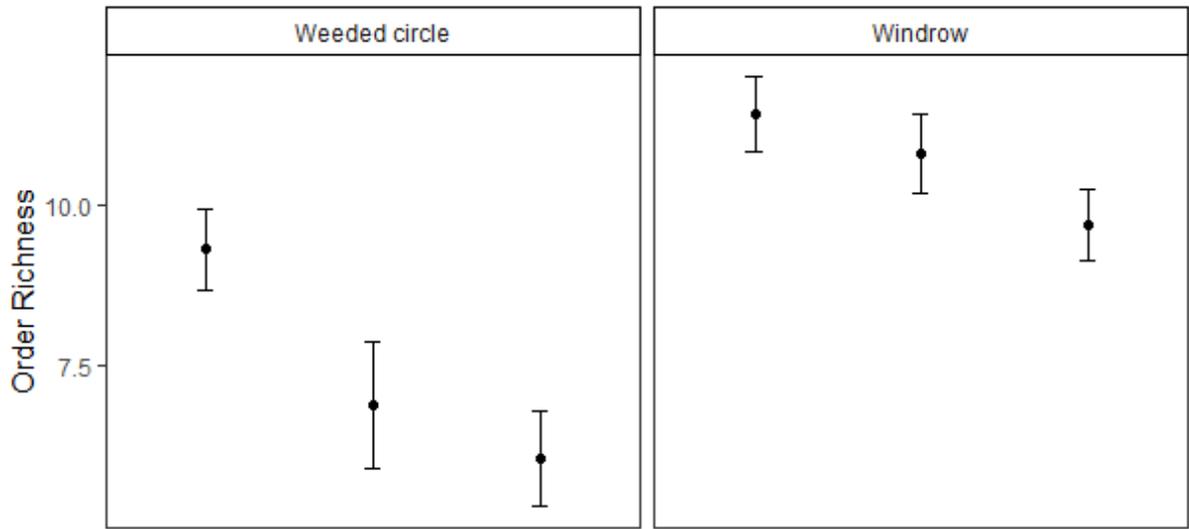


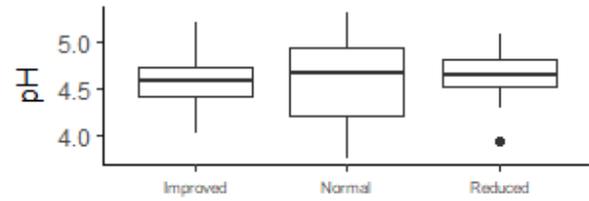
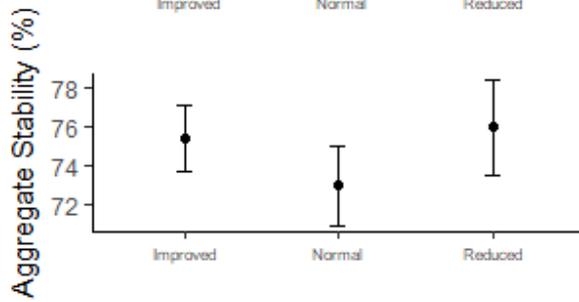
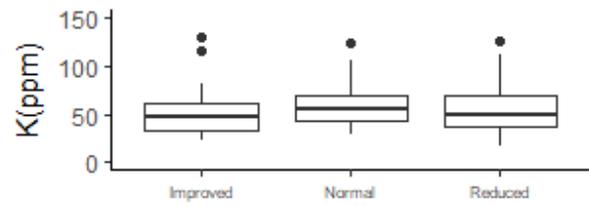
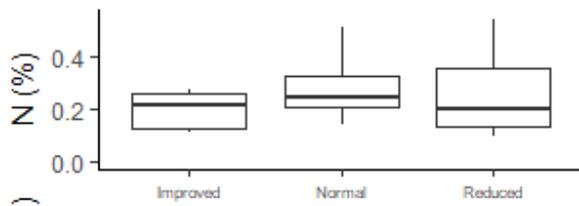
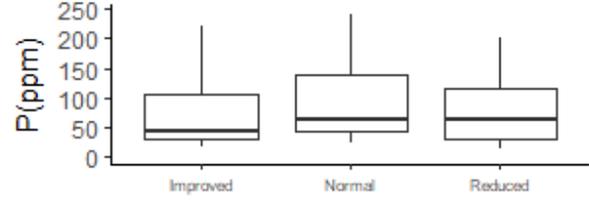
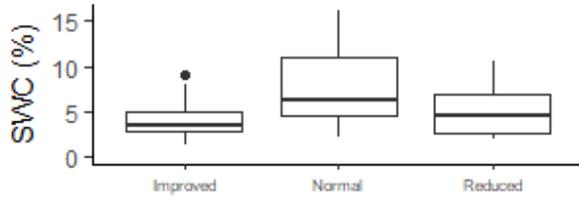
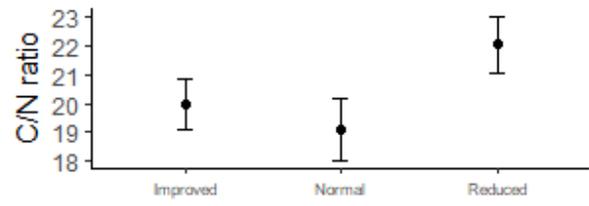
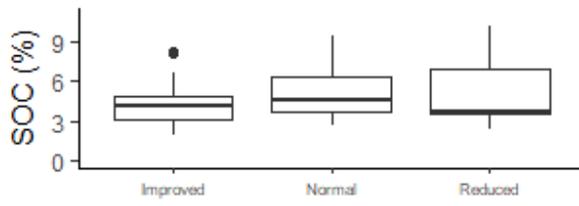
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Table 1. Model outputs of LMMs and GLMM comparing macrofauna order richness, abundance, vegetation cover and vegetation richness between Enhanced, Normal and Reduced treatment.

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
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
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.

<i>Predictors</i>	water			N			C			K		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
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

<i>Predictors</i>	P			stability			C N		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
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			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
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

