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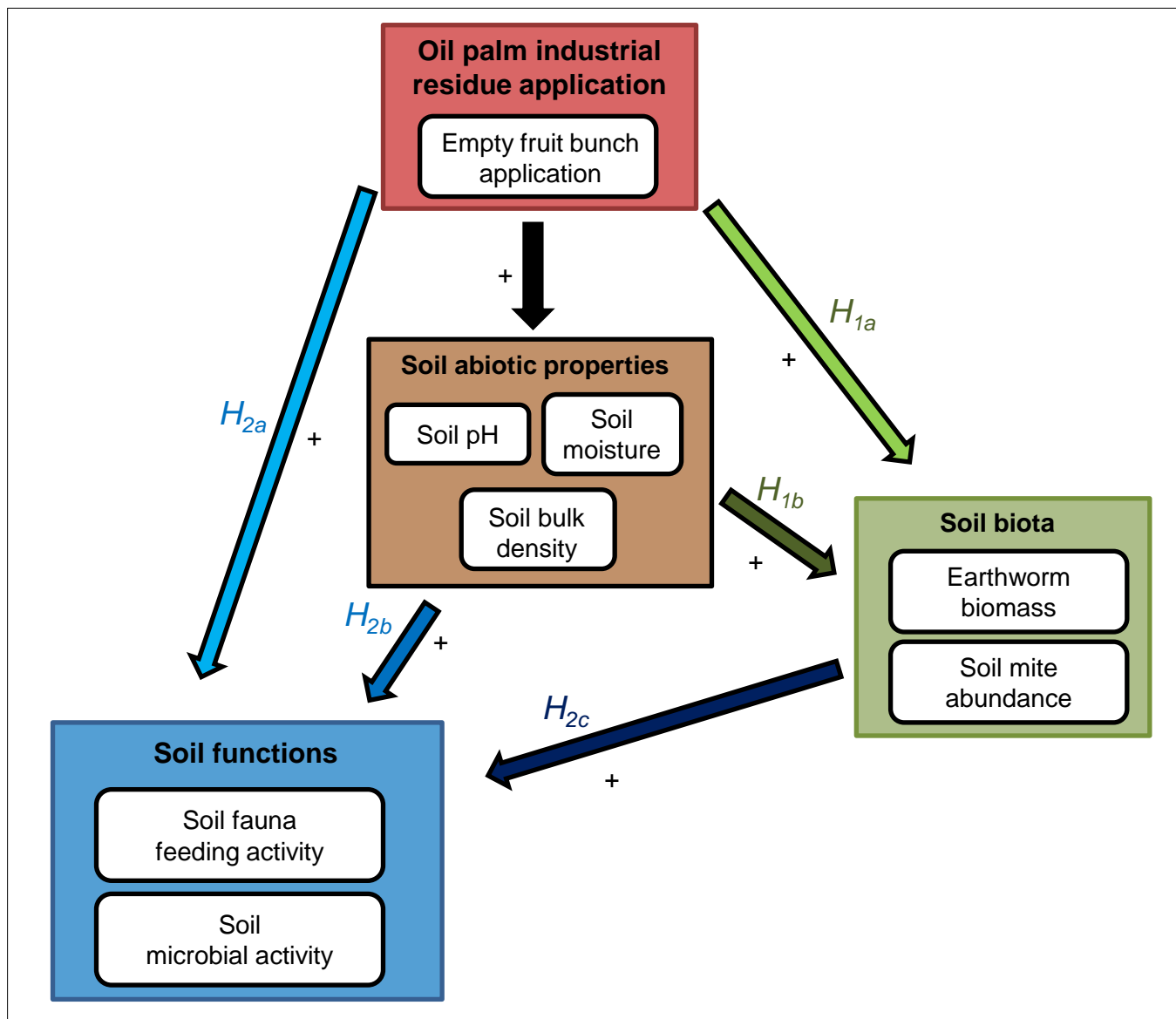
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Abstract: Oil palm (*Elaeis guineensis*) is an important tropical crop which provides one-fifth of the world's vegetable oil, yet its rapid expansion can negatively influence the soil ecosystem. Identifying suitable agronomic management such as crop residue application is important for the sustainable development of oil palm. We examined the effects of adding empty fruit bunches (EFB), a major oil palm residue, on multiple soil abiotic properties, soil biota, and indicators of soil functions. We compared treatments of EFB applications with three application rates, and a chemical fertilizer treatment in a 15-year trial in Central Sumatra, Indonesia. EFB application increased pH and aggregate stability in 0-10 cm soils and decreased the soil bulk density. EFB application increased the abundance of soil detritivore mites, soil fauna feeding activity, and soil microbial activity. EFB application decreased the biomass of a dominant invasive earthworm species, *Pontoscolex corethrurus* (Müller, 1857). Results from structural equation modelling suggested that EFB directly affected soil biota and functions, rather than through altering soil abiotic properties. The effects of EFB application on most soil abiotic properties, soil biota and function indicators were independent of the application rate. Our results revealed that EFB application has a high potential to enhance soil biota and functions in oil palm plantations.



Conceptual model indicating hypothesized effects of empty fruit bunch application on soil abiotic properties, soil biota and functions. Applying empty fruit bunch may influence soil biota through direct provision of resources (H_{1a}), or by altering soil abiotic properties (H_{1b}). Applying empty fruit bunch may influence soil function indicators through direct provision of energy resource (H_{2a}), or by altering soil abiotic properties (H_{2b}) and soil biota (H_{1c}).

1 Application of oil palm empty fruit bunch effects on soil biota and functions: a
2 case study in Sumatra, Indonesia

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19 ABSTRACT

20 Oil palm (*Elaeis guineensis*) is an important tropical crop which provides one-fifth of the
21 world's vegetable oil, yet its rapid expansion can negatively influence the soil ecosystem.
22 Identifying suitable agronomic management such as crop residue application is important
23 for the sustainable development of oil palm. We examined the effects of adding empty
24 fruit bunches (EFB), a major oil palm residue, on multiple soil abiotic properties, soil
25 biota, and indicators of soil functions. We compared treatments of EFB applications with
26 three application rates, and a chemical fertilizer treatment in a 15-year trial in Central
27 Sumatra, Indonesia. EFB application increased pH and aggregate stability in 0–10 cm soils
28 and decreased the soil bulk density. EFB application increased the abundance of soil
29 detritivore mites, soil fauna feeding activity, and soil microbial activity. EFB application
30 decreased the biomass of a dominant invasive earthworm species, *Pontoscolex corethrurus*
31 (Müller, 1857). Results from structural equation modelling suggested that EFB directly
32 affected soil biota and functions, rather than through altering soil abiotic properties. The
33 effects of EFB application on most soil abiotic properties, soil biota and function
34 indicators were independent of the application rate. Our results revealed that EFB
35 application has a high potential to enhance soil biota and functions in oil palm plantations.

36 1. INTRODUCTION

37 Soil provides crucial functions and ecosystem services to enhance food security, land
38 restoration, and climate change mitigation, which are key Sustainable Development Goals
39 of United Nations (S. D. Keesstra et al., 2016). Various interacting soil organisms and their
40 processes contribute to key soil ecosystem functions, such as nutrient cycling, carbon
41 sequestration, and soil structure maintenance (Bardgett and van der Putten, 2014). In
42 agricultural ecosystems, management practices may influence abiotic soil environment and
43 soil biota, which then alter key soil ecosystem functions and crop production (Birkhofer et
44 al., 2008).

45 Identifying sustainable management is especially important for tropical production systems
46 which produce 1.7 tons of dry crop yield annually (West et al., 2010). Oil palm (*Elaeis*
47 *guineensis*) is a wide spread economic crop in Southeast Asia which produces one-fifth of
48 vegetable oil globally (Kurnia et al., 2016; Sayer et al., 2012). The global oil palm land
49 area covers 16.4 million ha, equivalent to ten percent of the world's permanent croplands
50 (FAO, 2015). Land conversion from forest to oil palm can reduce soil biodiversity,
51 increase nutrient leaching, and negatively influence soil carbon storage and fertility
52 (Dislich et al., 2017). To identify and implement suitable soil management for mitigating
53 these negative environmental impacts is important; however, few studies have examined
54 these management practices and their effects on soil biodiversity and ecosystem functions
55 in oil palm plantations (Bessou et al., 2017; Carron et al., 2015; Tao et al., 2016).

56 In most oil palm plantations in Southeast Asia, chemical fertilizer is used as a major source
57 of nutrients. More recently, crop residues from oil palm have been used as organic
58 fertilizers and mulch substrates to reduce the quantity of mineral fertilizers needed. One of
59 the main oil palm residues from the palm oil extraction process are the empty fruit bunches

60 (EFB), which are the structural part of the fruit bunches (Chang, 2014). Several studies
61 have reported the effects of EFB application on soil fertility and yield in Indonesian and
62 Malaysian oil palm (Comte et al., 2013; Abolfath Moradi et al., 2014; Tao et al., 2017).
63 However, there is little information on the effects of EFB application on soil biota and
64 ecosystem functions (Carron et al., 2015; Tao et al., 2016), and whether the effects are
65 direct or through altering soil abiotic properties. It is also unknown whether the effects are
66 quantity-dependent, i.e., whether the magnitude of the effects depends on the application
67 rate of EFB. For other crops such as apricot, olive, and persimmon, applying crop residue
68 mulch has shown to reduce soil degradation (S. Keesstra et al., 2016; Parras-Alcántara et
69 al., 2016; Ritsema, 2016). Relevant information for oil palm is crucial for plantation
70 managers and policymakers to promote and implement suitable soil management practices
71 to achieve sustainable intensification of oil palm.

72 Among soil organisms, earthworms can be litter transformers and soil engineers which
73 structure the environment of other soil organisms, whereas soil mites directly feed on crop
74 residues and microorganisms (Coleman et al., 2004). Crop residue application may
75 influence soil microbial respiration and soil faunal feeding activities either by providing
76 food resources, or by altering soil abiotic properties and microhabitats for soil biota; yet
77 such mechanisms have rarely been explored in tropical agroecosystems especially for
78 perennial crops (Kurzatkowski et al., 2004; Römbke et al., 2006). Moreover, the majority
79 of research has focused on the effects of crop residue application on the litter layer rather
80 than the soil mineral layer, despite the fact that carbon sequestration and nutrient cycling
81 also happen in the soil layer (Ashford et al., 2013).

82 This study aimed to examine the long-term effects of oil palm residue addition on soil
83 biota and functions in the top soil layer. Specifically, we asked: 1) does EFB application

84 influence key soil biota and function indicators? 2) does EFB application directly influence
85 soil biota and functions, or indirectly through altering soil abiotic properties? and 3) do the
86 effects of EFB application on soil biota and functions depend on the application rate? We
87 examined six soil abiotic properties, two soil biota groups, and two indicators of soil
88 functions in a 15-year field trial in an oil palm plantation in Sumatra, Indonesia. We used a
89 structural equation modelling approach (Grace et al., 2012; Shipley, 2013) to examine the
90 potential causal relationships between soil abiotic properties, soil biota and functions. We
91 hypothesized that EFB application may influence soil biota and functions both by directly
92 providing resources, and by modifying soil abiotic properties. The soil biota could also
93 have cascading effects on other soil fauna groups and functions. In addition, we expected
94 that the responses of soil biota and functions to EFB application would be stronger at
95 higher application rates.

96 2. MATERIALS AND METHODS

97 2.1 Site description and experimental design

98 The study was carried out in an oil palm plantation in Sumatra, Indonesia (0° 56'0" N
99 101°18'0"E). The oil palm plantation was established in 1987 and has been certified by the
100 Roundtable on Sustainable Palm Oil (RSPO). The previous land use of this area was
101 secondary tropical forest dominated by *Dipterocarp* species. The climate of this region is
102 described as tropical humid, with a mean temperature of 26.8 °C and average rainfall of
103 2400 mm year⁻¹. The soils are Inceptisols (Typic Dystrudepts), within the loamy lowland
104 soil class (USDA soil classification system).

105 The 15-year trial began in 1998, when the age of oil palms was 11 years. Field sampling
106 and measurements were conducted at the end of the trial during September-October 2014.
107 The field trial was established at two adjacent oil palm commercial plots. The field trial

108 covered a total area of 36 hectares (1200 m length \times 300 m wide) and was composed of
109 five replicate blocks. Each replicate block was composed of four treatment plots, resulting
110 in a total of 20 treatment plots (5 replicate blocks \times 4 treatment plots). The replication
111 number was five in a nested design (See **Supplementary S1**).

112 Each treatment plot (80 m \times 40 m) was composed of 36 palm trees, arranged as eight palm
113 trees in four rows. The applications were applied throughout the treatment plot
114 continuously for 15 years. Soil sampling was undertaken at the end of 15 years at five oil
115 palms in the central two rows. There was at least one palm between two focal palms to
116 avoid spill over effects (**Supplementary S1**). Each treatment plot was surrounded by 1.5
117 m depth ditches to prevent interference by adjacent treatment plots.

118 The four treatment plots in each replicate block were: Low-EFB treatment applied with
119 EFB (210 kg tree⁻¹ yr⁻¹, equivalent to 30 t ha⁻¹ yr⁻¹) and urea (0.02 kg tree⁻¹ yr⁻¹);
120 Medium-EFB treatment applied with EFB (420 kg tree⁻¹ yr⁻¹, equivalent to 60 t ha⁻¹ yr⁻¹)
121 and urea (0.04 kg tree⁻¹ yr⁻¹); High-EFB treatment applied with EFB (630 kg tree⁻¹ yr⁻¹,
122 equivalent to 90 t ha⁻¹ yr⁻¹) and urea (0.06 kg tree⁻¹ yr⁻¹), and chemical fertilizer treatment
123 applied with a full quantity of chemical fertilizers without adding EFB. EFB as the
124 structural part of fruit bunches after fruit removal contains dry weight of 45-49 % C,
125 0.5-1.0 % N, 0.02-0.05 % P, 1.3-2.2 % K, and 0.2-0.4 % Mg (Budianta et al., 2010;
126 Chang, 2014; Kavitha et al., 2013; A. Moradi et al., 2014; Pardon et al., 2016). Chemical
127 fertilizer treatment included the application of 1.75 kg tree⁻¹ yr⁻¹ urea (46 % N), 0.5 kg
128 tree⁻¹ yr⁻¹ triple super phosphate (45 % P₂O₅, 15% Ca), 2.5 kg tree⁻¹ yr⁻¹ muriate of potash
129 (61% K₂O, 46% Cl), and 0.05 kg tree⁻¹ yr⁻¹ Kieserite (16% Mg, S:22%). For detailed
130 description of each treatment see **Supplementary S2**.

131 In EFB treatment plots, EFB was applied once a year for 15 years at one side of the
132 harvesting paths, followed by urea application on the top of EFB to regulate the EFB
133 decomposition rate. The application rate of the Low-EBF treatment was similar to standard
134 operations in the oil palm industry, whereas Medium-EBF and High-EBF treatments
135 represented alternative application rates of EFB. In the chemical fertilizer treatment, the
136 type and quantity of chemical fertilizers were similar to conventional standard estate
137 practices, and the fertilizers were applied within palm circles (1-2 m radius) twice a year
138 (i.e. during the February-March and September-October periods) throughout the trial
139 period. Harvesting path and palm circle account for approximately 5-15 % and 10-15% of
140 the total plantation area, respectively, as the majority of oil palm plantations in Southeast
141 Asia (Nelson et al., 2013).

142 2.2 Field measurements

143 We measured ten indicators for soil abiotic properties (soil pH, soil moisture, aggregate
144 stability, bulk density, soil organic carbon and total nitrogen), soil biota (earthworm
145 biomass and soil mite density), and soil ecosystem functions (soil fauna feeding activity
146 and soil microbial activity). We examined these soil properties at the soil mineral layer
147 rather than litter layer, since the response of soil-dwelling fauna communities and their
148 processes under soil management practices are relatively unknown in the oil palm
149 ecosystem (Tao et al., 2016). We examined these soil properties beneath EFB at one side
150 of harvesting paths of EFB treatment plots, and at the equivalent positions in chemical
151 fertilizer plots.

152 2.2.1 Measuring soil abiotic properties

153 We measured soil moisture using the WET sensor (Delta-T Device, UK). For soil pH, soil
154 organic carbon, soil total nitrogen, and soil aggregate stability, one soil sample was

155 collected at the depth of 0-15 cm under each focal palm. The resulting five soil samples for
156 each treatment plot were bulked to form a composite sample. Samples were air-dried for
157 4-7 days and sieved through 2 mm and 0.5 mm for soil chemical analysis. Soil organic
158 carbon concentration was measured using the Walkley-Black method (Nelson and
159 Sommers, 1982). Total nitrogen was determined by the Kjeldahl method (Bremmer and
160 Mulvaney, 1982). Soil pH was determined using a pH meter with a soil to water ratio of
161 1:1.

162 We analysed soil aggregate stability using the wet sieving method (Eijkelkamp, the
163 Netherlands). Soils particles under 0.25 mm were used for the measurement. Unstable
164 aggregates were extracted by physical shaking for fixed amounts of time, while stable
165 aggregate was extracted by sodium hydroxide. The aggregate stability was calculated as
166 the percentage of stable aggregates weight over total aggregate weight. For bulk density
167 measurement, three soil samples of fixed volume were collected using metal rings (5 cm
168 diameter and 5.1 cm depth) under each focal palm. The dry weight of the samples was
169 measured after over-dry for 105 degrees for 24 hr. The bulk density was calculated as the
170 weight per unit volume of a soil sample.

171

172 2.2.2 Measuring soil biota

173 Earthworms and soil mites were chosen as the focal soil biota groups in our study as they
174 contribute to key functions in nutrient cycling (Coleman et al., 2004), and their abundance
175 in the mineral layer of the soil. We used a modified Tropical Soil Biology and Fertility
176 (TSBF) approach to extract earthworms (Moreira et al., 2008). Under each focal palm, the
177 organic layer on the top-soil was removed by a shovel, and a soil monolith of 50 cm length
178 × 20 cm width × 10 cm depth was excavated. Earthworms were hand-sorted by a team of
179 five people in the field. The fresh weight of each earthworm was measured, stored in a

180 90% ethanol solution, and the taxonomy was identified by an expert (Dr Samuel Wooster
181 James, Maharishi University of Management, United States). The biomass of earthworms
182 (g m^{-2}) was obtained by dividing the fresh weights of earthworms by the surface area of
183 the soil monolith.

184 We sampled soil mite using a modified Berlese-Tullgren funnel approach (Moreira et al.,
185 2008). Three soil samples were collected using soil cores (7.5 cm diameter and 4.2 cm
186 length) at each focal tree and pooled for the extraction over a 48-hour period. We
187 identified soil mites into taxonomic groups at the suborder level (Krantz and Walter,
188 2009). We also collected other microarthropod groups i.e. Collembola and Formicidae
189 from the extraction, yet the number was low and was not used for further analysis. The
190 density of each Suborder (individuals/m^2) of each treatment plot was obtained by dividing
191 the number of mites of each Suborder by the surface area of three soil cores.

192 2.2.3 Measuring indicators of soil functions

193 Soil fauna feeding activity represents direct litter feeding rates of soil mesofauna and
194 macrofauna, therefore is an indicator for nutrient turnover in the soil. We measured soil
195 fauna feeding activity by the bait lamina method (Terra Protecta GmbH, Berlin, Germany)
196 (Von Torne 1990). The method uses thin PVC sticks (1 x 6 x 120 mm) with 16 apertures
197 of 1.5 mm diameter and 5 mm apart, filled with standardized bait made of cellulose
198 powder, bran flakes and active carbon in a ratio of 70:27:3. Under each of the focal palm,
199 we placed six bait lamina sticks 40 cm apart in a row. The sticks were inserted vertically
200 until the top aperture was just below the soil surface, and the bottom aperture was at a
201 depth of 8 cm below the soil surface. The sticks were left for 3 days and bait consumption
202 was recorded by assessing each aperture, i.e. feeding activity was recorded as 0 (without

203 perforation = no evidence of feeding) or 1 (partial or complete perforation = evidence of
204 feeding).

205 Soil microbial activity is the metabolic process of micro-organisms which associated with
206 oxidizing soil organic carbon and nitrogen-containing compounds. In this study, we
207 examined the potential of heterotrophic respiration under *ex-situ* conditions, by measuring
208 CO₂ burst after moistening dry soil for 24hr (Solvita CO₂-Burst Test, USA,
209 <https://solvita.com/co2-burst/>). This method is different from usual measurements of
210 *in-situ* basal soil respiration in field conditions which examine real-time soil respiration..
211 Rather, it measures potential of microbial respiration by water induction as used in various
212 ecological studies (Muñoz-Rojas et al., 2016a, 2016b; Ward et al., 2017). To perform the
213 test, each composite soil sample used for chemical property analysis was air-dried and
214 sieved through a 2mm mesh sieve. Subsequently, 40g of each sample was placed in a 50ml
215 plastic beaker and then inside a 240ml incubation jar. The soils were moistened by adding
216 20ml of water into the jar. A CO₂ probe was placed inside the jar before incubation at
217 room temperature for 24hr. After incubation, the CO₂ probe was taken out from the jar and
218 measured using a spectrometer (digital color reader). The background of atmospheric CO₂
219 was taken into account for the reading..

220 2.3 STATISTICAL ANALYSIS

221 All statistical analyses were performed in R.3.3.1 (R Core Team, 2016). We used linear
222 mixed effects models to examine the effects of EFB application on soil abiotic properties,
223 soil biota, and soil ecosystem functions. The treatment type (Low-EFB, Medium-EFB,
224 High-EFB, and chemical fertilizer treatment) was fitted as a fixed effect (categorical
225 variable). Treatment plots nested within replicate blocks were fitted as random effects. To
226 correct for heterogeneity in the residuals, earthworm biomass and soil mite density were

227 log (x+1)-transformed, bulk density and soil fauna feeding activity were square- root
228 transformed, and the rest of the variables were log-transformed. For soil mite, both the
229 total soil mite density and the Suborder of Oribatida were tested against the treatment type.
230 Significant overall effects of treatment type were further explored using a post-hoc Tukey
231 test. All the statistical tests were evaluated using $\alpha = 5\%$. Mixed effects modelling was
232 performed using the *lme* function of the *nlme* package (Bates et al., 2015), and the Tukey
233 test using the *multcomp* package (Hothorn et al., 2008).

234 Structural equation modelling was performed to test whether the EFB application
235 influenced soil biota and the soil ecosystem functions by direct provision of food
236 resources, or via modifying soil abiotic properties. This approach allows for evaluating
237 pre-existing theories using observational data, with a focus on exploring possible
238 mediation pathways (Eisenhauer et al., 2015; Grace et al., 2012). Among the ten
239 indicators, soil aggregate stability was not included in the structural equation modelling as
240 it positively correlated with soil bulk density. We thus used only soil bulk density to
241 represent soil structure. In addition, neither soil organic carbon nor total nitrogen were
242 included in the structural equation modelling, because they did not show significant
243 responses to the treatment type from prior data exploration. For the remaining seven
244 indicators (soil pH, soil moisture, bulk density, earthworm biomass, mite density, soil
245 fauna feeding activity, and soil microbial activity) an *a priori* model was built with
246 potential causal relations between variables based on theoretical knowledge and
247 hypotheses (**Supplementary S3**).

248 Subsequently, we built a component model for each of the seven indicators. The
249 component model was in a form of a mixed effect model, with fixed effects based on
250 hypothesized causal pathways in the *a priori* model, and random effects as treatment plots

251 nested within replicate blocks. The response variables were log (x+1)-transformed or
252 square-root transformed when necessary. The normal distribution and homogeneity of
253 variances of the residuals of each component model of the global path model were
254 graphically checked. From prior data exploration, the responses of most indicators to EFB
255 treatments were not dependent on the application rate of EFB. We thus assigned the
256 treatment type as a categorical variable with two levels (one level as the Low-EFB,
257 Medium-EFB, and High-EFB treatments, and the other level as the chemical fertilizer
258 treatment). The unbalanced sample size of the two levels was dealt with by mixed effects
259 models (Pinheiro and Bates, 2000). A structural equation model including the seven
260 component models was further simplified using a stepwise approach to remove
261 non-significant relationships (**Supplementary S4**). We tested the effects of these removals
262 on the Akaike Information Criterion (AIC), AIC with a correction for finite sample sizes
263 (AICc), and the model fit. During the model selection process, new causal relationships
264 between the soil variables which were not included in the *a priori* model appeared, and
265 were further included for examination. The most parsimonious model was selected where
266 deleting any variables generated $\Delta AICc < 3$ (Shipley, 2013) (**Supplementary S5**). The
267 model goodness-of-fit was examined by the Shipley's test of d-separation, using Fisher's
268 C statistics with X^2 distribution (Lefcheck, 2016). The structural equation modelling was
269 performed using the *piecewiseSEM* package (Lefcheck, 2016).

270 3. RESULTS

271 3.1 EFB application effects on soil abiotic properties

272 After 15 years of continuous treatment, soil pH, soil moisture, aggregate stability, and bulk
273 density at 0-15 cm soil depth significantly differed among treatments (**Figure 1**,
274 **Supplementary S6**). Soil pH and aggregate stability were significantly higher under EFB

275 treatments of all application rates, compared to the chemical fertilizer treatment. The
276 positive effects of EFB treatment on soil moisture increased with the application rate,
277 whereas this quantity-dependent response was not observed for soil pH and aggregate
278 stability. Bulk density was significantly lower under EFB treatments of all application
279 rates than in the chemical fertilizer treatment. Soil organic carbon and total nitrogen levels
280 did not significantly differ among the four treatments, yet this could be due to high
281 variations in the data.

282 3.2 EFB application effects on soil biota and functions

283 A total of 168 earthworms were collected, with a mean density of 1344 ind m⁻². The total
284 earthworm biomass under the Medium-EBF and High-EBF treatments was significantly
285 lower compared to the chemical fertilizer treatment, while the biomass was similar
286 between Low-EBF treatment and the chemical fertilizer treatment (**Figure 2,**
287 **Supplementary S6**). Across all the treatment plots, the dominant earthworm species was
288 the invasive endogeic species *Pontoscolex corethrurus* (Müller, 1857). No epigeic or
289 anecic earthworms were found in our study sites.

290 A total of 1168 mites were extracted, with a mean density of 909 ind m⁻². The total mite
291 density under the chemical fertilizer treatment was significantly lower than Low-EBF and
292 High-EBF treatments (**Figure 2, Supplementary S6**). The total mite density was similar
293 between Medium-EBF treatment and the chemical fertilizer treatment. The extracted mites
294 belonged to four main suborders: Astigmata, Oribatida, Mesostigmata, and Prostigmata.
295 Across the treatments, the dominant groups were Astigmata and Oribatida, with their
296 abundance accounted for 68% and 22% of all the specimens, respectively. The density of
297 Oribatida under the Low-EBF treatment was significantly higher than the chemical

298 fertilizer treatment and Medium-EFB treatment. The dominant group of Astigmata in our
299 samples was *Astigmata hypopus* (Supercohort Desmonomatides, Orbatida).

300 The soil fauna feeding activity under the Low-EFB and Medium-EFB treatments was
301 significantly higher than the chemical fertilizer treatment (**Figure 2, Supplementary S6**).
302 The High-EFB treatment had similar levels of soil fauna feeding activity as the chemical
303 fertilizer treatment. Soil microbial activity under all rates of EFB treatments was higher
304 than chemical fertilizer treatment (**Figure 2, Supplementary S6**).

305 3.3 Direct v.s. indirect effects of EFB application

306 We used structural equation modelling (SEM) to examine whether EFB treatment affected
307 soil biota and functions by providing resources, or through altering soil abiotic properties.
308 Compared to chemical fertilizer treatment, EFB treatment increased soil pH (path
309 coefficient=0.35, $P<0.001$) and soil moisture (path coefficient=0.19, $P<0.05$), and
310 decreased soil bulk density (path coefficient=-0.37, $P<0.001$) (**Figure 3**). EFB application
311 directly decreased the total biomass of *Pontoscolex corethrurus* (path coefficient=-0.23,
312 $P<0.05$). EFB application directly increased the abundance of detritivore mites (path
313 coefficient=0.25, $P<0.01$) and soil fauna feeding activity (path coefficient=0.19, $P<0.01$),
314 rather than indirectly through modifying soil abiotic properties. EFB application increased
315 soil microbial activity both by providing resources (path coefficient=0.26, $P<0.001$), and
316 through increasing the soil fauna feeding activity (path coefficient=0.18, $P<0.05$) (**Figure**
317 **3, Supplementary S5**). Linear mixed effects models confirmed that soil fauna feeding
318 activity positively influenced soil microbial activity ($F_{1,70}=8.75$, $P=0.0042$) (**Figure 4**).

319 4. DISCUSSION

320 This study examined the effects of EFB application on soil abiotic properties, soil biota,
321 and ecosystem functions in a 15-year trial in Central Sumatra, Indonesia. We used
322 structural equation modelling to understand whether the effects of EFB application directly
323 influenced soil biota and ecosystem functions, or indirectly through altering soil abiotic
324 properties. We synthesized whether the effects of EFB application on these soil ecosystem
325 indicators depended on the application rate of EFB.

326 4.1 EFB application effects on soil abiotic properties

327 EFB application over 15 years significantly increased soil pH (**Figure 1**), confirming the
328 capacity of EFB in releasing base cations to alleviate soil acidification and improve the
329 nutrient retention of the soil (Bakar et al., 2011; Comte et al., 2013). EFB application also
330 enhanced soil aggregate stability and decreased bulk density, suggesting its positive effects
331 on soil physical properties and structure (Abolfath Moradi et al., 2014). EFB application
332 did not markedly increase soil organic carbon levels at our study site. However, the high
333 variations in the data may cause the absence of statistic differences. Uneven distribution of
334 EFB at sampling palms and potential differences in microclimate between sampling palms
335 may have led to variations in EFB decomposition. Soil organic carbon appeared to decline
336 with higher rates of EFB treatment (**Figure 1**), suggesting that more inputs of urea with
337 higher rate of EFB treatments increased the decomposition of existing soil organic carbon.

338 4.2 EFB application effects on soil biota and functions

339 The total earthworm biomass was significantly reduced under EFB treatments of all
340 application rates, compared to the chemical fertilizer treatment. EFB contains high content
341 of lignin (285 g kg^{-1}) and releases a phenolic compound of 2,6- bis (1,1-dimethylethyl)
342 during field decomposition (A. Moradi et al., 2014; Sabrina et al., 2012). Some phenol

343 compounds are known to be toxic for earthworms (Sabrina et al., 2012) and thus may be a
344 cause of earthworm decline under EFB treatment in our study, yet further study is needed
345 to confirm this hypothesis. In addition, EFB mulched on the soil surface may create an
346 anoxic environment which inhibits earthworm populations (Carron et al., 2015). The
347 dominant earthworm population across all treatments was the invasive endogeic species,
348 *Pontoscolex corethrurus*. This species is known to act as a “compacting species” under
349 environments with scarce soil organic carbon, For example, it is reported to produce large
350 and compact casts, which result in increased soil bulk density and macro-aggregates in the
351 soil of some disturbed ecosystems (Alegre et al., 1996; Chauvel et al., 1999; Hallaire et al.,
352 2000). In contrast, the structural equation modelling did not show significant impacts of
353 earthworms on soil bulk density in our study. It is therefore likely that the small population
354 size of *P. corethrurus* in our study site had limited effects on soil structure, and that EFB
355 addition may directly decrease soil bulk density by protecting the soil from the compacting
356 effect of the heavy tropical rain.

357 The density of detritivorous mites of Astigmata and Oribatida were higher under the EFB
358 application compared to the chemical fertilizer treatment. The positive effects of crop
359 residue management on soil mites were also found in other cropping systems (Minor and
360 Norton, 2004; Sánchez-Moreno et al., 2009; Scheunemann et al., 2015). The effects of
361 organic matter addition on soil detritivorous mitea can be due to the provision of trophic or
362 energy sources, or by altering soil physico-chemical environment (Bedano et al., 2006;
363 Coleman et al., 2004). Soil animals such as endogeic earthworms may also have top-down
364 control on soil mite populations through resource competition, direct feeding, and
365 microhabitat disturbance (Eisenhauer, 2010; Mueller et al., 2016). Results from our
366 structural equation modelling suggested that the soil mite density was strongly influenced

367 by the bottom-up control of the EFB application, rather than top-down control by endogeic
368 earthworms.

369 Prostigmata, an important predatory mite taxa, was absent under the chemical fertilizer
370 treatment, while a few individuals were found under the EFB treatments. The appearance
371 of Prostigmata under EFB application suggests increased regulatory functions of the soil
372 food webs that are essential for energy and organic matter turnover (Wissuwa et al., 2012).

373 EFB application enhanced soil fauna feeding activity, coincided with another study
374 examining soil heterogeneity between different management zones of oil palm (Tao et al.,
375 2016). Soil macrofauna and mesofauna, such as earthworms, collembola, and soil mites
376 have been reported to be the major feeders on the bait lamina assay in temperate regions
377 and laboratory manipulations (Helling et al., 1998; Kratz, 1998). Our results suggested that
378 EFB application directly enhanced the soil fauna feeding activity, rather than indirectly
379 altering soil abiotic conditions or soil mite and earthworm populations. This result
380 suggested that the EFB may serve as a food/energy resources for soil biota groups other
381 than soil mites and earthworms (i.e. termites). The enhanced soil fauna feeding activity
382 under EFB application also implies a more rapid turnover of carbon and nutrient cycling
383 with the addition of EFB, which can be beneficial for long-term soil health and soil
384 fertility.

385 Soil microbial activity can be influenced by direct resource provision or by changes in the
386 soil abiotic environment (Cookson et al., 1998; Kaneko et al., 1998). Soil biota such as
387 earthworms may also have top-down control over soil microorganisms through direct
388 feeding, disruption of fungal hyphae, resource competition, or mechanical disturbance;
389 whereas soil mites may positively or negatively influence soil microbial activity by

390 altering the microbial population and turnover (Kaneko et al., 1998). We showed that EFB
391 application enhanced soil microbial activity through direct resource provision, as well as
392 through increasing soil fauna feeding activity. This finding suggested that the enhanced
393 soil fauna feeding activities under EFB application may have produced readily-available
394 nutrients for microbial utilization.

395 4.3 Effects of EFB application rate

396 The response of most soil abiotic properties, soil biota and ecosystem function indicators
397 were independent of the application rate of EFB treatments. Specifically, soil pH, soil
398 aggregate stability, earthworm biomass, total soil mite density, and microbial activity were
399 not statistically different between the Low-EFB, Medium-EFB, and High-EFB treatments.
400 Few soil ecosystem indicators showed higher enhancement under the Low-EFB treatment
401 than the Medium-EFB treatment or the High-EFB treatment. For example, the soil mite
402 Suborder of Oribatida under the Low-EFB treatment was higher than the Medium-EFB
403 treatment. Similarly, the soil fauna feeding activity under the Low-EFB treatment was
404 higher than the High-EFB treatment. The application rate of the Low-EFB treatment was
405 similar to standard operations in the oil palm industry, whereas Medium-EFB and
406 High-EFB treatments represented alternative application rates of EFB. These results
407 suggest that better soil abiotic properties, soil biota and ecosystem functions may be
408 enhanced by the low, industry standard EFB treatment without the need to increase the
409 application rate.

410 5. CONCLUSIONS

411 Applying a major oil palm industrial residue empty fruit bunch (EFB) for 15 years in
412 Indonesia improved soil abiotic properties and increased soil detritivore mites abundance,
413 soil fauna feeding activity, and soil microbial activity. EFB affected soil biota and function

414 indicators by providing resources, rather than through altering soil abiotic properties. The
415 effects of EFB application on most of measured soil parameters were independent of the
416 application rate. These results suggest that the current practice of EFB application in some
417 oil palm plantations has a high potential to enhance soil abiotic properties, soil biota and
418 functions. We highlight this practice as a promising approach to enhance sustainable
419 development of oil palm.

420

421 6. AUTHORS' CONTRIBUTIONS

422 All authors conceived the ideas and designed methodology; HHT collected the data and
423 wrote the manuscript; HHT and LH analysed the data. All authors contributed critically to
424 the drafts and gave final approval for publication.

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628

629 9. FIGURE CAPTION

630 **Figure 1.** Soil pH (a), soil moisture (b), aggregate stability (c), bulk density (d), soil
631 organic carbon (e), and soil total nitrogen (f) under Chemical fertilizer treatment
632 (Chemical fertilizer), Low-EFB treatment (Low-EFB), Medium-EFB treatment
633 (Medium-EFB), and High-EFB treatment (High-EFB). The filled circles indicate
634 treatment means and bars indicate standard errors. Different letters indicate significant
635 Tukey's HSD differences between treatments. EFB: empty fruit bunch. ns:
636 non-significant difference.

637

638 **Figure 2.** Earthworm biomass (a), soil mite density (b), soil fauna feeding activity (c),
639 and soil microbial activity (d) under Chemical fertilizer treatment (Chemical fertilizer),
640 Low-EFB treatment (Low-EFB), Medium-EFB treatment (Medium-EFB), and High-EFB
641 treatment (High-EFB). The filled circles indicate treatment means and bars indicate
642 standard errors. Different letters indicate significant Tukey's HSD differences between
643 treatments. In (b), the lower case letters indicate statistical differences in the total density
644 of soil mites, while the upper case letters indicate the differences in the density of
645 Oribatida. EFB: empty fruit bunch.

646

647 **Figure 3.** Structural equation modelling for the effects of EFB application on soil abiotic
648 properties, soil biota, and functions. The models provided the best fit to the data and were
649 well supported (Fisher's $C=35.02$, $df=38$, $P\text{-value}=0.61$). The number besides each arrow
650 indicates path coefficient (standardized partial regression coefficient; +: positive effect, -:
651 negative effect). The significance of the effects were determined by the P -value (*, **
652 and *** indicate that F-value differs significantly from 0 at $P = 0.05$, 0.01 , and 0.001).
653 The arrows indicate unidirectional relationships between the variables. Black arrows
654 indicate positive effects, grey arrows indicate negative effects, and dashed arrows indicate

655 non-significant relationships. Arrow widths are proportional to the path coefficients. The
656 conditional coefficients of determination (r^2) for each endogenous variable is reported.

657

658 **Figure 4.** Log-transformed soil microbial activity as CO₂ concentration (mg C-CO₂ kg⁻¹
659 soil day⁻¹), as a function of square-root transformed soil fauna feeding activity (%). Points
660 are measured values from Chemical fertilizer treatment, Low-EFB, Medium-EFB, and
661 High-EFB treatments. The line indicates a fitted linear regression model ($y=2.99+1.31x$,
662 $R^2=0.13$, P -value <0.001). The grey band indicates 95% of the confidence interval. Linear
663 mixed effects model including random effects of treatment plot nested within replicate
664 block showed significant effects of soil fauna feeding activity on soil microbial
665 respiration ($F_{1,70}=8.75$, P -value=0.0042).

666

1 Application of oil palm empty fruit bunch effects on soil biota and functions: a
2 case study in Sumatra, Indonesia

3
4 ~~DOES CROP RESIDUE APPLICATION ENHANCE SOIL ECOSYSTEM~~
5 ~~IN OIL PALM? A CASE STUDY IN SUMATRA, INDONESIA~~
6

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22 ABSTRACT

23 Oil palm (*Elaeis guineensis*) is an important tropical crop which provides one-fifth of the
24 world's vegetable oil, yet its rapid expansion can negatively influence the soil ecosystem.
25 Identifying suitable agronomic management such as crop residue application is important
26 for the sustainable development of oil palm. We examined the effects of adding empty
27 fruit bunches (EFB), a major oil palm residue, on multiple soil abiotic properties, soil
28 biota, and ~~indicators of soil soil-ecosystem~~ functions. We compared treatments of EFB
29 applications with three application rates, and a chemical fertilizer treatment in a 15-year
30 trial in Central Sumatra, Indonesia. EFB application increased pH ~~and moisture~~, aggregate
31 stability in 0–10 cm soils and decreased the soil bulk density. EFB application increased
32 the abundance of soil detritivore mites, soil fauna feeding activity, and soil microbial
33 activity. EFB application decreased the biomass of a dominant invasive earthworm
34 species, *Pontoscolex corethrurus* (Müller, 1857). Results from structural equation
35 modelling suggested that EFB directly affected soil biota and ~~ecosystem~~ functions, rather
36 than through altering soil abiotic properties. The effects of EFB application on most soil
37 ~~abiotic properties, soil biota and function ecosystem~~ indicators were independent of the
38 application rate. Our results revealed that EFB application has a high potential to enhance
39 soil ~~ecosystem~~ biota and functions in oil palm plantations.

40 1. INTRODUCTION

41 Soil provides crucial functions and ecosystem services to enhance food security, land
42 restoration, and climate change mitigation, which are key Sustainable Development Goals
43 of United Nations (S. D. Keesstra et al., 2016). Various interacting soil organisms and their
44 processes contribute to key soil ecosystem functions, such as nutrient cycling, carbon
45 sequestration, and soil structure maintenance (Bardgett and van der Putten, 2014). In
46 agricultural ecosystems, management practices may influence abiotic soil environment and
47 soil biota, which then alter key soil ecosystem functions and crop production (Birkhofer et
48 al., 2008).

49 Identifying sustainable management is especially important for tropical production systems
50 which produce 1.7 tons of dry crop yield annually (West et al., 2010). Oil palm (*Elaeis*
51 *guineensis*) is a wide spread economic crop in Southeast Asia which produces one-fifth of
52 vegetable oil globally (Kurnia et al., 2016; Sayer et al., 2012) (~~Kurnia et al., 2016; Sayer et~~
53 ~~al., 2012; Sheil et al., 2009~~). The global oil palm land area covers 16.4 million ha,
54 equivalent to ten percent of the world's permanent croplands (FAO, 2015) (~~FAO, 2015;~~
55 ~~Sheil et al., 2009~~). Land conversion from forest to oil palm can reduce soil biodiversity,
56 increase nutrient leaching, and negatively influence soil carbon storage and fertility
57 (Dislich et al., 2017) (~~Barnes et al., 2014; Fitzherbert et al., 2008; Guillaume et al., 2015;~~
58 ~~Violita et al., 2015~~). To identify and implement suitable soil management for mitigating
59 these negative environmental impacts is important; however, few studies have examined
60 these management practices and their effects on soil biodiversity and ecosystem functions
61 in oil palm plantations (Bessou et al., 2017; Carron et al., 2015; Tao et al., 2016) (~~Bessou et~~
62 ~~al., 2017; Gray et al., 2015; Gray and Lewis, 2014; Hartemink, 2005~~).

63 In most oil palm plantations in Southeast Asia, chemical fertilizer is used as a major source
64 of nutrients. More recently, crop residues from oil palm have been used as organic
65 fertilizers and mulch substrates to reduce the quantity of mineral fertilizers needed. One of
66 the main oil palm residues from the palm oil extraction process are the empty fruit bunches
67 (EFB), which are the structural part of the fruit bunches_(Chang, 2014)~~(Chang, 2014;~~
68 ~~Wiloso et al., 2014)~~. Several studies have reported the effects of EFB application on soil
69 fertility and yield in Indonesian and Malaysian oil palm_(Comte et al., 2013; Abolfath
70 Moradi et al., 2014; Tao et al., 2017)~~(Bakar et al., 2011; Comte et al., 2013; Moradi et al.,~~
71 ~~2015; Tao et al., 2016)~~. However, there is little information on the effects of EFB
72 application on soil biota and ecosystem functions_(Carron et al., 2015; Tao et al., 2016),
73 and whether the effects are direct or through altering soil abiotic properties~~(Carron et al.,~~
74 ~~2015; Tao et al., 2016)~~. It is also unknown whether the effects are quantity-dependent, i.e.,
75 whether the magnitude of the effects depends on the application rate of EFB. For other
76 crops such as apricot, olive, and persimmon, applying crop residue mulch has shown to
77 reduce soil degradation (S. Keesstra et al., 2016; Parras-Alcántara et al., 2016; Ritsema,
78 2016). Relevant This information for oil palm is crucial for plantation managers and
79 policymakers to promote and implement suitable soil management practices to achieve
80 sustainable intensification of oil palm. ▲

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81 Among soil organisms, earthworms can be litter transformers and soil engineers which
82 structure the environment of other soil organisms, whereas soil mites directly feed on crop
83 residues and microorganisms_(Coleman et al., 2004)~~(D. Coleman et al., 2004;~~
84 ~~Corral Hernández et al., 2015)~~. ~~In temperate regions,~~ Crop residue application ~~has been~~
85 ~~reported to~~ may positively influence soil microbial respiration and soil faunal feeding
86 activities; either by providing food resources, or by altering soil abiotic properties and

87 microhabitats for soil biota; ~~yet~~ (Kurzatkowski et al., 2004; Reinecke et al., 2008;
88 ~~Simpson et al., 2012~~). However, such mechanisms have rarely been explored ~~been~~
89 ~~relatively under studied~~ in tropical agroecosystems; especially for perennial crops
90 (Kurzatkowski et al., 2004; Römbke et al., 2006). Moreover, the majority of research has
91 focused on the effects of crop residue application on the litter layer rather than the soil
92 mineral layer, despite the fact that carbon sequestration and nutrient cycling also happen in
93 the soil layer (Ashford et al., 2013).

94 This study aimed to examine the long-term effects of oil palm residue addition on ~~the~~ soil
95 biota and ecosystem functions ~~in~~ the top soil layer. Specifically, we asked: 1) does EFB
96 application influence key soil biota and ~~ecosystem~~ function indicators? 2) does EFB
97 application directly influence soil biota and ~~ecosystem~~ functions, or indirectly through
98 altering soil abiotic properties? and 3) do the effects of EFB application on soil biota and
99 ~~ecosystem~~ functions depend on the application rate? We examined key indicators for six
100 soil abiotic properties, two soil biota groups, and two indicators of ecosystem soil
101 functions in a 15-year field trial in an oil palm plantation in Sumatra, Indonesia. We used a
102 structural equation modelling approach (Grace et al., 2012; Shipley, 2013) to examine the
103 potential causal relationships between soil abiotic properties, soil biota, and ~~ecosystem~~
104 functions (~~Grace et al., 2012; Shipley, 2013~~). We hypothesized that EFB application has
105 positive impacts on key soil ecosystem indicators. ~~EFB application~~ may influence soil
106 biota and ~~ecosystem~~ functions both by directly providing resources, and by modifying soil
107 abiotic properties. The soil biota could also have cascading effects on other soil fauna
108 groups and ~~ecosystem~~ functions (**Figure 1**). In addition, we expected that the responses of
109 soil biota and ~~ecosystem~~ functions to EFB application would be stronger at higher
110 application rates.

111 2. MATERIALS AND METHODS

112 2.1 Site description and experimental design

113 The study was carried out in an oil palm plantation in Sumatra, Indonesia (0° 56'0" N
114 101°18'0"E). The oil palm plantation was established in 1987 and has been certified by the
115 Roundtable on Sustainable Palm Oil (RSPO). The previous land use of this area was
116 secondary tropical forest dominated by *Dipterocarp* species. The climate of this region is
117 described as tropical humid, with a mean temperature of 26.8 °C and average rainfall of
118 2400 mm year⁻¹. The soils are Inceptisols (Typic Dystrudepts), within the loamy lowland
119 soil class (USDA soil classification system).

120 The 15-year trial began in 1998, when the age of oil palms was 11 years. Field sampling
121 and measurements were conducted at the end of the trial during September-October 2014.
122 The field trial was established at two adjacent oil palm commercial plots. The field trial
123 covered a total area of 36 hectares (1200 m length × 300 m wide) and was composed of
124 five replicate blocks. Each replicate block was composed of four treatment plots, resulting
125 in a total of 20 treatment plots (5 replicate blocks × 4 treatment plots). The replication
126 number was five in a nested design (See **Supplementary S1**).

127 Each treatment plot (80 m × 40 m) was composed of 36 palm trees, arranged as eight palm
128 trees in four rows. The applications were applied throughout the treatment plot
129 continuously for 15 years. Soil sampling was undertaken at the end of 15 years at five oil
130 palms in the central two rows. There was at least one palm between two focal palms to
131 avoid spill over effects (**Supplementary S1**). Each treatment plot was surrounded by 1.5
132 m depth ditches to prevent interference by adjacent treatment plots.

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133 The four treatment plots in each replicate block were: Low-EFB treatment applied with
134 EFB (210 kg tree⁻¹ yr⁻¹, equivalent to 30 t ha⁻¹ yr⁻¹) and urea (0.02 kg tree⁻¹ yr⁻¹);
135 Medium-EFB treatment applied with EFB (420 kg tree⁻¹ yr⁻¹, equivalent to 60 t ha⁻¹ yr⁻¹)
136 and urea (0.04 kg tree⁻¹ yr⁻¹); High-EFB treatment applied with EFB (630 kg tree⁻¹ yr⁻¹,
137 equivalent to 90 t ha⁻¹ yr⁻¹) and urea (0.06 kg tree⁻¹ yr⁻¹), and chemical fertilizer treatment
138 applied with a full quantity of chemical fertilizers without adding EFB. EFB as the
139 structural part of fruit bunches after fruit removal contains dry weight of 45-49 % C,
140 0.5-1.0 % N, 0.02-0.05 % P, 1.3-2.2 % K, and 0.2-0.4 % Mg (Budianta et al., 2010;
141 Chang, 2014; Kavitha et al., 2013; A. Moradi et al., 2014; Pardon et al., 2016). Chemical
142 fertilizer treatment included the application of 1.75 kg tree⁻¹ yr⁻¹ urea (46 % N), 0.5 kg
143 tree⁻¹ yr⁻¹ triple super phosphate (45 % P₂O₅, 15% Ca), 2.5 kg tree⁻¹ yr⁻¹ muriate of potash
144 (61% K₂O, 46% Cl), and 0.05 kg tree⁻¹ yr⁻¹ Kieserite (16% Mg, S:22%). For detailed
145 nutrient inputs description of each treatment see **Supplementary S2**.

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146 In EFB treatment plots, EFB was applied once a year for 15 years at one side of the
147 harvesting paths, followed by urea application on the top of EFB to regulate the EFB
148 decomposition rate. The application rate of the Low-EFB treatment was similar to standard
149 operations in the oil palm industry, whereas Medium-EFB and High-EFB treatments
150 represented alternative application rates of EFB. In the chemical fertilizer treatment, the
151 type and quantity of chemical fertilizers were similar to conventional standard estate
152 practices, and the fertilizers were applied within palm circles (1-2 m radius) twice a
153 year (i.e. during the February-March and September-October periods) throughout the trial
154 period. Harvesting path and palm circle account for approximately 5-15 % and 10-15% of
155 the total plantation area, respectively, as the majority of oil palm plantations in Southeast
156 Asia (Nelson et al., 2013).

157 2.2 Field measurements

158 We measured ten indicators for soil abiotic properties (soil pH, soil moisture, aggregate
159 stability, bulk density, soil organic carbon and total nitrogen), soil biota (earthworm
160 biomass and soil mite density), and soil ecosystem functions (soil fauna feeding activity
161 and soil microbial activity). We examined these soil properties at the soil mineral layer
162 rather than litter layer, since the response of soil-dwelling fauna communities and their
163 processes under soil management practices are relatively unknown in the oil palm
164 ecosystem (Tao et al., 2016). We examined these soil properties beneath EFB at one side
165 of harvesting paths of EFB treatment plots, and at the equivalent positions in chemical
166 fertilizer plots.

167 2.2.1 Measuring soil abiotic properties

168 We measured soil moisture using the WET sensor (Delta-T Device, UK). For soil pH, soil
169 organic carbon, soil total nitrogen, and soil aggregate stability, one soil sample was
170 collected at the depth of 0-15 cm under each focal palm. The resulting five soil samples for
171 each treatment plot were bulked to form a composite sample. Samples were air-dried for
172 4-7 days and sieved through 2 mm and 0.5 mm for soil chemical analysis. Soil organic
173 carbon concentration was measured using the Walkley-Black method (Nelson and
174 Sommers, 1982). Total nitrogen was determined by the Kjeldahl method (Bremmer and
175 Mulvaney, 1982). Soil pH was determined using a pH meter with a soil to water ratio of
176 1:1.

177 We analysed soil aggregate stability using the wet sieving method (Eijkkelkamp, the
178 Netherlands). Soils particles under 0.25 mm were used for the measurement. Unstable
179 aggregates were extracted by physical shaking for fixed amounts of time, while stable
180 aggregate was extracted by sodium hydroxide. The aggregate stability was calculated as

181 the percentage of stable aggregates weight over total aggregate weight. For bulk density
182 measurement, three soil samples of fixed volume were collected using metal rings (5 cm
183 diameter and 5.1 cm depth) under each focal palm. The dry weight of the samples was
184 measured after over-dry for 105 degrees for 24 hr. The bulk density was calculated as the
185 weight per unit volume of a soil sample.

186

187 2.2.2 Measuring soil biota

188 Earthworms and soil mites were chosen as the focal soil biota groups in our study as they
189 contribute to key functions in nutrient cycling (Coleman et al., 2004), and their abundance
190 in the mineral layer of the soil. We used a modified Tropical Soil Biology and Fertility
191 (TSBF) approach to extract earthworms (Moreira et al., 2008). Under each focal palm, the
192 organic layer on the top-soil was removed by a shovel, and a soil monolith of 50 cm length
193 × 20 cm width × 10 cm depth was excavated. Earthworms were hand-sorted by a team of
194 five people in the field. The fresh weight of each earthworm was measured, stored in a
195 90% ethanol solution, and the taxonomy was identified by an expert (Dr Samuel Wooster
196 James, Maharishi University of Management, United States). ~~We also used mustard
197 extraction approach to catch anecic earthworm, although no earthworm was found by this
198 approach.~~The biomass of earthworms (g/m^2) was obtained by dividing the fresh weights
199 of earthworms by the surface area of the soil monolith.

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200 We sampled soil mite using a modified Berlese-Tullgren funnel approach (Moreira et al.,
201 2008). Three soil samples were collected using soil cores (7.5 cm diameter and 4.2 cm
202 length) at each focal tree and pooled for the extraction over a 48-hour period. We
203 identified soil mites into taxonomic groups at the suborder level (Krantz and Walter,
204 2009). We also collected other microarthropod groups i.e. Collembola and Formicidae
205 from the extraction, yet the number was low and was not used for further analysis. The

206 density of each Suborder (individuals/m²) of each treatment plot was obtained by dividing
207 the number of mites of each Suborder by the surface area of three soil cores.

208 2.2.3 Measuring indicators of soil ecosystem functions

209 Soil fauna feeding activity represents direct litter feeding rates of soil mesofauna and
210 macrofauna, therefore is an indicator for nutrient turnover ~~and litter decomposition rate in~~
211 ~~the soil~~ (Reinecke et al., 2008; Simpson et al., 2012). We measured soil fauna feeding
212 activity by the bait lamina method (Terra Protecta GmbH, Berlin, Germany) (Von Torne
213 1990). The method uses thin PVC sticks (1 x 6 x 120 mm) with 16 apertures of 1.5 mm
214 diameter and 5 mm apart, filled with standardized bait made of cellulose powder, bran
215 flakes and active carbon in a ratio of 70:27:3. Under each of the focal palm, we placed six
216 bait lamina sticks 40 cm apart in a row. The sticks were inserted vertically until the top
217 aperture was just below the soil surface, and the bottom aperture was at a depth of 8 cm
218 below the soil surface. The sticks were left for 3 days and bait consumption was recorded
219 by assessing each aperture, i.e. feeding activity was recorded as 0 (without perforation =
220 no evidence of feeding) or 1 (partial or complete perforation = evidence of feeding).

221 Soil microbial activity is the metabolic process of micro-organisms which associated with
222 oxidizing soil organic carbon and nitrogen-containing compounds. In this study, we
223 examined the potential of heterotrophic respiration under *ex-situ* conditions, by measuring
224 CO₂ burst after moistening dry soil for 24hr (Solvita CO₂-Burst Test, USA,
225 <https://solvita.com/co2-burst/>). This method is different from usual measurements of
226 *in-situ* basal soil respiration in field conditions which examine real-time soil respiration. ~~It~~
227 ~~can be measured by CO₂ respiration as a function of substrate availability and serves as an~~
228 ~~useful indicator for organic matter decomposition (Hanson et al., 2000). We examined soil~~
229 ~~microbial respiration by Solvita laboratory respiration kit, which measures CO₂ burst~~

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230 ~~produced by microbes (Haney et al., 2008; Haney and Haney, 2010). Rather, it measures~~
231 ~~potential of microbial respiration by water induction as used in This method has been used~~
232 ~~in various ecological studies (Muñoz-Rojas et al., 2016a, 2016b; Ward et al., 2017) and is~~
233 ~~considered as a reliable, efficient and cost-effective method which results are comparable~~
234 ~~with other methods (Haney et al., 2008; Haney and Haney, 2010). To perform the test,~~
235 ~~each composite soil sample used for chemical property analysis was one soil sample of~~
236 ~~0–10 cm depth was collected under each focal palm and air-dried for one week. Each soil~~
237 ~~sample was and~~ sieved through a 2mm mesh sieve. Subsequently, 40g of each sample was
238 placed in a 50ml plastic beaker and then inside a 240ml incubation jar. The soils were
239 moistened by adding 20ml of water into the jar. A CO₂ probe was placed inside the jar
240 before incubation at room temperature for 24hr. ~~After incubation, the CO₂ probe was taken~~
241 ~~out from the jar and measured using The accumulated concentration of CO₂ was then~~
242 ~~measured using~~ a spectrometer (digital color reader). ~~The background of atmospheric CO₂~~
243 ~~was taken into account for the reading. The resulting values allowed for comparing relative~~
244 ~~differences between the treatments.~~

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245 2.3 STATISTICAL ANALYSIS

246 All statistical analyses were performed in R.3.3.1 (R Core Team, 2016). We used linear
247 mixed effects models to examine the effects of EFB application on soil abiotic properties,
248 soil biota, and soil ecosystem functions. The treatment type (Low-EFB, Medium-EFB,
249 High-EFB, and chemical fertilizer treatment) was fitted as a fixed effect (categorical
250 variable). Treatment plots nested within replicate blocks were fitted as random effects. To
251 correct for heterogeneity in the residuals, earthworm biomass and soil mite density were
252 log (x+1)-transformed, bulk density ~~and soil fauna feeding activity were~~ square- root
253 transformed, and the rest of the variables were log-transformed. For soil mite, both the

254 total soil mite density and the Suborder of Oribatida were tested against the treatment type.
255 Significant overall effects of treatment type were further explored using a post-hoc Tukey
256 test. All the statistical tests were evaluated using $\alpha = 5\%$. Mixed effects modelling was
257 performed using the *lme* function of the *nlme* package (Bates et al., 2015), and the
258 ~~post-hoc~~ Tukey test using the *multcomp* package (Hothorn et al., 2008).

259 Structural equation modelling was performed to test whether the EFB application
260 influenced soil biota and the soil ecosystem functions by direct provision of food
261 resources, or via modifying soil abiotic properties. This approach allows for evaluating
262 pre-existing theories using observational data, with a focus on exploring possible
263 mediation pathways (Eisenhauer et al., 2015; Grace et al., 2012). Among the ten
264 indicators, soil aggregate stability was not included in the structural equation modelling as
265 it positively correlated with soil bulk density. We thus used only soil bulk density to
266 represent soil structure. In addition, neither soil organic carbon nor total nitrogen were
267 included in the structural equation modelling, because they did not show significant
268 responses to the treatment type from prior data exploration. For the remaining seven
269 indicators (soil pH, soil moisture, bulk density, earthworm biomass, mite density, soil
270 fauna feeding activity, and soil microbial activity) an *a priori* model was built with
271 potential causal relations between variables based on theoretical knowledge and
272 hypotheses (**Supplementary S3**).

273 Subsequently, we built a component model for each of the seven indicators. ~~The~~ The
274 component model was in a form of a mixed effect model, with fixed effects based on
275 hypothesized causal pathways in the *a priori* model, and random effects as treatment plots
276 nested within replicate blocks. The response variables were log (x+1)-transformed or
277 square-root transformed when necessary. The normal distribution and homogeneity of

278 variances of the residuals of each component model of the global path model were
279 graphically checked. From prior data exploration, the responses of most indicators to EFB
280 treatments were not dependent on the application rate of EFB. We thus assigned the
281 treatment type as a categorical variable with two levels (one level as the Low-EFB,
282 Medium-EFB, and High-EFB treatments, and the other level as the chemical fertilizer
283 treatment). The unbalanced sample size of the two levels was dealt with by mixed effects
284 models (Pinheiro and Bates, 2000). A structural equation model including the seven
285 component models was further simplified using a stepwise approach to remove
286 non-significant relationships ([Supplementary S4](#)). We ~~then~~-tested the effects of these
287 removals on the Akaike Information Criterion (AIC), AIC with a correction for finite
288 sample sizes (AICc), and the model fit. During the model selection process, new causal
289 relationships between the soil variables which were not included in the *a priori* model
290 appeared, and were further included for examination. The most parsimonious model was
291 selected where deleting any variables generated $\Delta AICc < 3$ (Shibley, 2013)
292 ([Supplementary S5](#)). The model goodness-of-fit was examined by the Shipley's test of
293 d-separation, using Fisher's C statistics with X^2 distribution (Lefcheck, 2016). The
294 structural equation modelling was performed using the *piecewiseSEM* package (Lefcheck,
295 2016).

296 3. RESULTS

297 3.1 EFB application effects on soil abiotic properties

298 After 15 years of continuous treatment, soil pH, soil moisture, aggregate stability, and bulk
299 density at 0-15 cm soil depth significantly differed among treatments (**Figure 12**,
300 **Supplementary S64**). ~~The post-hoc comparisons showed that S~~soil pH, ~~soil moisture~~, and
301 aggregate stability were significantly higher under EFB treatments of all application rates,

302 compared to the chemical fertilizer treatment. The positive effects of EFB treatment on
303 soil moisture increased with the application rate, whereas this quantity-dependent response
304 was not observed for soil pH and aggregate stability. Bulk density was significantly lower
305 under EFB treatments of all application rates than in the chemical fertilizer treatment. Soil
306 organic carbon and total nitrogen levels did not significantly differ among the four
307 treatments, ~~yet this could be due to high variations in the data.~~

308 3.2 EFB application effects on soil biota and ~~ecosystem~~-functions

309 A total of 168 earthworms were collected, with a mean density of 1344 ind m⁻². The total
310 earthworm biomass under the Medium-EBF and High-EBF treatments was significantly
311 lower compared to the chemical fertilizer treatment, while the biomass was similar
312 between Low-EBF treatment and the chemical fertilizer treatment (**Figure 23,**
313 **Supplementary S64**). Across all the treatment plots, the dominant earthworm species was
314 the invasive endogeic species *Pontoscolex corethrurus* (Müller, 1857). No epigeic or
315 anecic earthworms were found in our study sites.

316 A total of 1168 mites were extracted, with a mean density of 909 ind m⁻². The ~~post-hoc~~
317 ~~comparisons showed that the~~ total mite density under the chemical fertilizer treatment was
318 significantly lower than Low-EBF and High-EBF treatments (**Figure 23, Supplementary**
319 **S64**). The total mite density was similar between Medium-EBF treatment and the chemical
320 fertilizer treatment. The extracted mites belonged to four main suborders: Astigmata,
321 Oribatida, Mesostigmata, and Prostigmata. Across the treatments, the dominant groups
322 were Astigmata and Oribatida, with their abundance accounted for 68% and 22% of all the
323 specimens, respectively. The density of Oribatida under the Low-EBF treatment was
324 significantly higher than the chemical fertilizer treatment and Medium-EBF treatment. The

325 dominant group of Astigmata in our samples was *Astigmata hypopus* (Supercohort
326 Desmonomatides, Orbatida).

327 The soil fauna feeding activity under the Low-EFB and Medium-EFB treatments was
328 significantly higher than the chemical fertilizer treatment (**Figure 23, Supplementary**
329 **S64**). The High-EFB treatment had similar levels of soil fauna feeding activity as the
330 chemical fertilizer treatment. Soil microbial activity under all rates of EFB treatments was
331 higher than chemical fertilizer treatment (**Figure 23, Supplementary S64**).

332 3.3 Direct v.s. indirect effects of EFB application

333 ~~We used s~~Structural equation modelling (SEM) ~~was used~~ to examine whether EFB
334 treatment ~~directly~~ affected soil biota and ~~soil ecosystem~~ functions by providing ~~food~~
335 resources, or ~~indirectly by through~~ altering soil abiotic properties. ~~C~~ompared to chemical
336 fertilizer treatment, ~~revealed that~~ EFB treatment increased ~~the soil pH~~ (path
337 coefficient=0.35, $P<0.001$) ~~and soil~~ moisture (path coefficient=0.19, $P<0.05$), ~~and of~~
338 ~~the soil but~~ decreased ~~the soil~~ bulk density (path coefficient=~~-~~0.37, $P<0.001$) (**Figure 3**)
339 (**Figure 4**). ~~The full model contained seven component models, which were built with all~~
340 ~~the possible causal links based on prior knowledge and hypotheses (Supplementary S3).~~
341 ~~The stepwise deletion approach resulted in the most parsimonious model, and the model fit~~
342 ~~was examined by the Fisher's C and χ^2 distribution (Supplementary S5, S6).~~ Consistent
343 ~~with the results from linear mixed effects models, In terms of soil biota and ecosystem~~
344 ~~functions,~~ EFB application directly decreased the total biomass of *Pontoscolex corethrurus*
345 (path coefficient=~~-~~0.23, $P<0.05$). EFB application directly increased the abundance of
346 detritivore mites (path coefficient=0.25, $P<0.01$) and soil fauna feeding activity (path
347 coefficient=0.19, $P<0.01$), rather than indirectly through modifying soil abiotic properties.
348 EFB application increased soil microbial activity both by ~~directly~~ providing ~~food~~ resources

349 ~~(path coefficient=0.26, $P<0.001$), as well as and through indirectly, by~~ increasing the soil
350 fauna feeding activity ~~(path coefficient=0.18, $P<0.05$)~~ (Figure 34, Supplementary S56).
351 ~~The causal relationships between the soil microbial activity and soil fauna feeding activity~~
352 ~~were not included in the *a priori* model but was detected during the model selection process~~
353 ~~of structural equation modelling.~~ Linear mixed effects models confirmed that soil fauna
354 feeding activity positively influenced soil microbial activity ~~was positively influenced by~~
355 ~~soil fauna feeding activity~~ ($F_{1,70}=8.75$, $p\text{-value}=0.0042$) (Figure 45).

356 4. DISCUSSION

357 This study examined the effects of EFB application on soil abiotic properties, soil biota,
358 and ecosystem functions in a 15-year trial in Central Sumatra, Indonesia. We used
359 structural equation modelling to understand whether the effects of EFB application directly
360 influenced soil biota and ecosystem functions, or indirectly through altering soil abiotic
361 properties. We synthesized whether the effects of EFB application on these soil ecosystem
362 indicators depended on the application rate of EFB.

363 4.1 EFB application effects on soil abiotic properties

364 EFB application over 15 years significantly increased soil pH ~~and soil moisture~~ (Figure
365 12), confirming the capacity of EFB in releasing base cations to alleviate soil acidification
366 and improve the nutrient retention of the soil (Bakar et al., 2011; Comte et al., 2013). EFB
367 application also enhanced soil aggregate stability and decreased bulk density, suggesting
368 its positive effects on soil physical properties and structure (Abolfath Moradi et al., 2014).
369 EFB application did not markedly increase soil organic carbon levels at our study site.
370 However, the high variations in the data may cause the absence of statistic differences.
371 Uneven distribution of EFB at sampling palms and potential differences in microclimate
372 between sampling palms may have led to variations in EFB decomposition. Soil organic

373 carbon appeared to decline with higher rates of EFB treatment (Figure 1), suggesting that
374 more inputs of urea with higher rate of EFB treatments increased the decomposition of
375 existing soil organic carbon.

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376 ~~which could be due to an increase in the decomposition rate of existing soil organic carbon~~
377 ~~(Berhe et al., 2007; Guillaume et al., 2015; Smith et al., 2012).~~

378 4.2 EFB application effects on soil biota and ~~ecosystem~~ functions

379 The total earthworm biomass was significantly reduced under EFB treatments of all
380 application rates, compared to the chemical fertilizer treatment. EFB contains high content
381 of lignin (285 g kg⁻¹) and releases a phenolic compound of 2,6- bis (1,1-dimethylethyl)
382 during field decomposition (A. Moradi et al., 2014; Sabrina et al., 2012). Some phenol
383 compounds are known to be toxic for earthworms (Sabrina et al., 2012) and thus may be a
384 cause of earthworm decline under EFB treatment in our study, yet further study is needed
385 to confirm this hypothesis. One possible explanation is that EFB decomposition releases
386 phenol compounds, which can be toxic to earthworms (Sabrina et al., 2012, 2009). In
387 addition, EFB mulched on the soil surface may create an anoxic environment which
388 inhibits earthworm populations (Carron et al., 2015). The dominant earthworm population
389 across all treatments was the invasive endogeic species, *Pontoscolex corethrurus*. This
390 species is known to act as a “compacting species” under environments with scarce soil
391 organic carbon, For example, it is reported to produce large and compact casts, which
392 result in increased soil bulk density and macro-aggregates in the soil of some disturbed
393 ecosystems (Alegre et al., 1996; Chauvel et al., 1999; Hallaire et al., 2000). ~~We could thus~~
394 ~~expect that the suppressed *P. corethrurus* population under EFB treatments would enhance~~
395 ~~soil physical properties, i.e., reduce the soil bulk density.~~ In contrast, the structural
396 equation modelling did not show significant impacts of earthworms on soil bulk density in

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397 | our study. It is therefore likely that the small population size of *P. corethrurus* in our study
398 | site had limited effects on soil structure, and that EFB addition may directly decrease soil
399 | bulk density by protecting the soil from the compacting effect of the heavy tropical rain.

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400 | The density of detritivorous mites of Astigmata and Oribatida were higher under the EFB
401 | application compared to the chemical fertilizer treatment. The positive effects of crop
402 | residue management on soil mites were also found in other cropping systems (Minor and
403 | Norton, 2004; Sánchez-Moreno et al., 2009; Scheunemann et al., 2015). The effects of
404 | organic matter addition on soil detritivorous mitea can be due to the provision of trophic or
405 | energy sources, or by altering soil physico-chemical environment (Bedano et al., 2006;
406 | Coleman et al., 2004). Soil animals such as endogeic earthworms may also have top-down
407 | control on soil mite populations through resource competition, direct feeding, and
408 | microhabitat disturbance (Eisenhauer, 2010; Mueller et al., 2016). Results from our
409 | structural equation modelling suggested that the soil mite density was strongly influenced
410 | by the bottom-up control of the EFB application, rather than top-down control by endogeic
411 | earthworms.

412 | Prostigmata, an important predatory mite taxa, was absent under the chemical fertilizer
413 | treatment, while a few individuals were found under the EFB treatments. The appearance
414 | of Prostigmata under EFB application suggests increased regulatory functions of the soil
415 | food webs that are essential for energy and organic matter turnover (Wissuwa et al., 2012).

416 | EFB application enhanced soil fauna feeding activity, coincided with another study
417 | examining soil heterogeneity between different management zones of oil palm (Tao et al.,
418 | 2016). Soil macrofauna and mesofauna, such as earthworms, collembola, and soil mites
419 | have been reported to be the major feeders on the bait lamina assay in temperate regions

420 and laboratory manipulations (Helling et al., 1998; Kratz, 1998) ~~(Birkhofer et al., 2011;~~
421 ~~Helling et al., 1998; Kratz, 1998)~~. Our results suggested that EFB application directly
422 enhanced the soil fauna feeding activity, rather than indirectly altering soil abiotic
423 conditions or soil mite and earthworm populations. This result suggested that the EFB may
424 serve as a food/energy resources for soil biota groups other than soil mites and earthworms
425 ~~(i.e. termites). For example, a potential feeder on bait lamina in oil palm ecosystems are~~
426 ~~termites, which have been reported as an important litter decomposer in oil palm~~
427 ~~plantations (Foster et al., 2011)~~. The enhanced soil fauna feeding activity under EFB
428 application also implies a more rapid turnover of carbon and nutrient cycling with the
429 addition of EFB, which can be beneficial for long-term soil health and soil fertility.

430 Soil microbial activity can be influenced by direct resource provision or by changes in the
431 soil abiotic environment (Cookson et al., 1998; Kaneko et al., 1998) ~~(Cookson et al.,~~
432 ~~1998; Kaneko et al., 1998; Torbert and Wood, 1992)~~. Soil biota such as earthworms may
433 also have top-down control over soil microorganisms through direct feeding, disruption of
434 fungal hyphae, resource competition, or mechanical disturbance; whereas soil mites may
435 positively or negatively influence soil microbial activity by altering the microbial
436 population and turnover (Kaneko et al., 1998). We showed that EFB application enhanced
437 soil microbial activity through direct resource provision, as well as through increasing soil
438 fauna feeding activity. This finding suggested that the enhanced soil fauna feeding
439 activities under EFB application may have produced readily-available nutrients for
440 microbial utilization.

441 4.3 Effects of EFB application rate

442 The response of most soil abiotic properties, soil biota and ecosystem function indicators
443 were independent of the application rate of EFB treatments. Specifically, soil pH, soil

444 aggregate stability, earthworm biomass, total soil mite density, and microbial activity were
445 not statistically different between the Low-EFB, Medium-EFB, and High-EFB treatments.
446 Few soil ecosystem indicators showed higher enhancement under the Low-EFB treatment
447 than the Medium-EFB treatment or the High-EFB treatment. For example, the soil mite
448 Suborder of Oribatida under the Low-EFB treatment was higher than the Medium-EFB
449 treatment. Similarly, the soil fauna feeding activity under the Low-EFB treatment was
450 higher than the High-EFB treatment. The application rate of the Low-EFB treatment was
451 similar to standard operations in the oil palm industry, whereas Medium-EFB and
452 High-EFB treatments represented alternative application rates of EFB. These results
453 suggest that better soil abiotic properties, soil biota and ecosystem functions may be
454 enhanced by the low, industry standard EFB treatment without the need to increase the
455 application rate.

456 5. CONCLUSIONS AND MANAGEMENT IMPLICATIONS

457 ~~Three key results emerged from our study in a 15-year field trial in Indonesia: first, EFB~~
458 ~~application increased soil pH, soil moisture, and soil aggregate stability, while decreasing~~
459 ~~soil bulk density. EFB application increased the abundance of soil detritivore mites, soil~~
460 ~~fauna feeding activity, and soil microbial activity. EFB application decreased the biomass~~
461 ~~of a dominant earthworm species *Pontoscolex corethrurus*. Second, EFB application~~
462 ~~appears to directly affect soil biota and ecosystem function indicators, rather than via~~
463 ~~altering soil abiotic properties. Third, Applying a major oil palm industrial residue empty~~
464 ~~fruit bunch (EFB) for 15 years in Indonesia improved soil abiotic properties and increased~~
465 ~~soil detritivore mites abundance, soil fauna feeding activity, and soil microbial activity.~~
466 ~~EFB affected soil biota and function indicators by providing resources, rather than through~~
467 ~~altering soil abiotic properties. The effects of EFB application on most of measured soil~~

468 ~~parameters were soil ecosystem indicators were~~ independent of the application rate. These
469 results suggest that ~~the current practice of the application of empty fruit bunches~~ EFB
470 ~~application~~ in ~~some~~ oil palm plantations has a high potential to enhance ~~the~~ soil ~~abiotic~~
471 ~~properties, soil biota and functions. We highlight this practice as a promising approach to~~
472 ~~enhance sustainable development of oil palm.~~

473
474 ~~ecosystem, compared to use chemical fertilizer as a sole nutrient supply. The~~
475 ~~implementation of this practice, however, largely depend on the availability of EFB,~~
476 ~~relative costs of field operations, and the potential in greenhouse gas emissions (Chang,~~
477 ~~2014; Chiew and Shimada, 2013; Wiloso et al., 2014). We highlight the importance of~~
478 ~~further research and technology development of relevant practices to enhance sustainable~~
479 ~~development of oil palm.~~

480 481 6. AUTHORS' CONTRIBUTIONS

482 All authors conceived the ideas and designed methodology; HHT collected the data and
483 wrote the manuscript; HHT and LH analysed the data. All authors contributed critically to
484 the drafts and gave final approval for publication.

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688 |

689 9. FIGURE CAPTION

690 **Figure 12.** Soil pH (a), soil moisture (b), aggregate stability (c), bulk density (d), soil
691 organic carbon (e), and soil total nitrogen (f) under Chemical fertilizer treatment
692 (Chemical fertilizer), Low-EFB treatment (Low-EFB), Medium-EFB treatment
693 (Medium-EFB), and High-EFB treatment (High-EFB). The filled circles indicate
694 treatment means and bars indicate standard errors. ~~four treatments (mean ± SE).~~ Different
695 letters indicate significant Tukey's HSD differences between ~~the~~ treatments. EFB: empty
696 fruit bunch. ns: non-significant difference ~~between treatments.~~

697
698 **Figure 23.** Earthworm biomass (a), soil mite density (b), soil fauna feeding activity (c),
699 and soil microbial activity (d) under Chemical fertilizer treatment (Chemical fertilizer),
700 Low-EFB treatment (Low-EFB), Medium-EFB treatment (Medium-EFB), and High-EFB
701 treatment (High-EFB). The filled circles indicate treatment means and bars indicate
702 standard errors. ~~four treatments (mean ± SE).~~ Different letters indicate significant Tukey's
703 HSD differences between ~~four~~ treatments ~~at α=5 %~~. In (b), the lower case letters ~~represent~~
704 indicate statistical differences in the total density of soil mites, while the upper case
705 letters ~~represent~~ indicate the differences in the density of Oribatida. EFB: empty fruit
706 bunch.

707
708 **Figure 34.** ~~The final, most parsimonious model for the effects of~~ Structural equation
709 modelling for the effects of ~~EFB~~ application on soil abiotic properties, soil biota, and
710 ~~soil ecosystem~~ functions. The models provided the best fit to the data and were well
711 supported (Fisher's C=35.02, df=38, P-value=0.61). The number besides each arrow
712 indicates path coefficient (standardized partial regression coefficient; +: positive effect, -:
713 negative effect). The significance of the effects were determined by the P-value (*, **
714 and *** indicate that F-value differs significantly from 0 at P = 0.05, 0.01, and 0.001).

715 ~~The Arrows represent indicate~~ unidirectional relationships ~~among between~~ the
716 variables. ~~Black arrows indicate positive effects, grey arrows indicate .~~ Positive
717 ~~relationships are denoted by blue arrows,~~ negative relationships ~~effects~~ by red arrows, and
718 ~~dashed arrows indicate non-non-significant relationships (p-value > 0.05) by dashed~~
719 ~~arrows. Arrow widths are proportional to the path coefficients. The Arrow widths are~~
720 ~~proportional to the standardized regression coefficients. c~~ Conditional coefficients of
721 determination (r^2) ~~for~~ each endogenous variable ~~is reported~~ are reported. The models
722 are well supported (Fisher's $C=35.02$, $df=38$, p -value=0.61).

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723
724 **Figure 45.** ~~Log-transformed S~~soil microbial activity as CO_2 concentration (mg C-CO_2
725 kg^{-1} soil day^{-1}), as a function of ~~square-root transformed~~ soil fauna feeding activity (%).
726 ~~Points are measured values from Chemical fertilizer treatment, Low-EFB, Medium-EFB,~~
727 ~~and High-EFB treatments. The blue line was indicates the a fitted~~ linear regression model
728 ($y=2.99+1.31x$, $R^2=0.13$, P -value <0.001). The grey band ~~indicates~~ represented 95% of the
729 confidence interval. ~~Linear mixed effects model including random effects of treatment~~
730 ~~plot nested within replicate block showed significant effects of soil fauna feeding activity~~
731 ~~on soil microbial respiration from a mixed effects model~~ ($F_{1,70}=8.75$, P -value=0.0042).

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Figure 1
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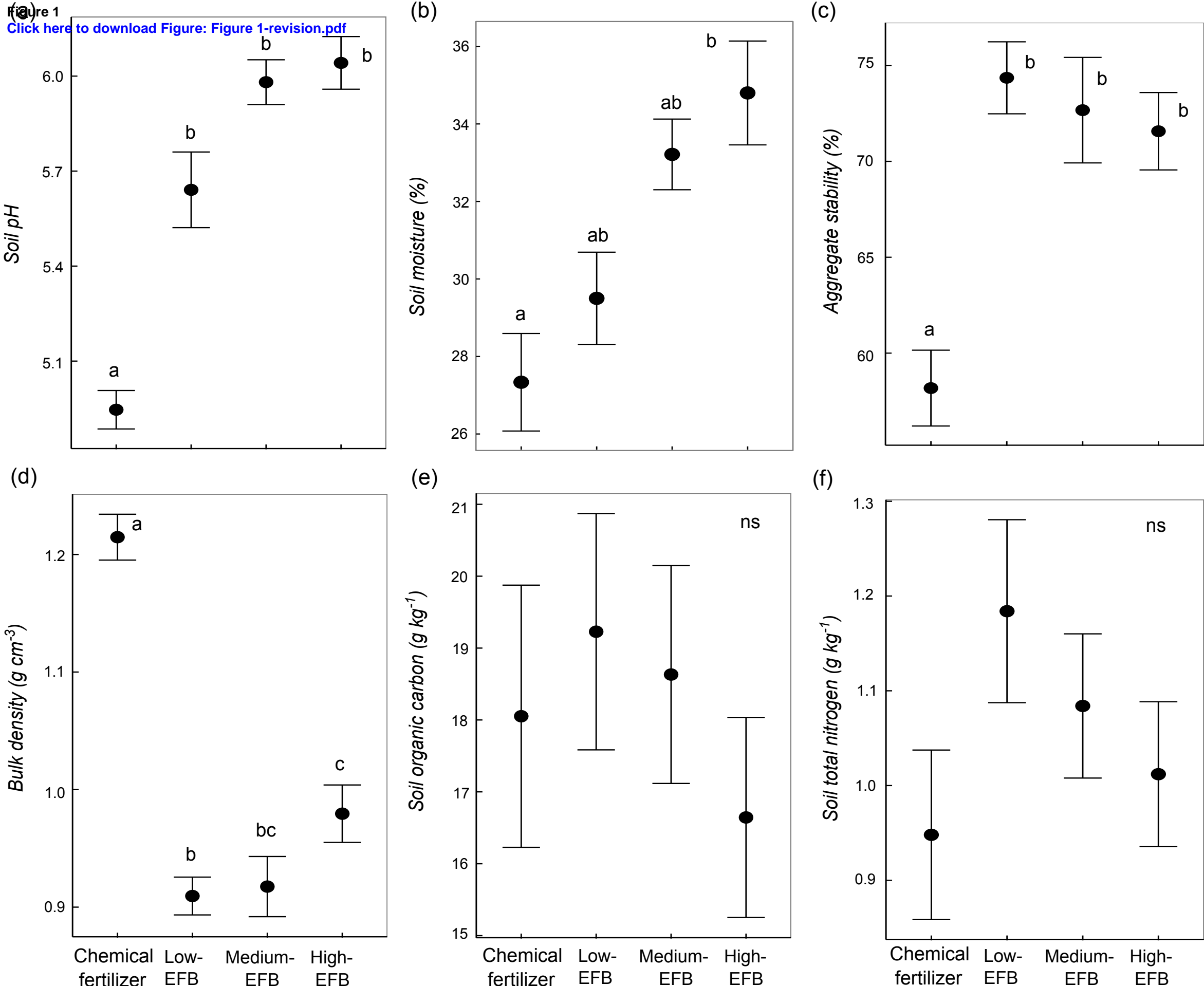


Figure 2
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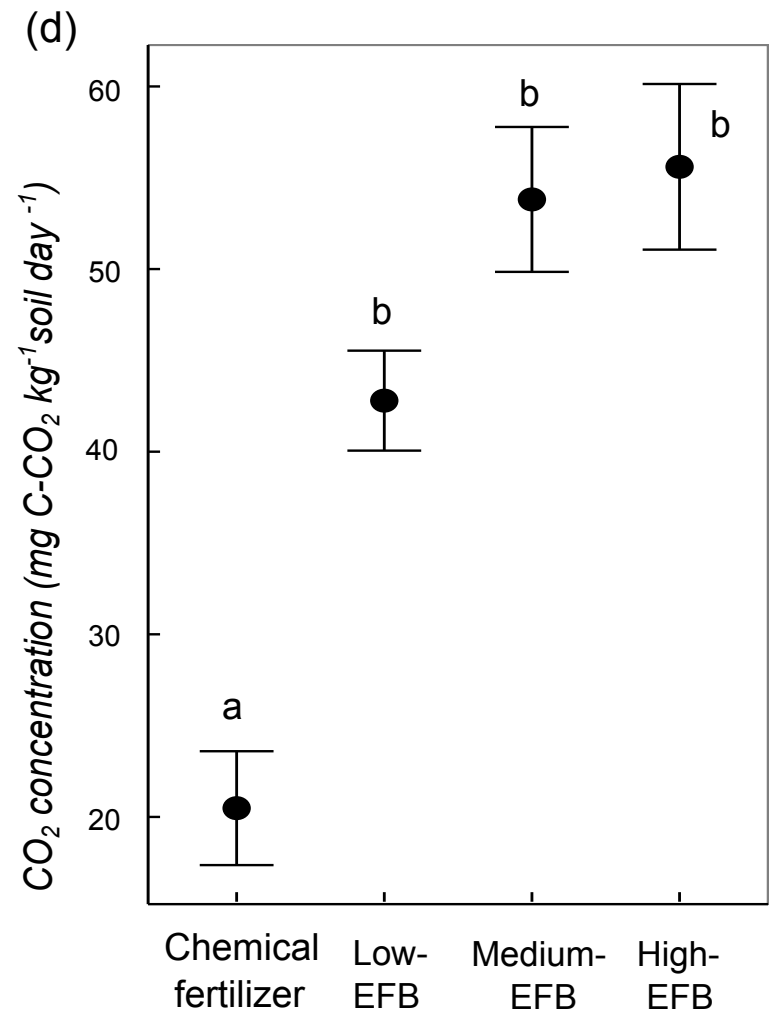
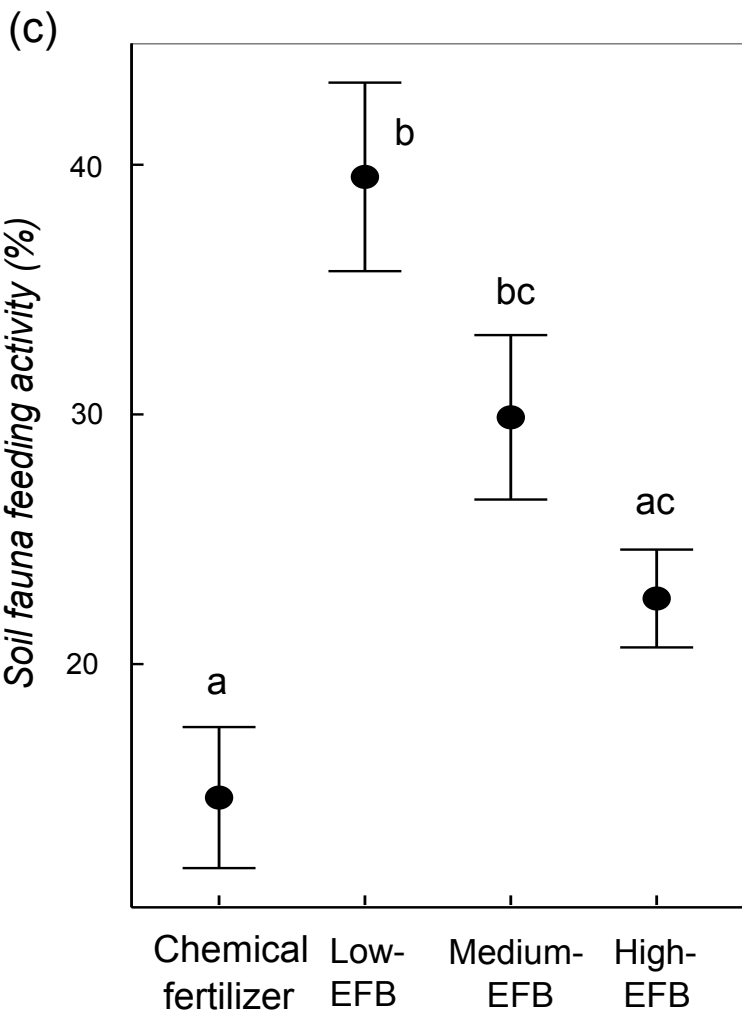
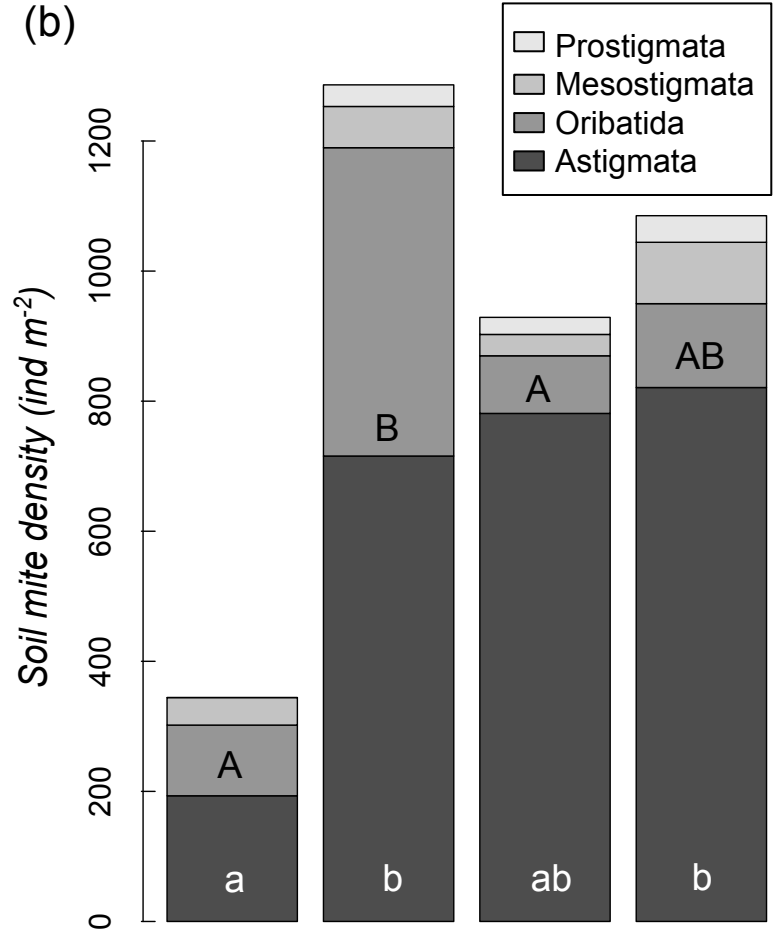
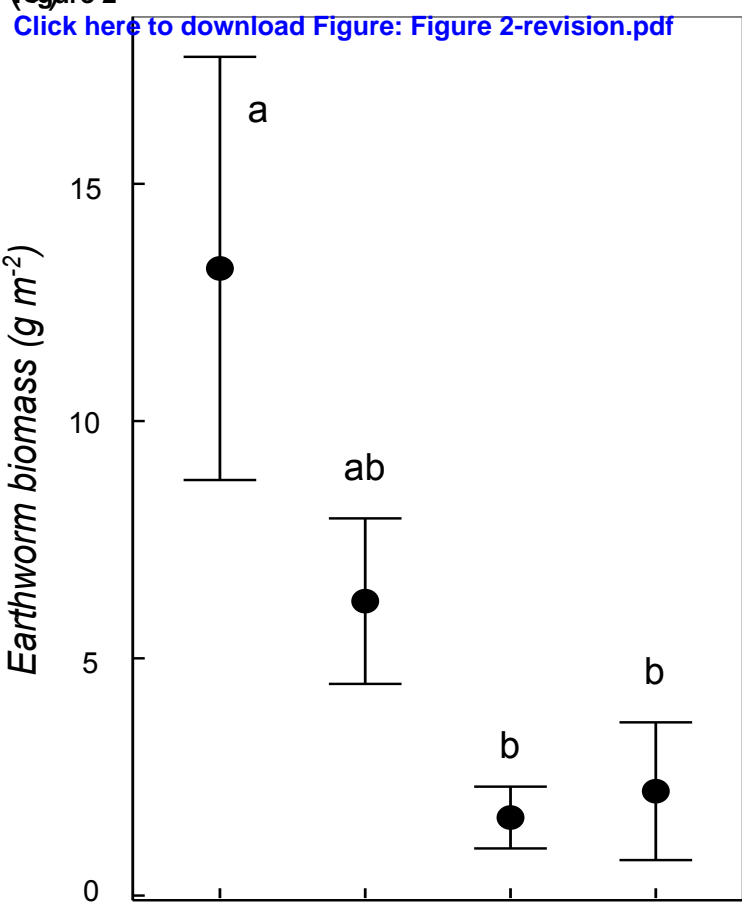
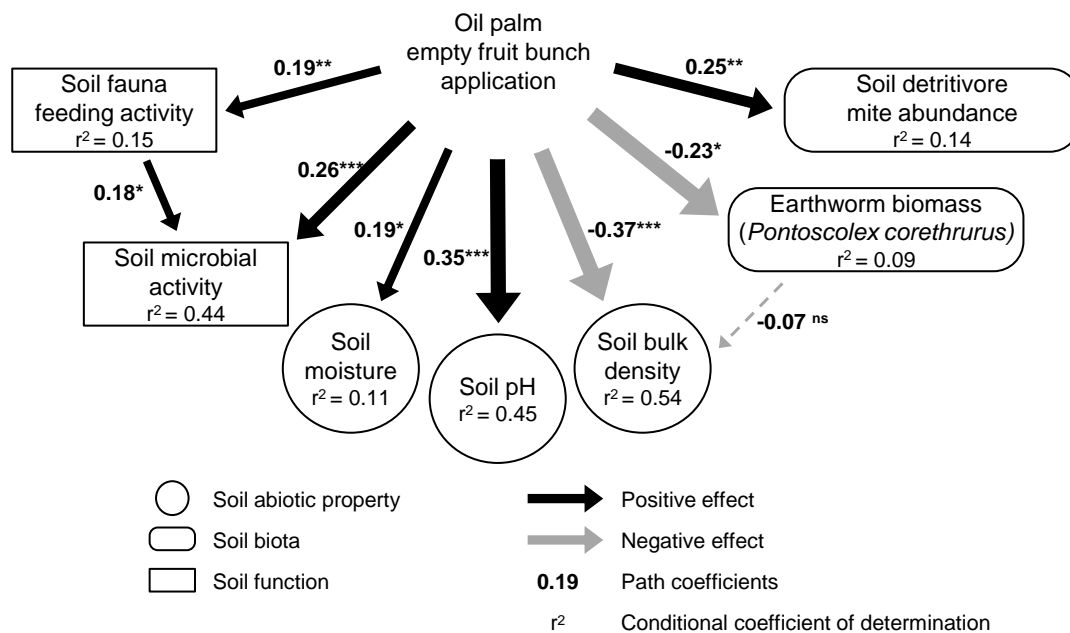


Figure 3

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