Environmental impacts as affected by different oil palm cropping systems in tropical peatlands

Selvakumar Dhandapani[a,b(#)], Karl Ritz[a], Stephanie Evers[c,d,e], Sofie Sjögersten[a].

Affiliations

[a]School of Biosciences, University of Nottingham, Sutton Bonington, UK.

[b]Crops For the Future, Semenyih, Selangor, Malaysia,

[c]School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, UK.

[d]School of Biosciences, University of Nottingham Malaysia Campus, Semenyih, Malaysia.

[e]Tropical Catchment Research Initiative (TROCARI)

(#) Corresponding author

Selvakumar Dhandapani,

Postal address: [b]School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool L3 3AF, UK.

Telephone: +44 7413649444

Email address: s.dhandapani@ljmu.ac.uk

Abstract

Tropical peatlands are globally important for their high carbon storage and unique biodiversity, but are currently under severe threat in South East Asia from expansion of oil palm plantations. A large part of this expansion in Peninsular Malaysia arises from small-holder oil palm plantations that follow varied cropping practices, yet their impact on the environment is largely unexplored. This research aimed to study and evaluate the environmental and belowground microbial impacts of different smallholder cropping systems relative to forested peatlands in North Selangor, Peninsular Malaysia. Specifically, GHG measurements using closed chambers, and peat sampling were carried out in both wet and dry seasons. Microbial phenotypic community structure was determined using phospholipid fatty acid (PLFA) analysis. Relative to forested peatlands, the agricultural plantations had increased pH, temperature and bulk density, decreased organic content, and peat moisture, with a pineapple intercropping site as the only exception. These effects were most pronounced in 2nd generation mono-cropping systems. Soil microbial community structure, dominated by Gram-positive bacteria under all land-use types, differed significantly between agricultural sites and forest, and also showed significant seasonal variation. There was a general increase in non-specific fatty acids and a decrease in Gram-positive fatty acids in agricultural sites from forest, however microbial community structure were similar in most agricultural sites. CO_2 emissions were greatest at the forest site and showed no seasonal variations, however most of the forest CO_2 emissions were most likely due to high autotrophic contribution from roots. CH_4 emissions were under 1 mg m^{-2} hr^{-1} for all the agricultural sites, while forest peat surface absorbed similar low quantity of CH_4. Overall, the changes in peat properties and loss of C was greatest in the 2nd generation mono-cropping, while the intercropping systems ameliorated these effects by maintaining most of the forest peat organic content and causing relatively smaller changes in pH, moisture and bulk density.

It is clear that oil palm intercropping have an ameliorating effect on environmental impacts caused by the expansion of oil palm plantations into peatlands.

Keywords: Tropical Peatlands; Oil palm mono-cropping; Oil palm intercropping; Microbial community structure.

1. Introduction

Tropical peatlands are globally important, yet are endangered ecosystems with high C storage capability and endemic biodiversity (Jackson *et al.*, 2009; Yule, 2010; Dohong *et al.*, 2017). Acidic, nutrient-poor and water-logged conditions in natural peatlands inhibit aerobic microbial decomposition, resulting in the accumulation of partially-decomposed plant materials arising from their inherently high primary production (Parish *et al.*, 2008; Sjögersten *et al.*, 2011; Miettinen *et al.*, 2012). Even though natural peatlands are known to have high methane (CH_4) emissions, high carbon (C) storage means that they act as important long-term C sinks (Page *et al.*, 2011; Schrier-Uijl *et al.*, 2013). About 56% of all tropical peatlands are in South East Asia (SEA), with greatest cover in Indonesia and Malaysia, mostly on low-lying coastal plains (Yule, 2010; Lo and Parish, 2013; Rashid *et al.*, 2013; Hergoualc'h and Verchot, 2014; Xu *et al.*, 2018). SEA peatlands store about 69 Gt of C (Miettinen and Liew, 2010; Dohong *et al.*, 2017) and absorb at least 2.6 tonnes of carbon dioxide (CO_2) per hectare a year (Norwana *et al.*, 2011).

Anthropogenic disturbances in SEA peatlands over the last few decades increasingly affect the balance of the environmental, biological and climatic conditions that maintain peatlands, resulting in their degradation and C loss (Couwenberg *et al.*, 2010). The SEA region has experienced relatively high deforestation rates in the 21st century, with Malaysia having the greatest deforestation rate of all the countries in the world (Hansen *et al.*, 2013) and now

undisturbed peat swamp forest are nearly extinct in Peninsular Malaysia (Miettinen *et al.*, 2016). It is estimated that 25% of all forest degradation in SEA occurs in peatlands (Lo and Parish, 2013). Most of these anthropogenic disturbances were associated with agricultural expansion, especially oil palm plantations. Oil palm plantations currently cover 7.6 M ha and 4.6 M ha in Indonesia and Malaysia, respectively (Dislich *et al.*, 2017) and are only expected to increase (Miettinen *et al.*, 2016). Around 75% of all peat forest loss in Peninsular Malaysia, Sumatra and Borneo between 2007 and 2015 were due to oil palm expansion (Miettinen *et al.*, 2016). The establishment of oil palm in peatlands requires draining and clearing of vegetation, severely altering the peatlands' physical and environmental conditions (Luskin and Potts, 2011). Degradation of these peatlands not only emits large quantities of CO_2, but also maintains high methane emissions through drainage ditches (Schrier-Uijl *et al.*, 2011). Increased use of fertilizers in oil palm plantations are known to increase both nitrous oxide (N_2O) and CO_2 emissions (Mohd Kusin *et al.*, 2015; Comeau *et al.*, 2016). Thus, the expansion of oil palm plantations into peatlands contributes to climate change, with increased emissions of three potent greenhouse gases.

Though industrial plantations are the leading land-use type for oil palm cultivation (Azhar *et al.*, 2011), about 3.5 M ha (22.4%) of peatlands in peninsular Malaysia, Sumatra and Borneo are small-holder plantations, and make up half of the managed peatlands in Peninsular Malaysia (Miettinen *et al.*, 2016). Unlike industrial plantations, smallholder farmers follow a diverse range of management practices and cropping systems such as intercropping, depending on personal convenience and their local needs (Global Environment Centre, personal communication). The smallholders' plantations are less productive and lack modern infrastructure (Azhar *et al.*, 2011), but have greater landscape heterogeneity (Azhar *et al.*, 2015). Microbial communities are an important biological factor for the formation and maintenance of peatlands and peat functions, by directly controlling C turnover and nutrient

97 mineralization supporting high primary production (Andersen *et al.*, 2013). Most of the C
98 utilised by bacterial groups in tropical peatlands is obtained via dissolved organic C leaching
99 from the surface leaf-litter layers (Yule, 2010). Several studies have shown that oil palm
100 plantations lack leaf litter and a humus layer (Bruhl and Eltz, 2010; Fayle *et al.*, 2010;
101 Cusack, 2011; Faruk *et al.*, 2013), and lack the leaf-litter heterogeneity that forests provide
102 through high plant biodiversity. This could have detrimental effects on peat microbial
103 communities, impacting nutrient cycling and biodiversity dependent on the microbial C food
104 chain. The multiple cropping systems could influence the microbial communities in broadly
105 two ways: (1) Above- and below-ground linkages through rhizosphere microbial
106 communities, root exudates and through quality and quantity of vegetative C sources added to
107 the soil (Aneja *et al.*, 2006; Jin *et al.*, 2010); (2) changes in microhabitat and microclimatic
108 conditions due to the heterogeneity of aboveground plant structure (Zhang *et al.*, 2010).

109 Given the importance of microbial communities in tropical peatlands and the anthropogenic
110 pressure they are exposed to, there is an increasing need to understand how land-use change
111 in tropical peatlands affects these microbial communities and their consequent effects on
112 biogeochemical cycles. The impact of different oil palm cropping systems in peatlands
113 remain poorly understood.

114 Most of the published studies on GHG emissions have been limited to peat forest and
115 industrial oil palm monoculture, ignoring the different kinds of management and cropping
116 systems increasingly used by oil palm smallholders throughout SEA. Microbial community
117 composition in tropical peatlands are generally poorly understood, while their responses to
118 land use change, seasonal variations and their relationship with GHG emissions are virtually
119 unknown (Yule, 2010). The aim of this study was therefore to determine the changes and
120 seasonal variations in peat properties and the responses of peat microbial community

structure and functions, specifically GHG emissions and C storage in different oil palm cropping systems.

We hypothesised that peat properties are altered in oil palm plantations relative to forest, and predict that peat properties such as organic matter content, moisture content, bulk density, pH and temperature are progressively affected more from 1st to 2nd generation cropping systems, while the intercropping systems (with their more complex microhabitats and litter inputs) are anticipated to ameliorate such damage to peat properties. We postulated the impact on peat properties in turn influences soil microbial communities and GHG emissions, which are additionally impacted by the difference in above ground vegetation in different cropping systems. We hypothesised seasonal changes in rainfall also impact soil microbial communities, subsequently effecting changes in GHG emissions, given the short response time of microbial communities to environmental changes (Andersen *et al.*, 2013).

2. Material and Methods

2.1 Study sites

The study sites are located in a single big peat dome in North Selangor, Malayasia. They are the largest peatlands in the state of Selangor with an area of 81,304 ha with the main peat soil areas comprising 2 protected forest reserves namely Raja Musa forest reserve, Sungai Karang forest reserve (Selangor State Forestry Department, 2014). The peat depth at the sites ranged from 1.3 to 6 m. The mean annual rainfall in NSPSF varies from 1359 mm to 2480 mm, peaking in October-November and driest in May-September (Global Environmental Centre, 2014). In the sampling periods during 2016-2017, it rained several times a week during wet season measurements, with rainfall in the region amounting for 442.9 mm, 270.8 mm and 482.5 mm for November 2016, December 2016 and January 2017 respectively (World Weathers Online, 2018), while it had rained only twice during the whole sampling period for

145 the dry season, with rainfall in the region accounting for 127.4 mm in July 2017 (World
146 Weathers Online, 2018)

147 The forest site (3°41'39.5"N 101°11'05.4"E) is located in the northern edge of Sungai Karang
148 forest reserve that received protection status in 1990 (Tonks, 2017). The site has not been
149 logged for at least last 40 years, but still contains old channels for timber extraction, many of
150 which are blocked today. The forest vegetation is composed of *Macaranga pruinosa* (Miq.)
151 Müll.Arg, *Campnosperma coriaceum* (Jack) Hallier f., *Blumeodendron tokbrai* (Blume)
152 Kurz, *Shorea platycarpa* F.Heim, *Parartocarpus venenosus* Becc., *Ixora grandiflora* Ker
153 Gawl, *Pternandra galeata* Ridl., *Stenoclaena palustris* (Burm. f.) Bedd., *Asplenium*
154 *longissimum* Baker, *Nephrolepsis biserrata* (Sw.) Schott, *Crytostachys sp., Cyperus rotundus*
155 L., and *Pandanus atrocarpus* Griff. (Yule and Gomez, 2009). The forest floor surface was
156 covered with leaf litter. There was no observable change in the physical environment above
157 ground such as vegetation, water level and leaf litter, at this site between wet season and dry
158 season sampling periods. All the other study sites are small-scale agricultural plantations in
159 Kampung Raja Musa village, located at the southern edge of Raja Musa forest reserve. Site
160 description and locations are given in Table 1, in the order of age of conversion from forest,
161 starting from 1st generation oil palm mono-cropping. Site pictures are given in Supplementary
162 information 1. All the smallholding agricultural plantations in the village are of similar size at
163 about 2 ha, that includes all the non-forest sites in this study. The sampling area in the forest
164 were larger than 2 ha, covering 6 different locations around the area shown in Fig.1.

165 2.2 Sampling strategy

166 Sampling was carried out during both the wet and dry season. The wet season sampling was
167 carried out during November 2016 to January 2017 and the dry season sampling was carried
168 out during July 2017. Each site was visited three times during each season. At each time,
169 samples were collected from 25 random points distributed over the site. Complete random

sampling as described in Dhandapani *et al.* (2019) was used over other sampling methods to quantify the impact of ecosystem or land-use type as a whole, opposed to identify any particular effects. At each sampling point, greenhouse gas measurements were taken and the surface peat (0-5 cm) samples were collected for laboratory analyses. This resulted in 150 independent sampling points per site, with 75 samples from each season. Of these, five random samples were taken from each visit for phospholipid fatty acid (PLFA) analysis and a different set of 10 random samples from each visit were used for CN analysis.

2.3 Peat analysis

All the procedures used for laboratory peat analysis were described Dhandapani *et al.* (2019). Peat temperature and moisture were measured *in situ*, using a digital thermometer from Fischer Scientific (Loughborough, UK) and a digital volumetric moisture meter, theta probe® (Delta-T Devices, Cambridge, UK) respectively. For some sampling times peat samples were collected for measuring gravimetric moisture due to failure of theta probe. For this fresh peat was dried in an oven at 105ºC for 48 hours. The gravimetric moisture was calculated as follows. Bulk density samples were collected by inserting a tube of known volume (20 ml) into the peat surface. The collected peat was then dried in an oven at 105ºC for 48 hours and the dry weight was recorded. The calculated gravimetric moisture was then converted to volumetric moisture using bulk density data.

For pH measurements, about 5 ml volume of peat sample was diluted in 10 ml deionised water in a centrifuge tube and shaken in a rotary shaker for 30 minutes. The pH of the supernatant was then measured using a pH meter (Mettler Toledo Leicester, UK).

Oven dried peat samples (105ºC for 48 h) were used to calculate the organic matter content. Dried peat samples were placed in silica crucibles and then transferred to a muffle furnace and maintained at 550ºC for 4 h. The organic matter content was then determined by

194 calculating the loss on ignition as follows, organic matter content (%) = [(weight of oven
195 dried soil – weight of ash) / weight of oven dried soil] ×100.

196 For analysing total C and N content, all samples were oven dried (105^{o}C for 48 h) and finely
197 ground using a ball mill. Approximately 10 mg of sample was weighed into a Al foil cup and
198 the exact weight was recorded. The samples were then transferred to an auto sampler on
199 Flash 2000 CHNS-O elemental analyser supplied by Thermo Scientific (Loughborough, UK)
200 to measure total C and N. The analyser was set at 55^{o}C oven temperature, with helium as the
201 carrier gas at the flow rate of 140 ml min^{-1}. L-aspartic acid supplied by Sigma Aldrich (St
202 Louis, USA) was used as quality control and peaty soil standard supplied by Elemental
203 Microanalysis (Okeham, UK) was used as a standard.

204 ## 2.4 Phospholipid fatty acid analysis

205 Microbial community phenotypic structure was determined by phospholipid fatty acid
206 (PLFA) analysis. PLFAs were extracted from replicate 1 g freeze-dried tropical peat samples
207 using a modification of the method described by (Frostegard et al., 1991). The lipids from
208 peat were extracted using Bligh & Dyer extraction (Bligh & Dyer, 1959). The extracted lipids
209 were then separated into neutral lipids, glycol lipids and polar lipids (containing
210 phospholipids) fractions using Megabond Elut® silica gel column. The extracted polar lipids
211 were then methylated by mild alkaline methanolysis and converted into fatty acid methyl
212 esters, which were then analysed using gas chromatography.

213 The dried fatty acid methyl esters were suspended in 200 µl of hexane, ready for GC
214 injection. One µl of each sample was injected into the GC in split-less mode. The column
215 used in the GC for phospholipid analysis was ‘ZB-FFAP’ column, supplied by
216 Phenomenex®. The column was 30 m length x 0.25 mm inner diameter x 0.25 µm film
217 thickness. The carrier gas was helium with the constant pressure of 18 psi. The initial oven

218 temperature in GC was 120°C; this was maintained for 1 min and then programmed to 250°C
219 at the rate of 5°C min^{-1}. The constant temperature of 250°C was maintained throughout the
220 run. The results were displayed as a chromatogram of retention times of the compounds and
221 the mass spectroscopy provides the ion profile of each compounds.

222 The fatty acids i15:0, a15:0, i16:0, i17:0, a17:0 were considered as Gram-positive biomarkers
223 (Wilkinson et al., 2002). The fatty acids 10me16:0 and 10me18:0 were described as the
224 biomarkers for actinomycetes (Wilkinson et al., 2002, Moore-Kucera & Dick, 2008), a group
225 that belongs to Gram-positive bacteria. The relative abundance of Gram-negative bacteria
226 were calculated using 16:1n9, 16:1n7, cyc17:0, 18:1n7 and cyc19:0 as biomarkers (Wilkinson
227 et al., 2002, Kaiser et al., 2010). 18:2n6 and 18:1n9 were used as fungal biomarkers (Vestal
228 & White, 1989, Wilkinson et al., 2002, Kaiser et al., 2010). 14:0, 16:0, 18:0, a17:1 and 20:0
229 were non-specific fatty acids (Wilkinson et al., 2002). The fatty acids with similar mass
230 spectrum 18:1n9 and 18:1n7 were differentiated with the help of neutral lipid fatty acid
231 analysis, by the findings that fungal biomarker 18:1n9 should have much higher NLFA/PLFA
232 ratio that the Gram-negative biomarker 18:1n7 (Baath, 2003).

233 ## 2.5 Greenhouse gas measurement

234 CO_2 and CH_4 emissions from soil surface were measured using a Los Gatos® (San Jose,
235 USA) ultraportable greenhouse gas analyser. The gas analyser works on the principle of laser
236 absorption spectroscopy. The instrument gives the readings of CH_4, CO_2 and moisture in ppm
237 and gas temperature. The measurements were made using closed chamber method using a
238 chamber with a height of 15 cm and the inner diameter of 13.5 cm. The chamber had an inlet
239 and an outlet port that were connected to the gas analyser, using a quarter inch outer diameter
240 polytetrafluoroethylene (PTFE) tube. During each measurement the chamber was carefully
241 inserted into an un-vegetated area of peat to approximately 1cm depth to provide a gas seal.
242 Gas measurements were taken at 20 second intervals for 5 minutes, resulting in at least 12

recorded measurement points for each plot. The first minute of each measurement was ignored allowing the gas flux to settle down after initial disturbance of placing the chambers. The gas measurements in ppm were converted to mg CO_2 m^{-2} hr^{-1} and µg CH_4 m^{-2} hr^{-1} for CO_2 and CH_4 respectively, as described in (Samuel and Evers, 2016), using the ideal gas law. PV=nRT. Where: P = atmospheric pressure; V = volume of headspace; n = number of moles (mol); R = universal Gas Constant law (8.314 J $K^{-1}mol^{-1}$) and T = temperature in kelvin (K), with conversion factor, 1 mol of CO_2 = 44.01g and 1 mol CH_4 = 16.02g. The change in gas concentration within the chamber (volume in cm^3) for every 20 second (converted to hour) measuring points, for soil surface area (m^2) covered, were fitted into a linear regression. The slope from the linear regression represents the gas flux in mg m^{-2} hr^{-1}.

2.6 Statistical analyses

All the statistical analyses were carried out using Genstat® 17^{th} edition (VSN international, 2017). The significance of differences between sites for greenhouse gas emissions and other environmental parameters were evaluated using linear mixed models with restricted maximum likelihood (REML) incorporating seasons and sites as fixed effects and individual visits as random effects. For the data sets that were not normally distributed, the data were log transformed. If the log transformed data were still not normally distributed, the data were power transformed, using Box Cox transformation.

Principal component analysis (PCA) was performed on PLFA data using Mol% normalised spectra and the correlation matrix. Resultant PCs were analysed by one way analysis of variance (ANOVA), to get standard error of differences and means for PCA plots. Relative abundance of individual microbial groups, and ratios between groups, were calculated and were subjected to statistical analysis using restricted maximum likelihood (REML) models, to identify the interactions of individual microbial groups with site, season and combination of

site and season. Similar REML were also performed for PCs. REML was carried out using 'site' and 'season' were used as fixed model

Backward stepwise multiple regression was performed with relative abundance of each individual microbial groups and ratios as response and other environmental parameters as fixed. Similar backward stepwise multiple regression was also performed with CO_2 as response variates. To meet the normality assumptions means of each visit were used to find correlations between CH_4 and other environmental parameters. Linear regression was also performed to predict CO_2 emissions at each individual site from the measured volumetric moisture. Backward stepwise multiple regression was also carried out to determine the relationship for CO_2 and CH_4 emissions with relative abundance of different microbial groups.

3. Results

3.1 Peat properties

The surface organic matter content in first generation oil palm plantation was significantly reduced by ~10% from the forest (Table 2, Fig. 2a), but was almost halved to 50% of forest levels in the 2nd generation oil palm mono-cropping. However, in 2nd generation systems, the cleared and pineapple intercropping sites maintained similar level of organic matter content as forest, while Yam intercropping site had similar level of organic content as 1st generation mono-cropping oil palm. No seasonal changes in organic matter content were observed in any of the sites (Table 2).

The first generation mono-cropping had the lowest moisture level of all sites at *ca.* 31%. All the 2nd generation systems maintained moisture levels that were significantly higher than 1st generation but lower than forest, except for pineapple intercropping site that had moisture level higher than the forest during wet season. Volumetric moisture significantly varied

between seasons and these seasonal changes were observed only in the 2nd generation agricultural systems. The changes in moisture content between seasons were higher with increasing age from conversion.

pH exhibited different trends between the two seasons resulting in significant interaction between site and season (Table 2, Fig.2c). During the wet season, forest and the 1st generation oil palm had similar pH, while pH were higher in all the 2nd generation cropping systems. During the dry season, pH at the 2nd generation mono-cropping was still the highest, however the cleared and pineapple intercropping sites had pH lower than that of the forest and 1st generation oil palm mono-cropping (Fig. 2c).

Peat surface temperatures were significantly higher at all agricultural sites compared to forest, (Fig. 2d, Table 2). Among the second generation sites, the cleared and yam intercropping sites maintained similar temperature level as 1st generation oil palm, while the pineapple intercropping and 2nd generation oil palm had lower surface temperatures in comparison, yet significantly higher than forest. During the dry season from the wet season, the temperature increased significantly at some agricultural sites but decreased in the forest and pineapple intercropping sites. Bulk density was significantly greater in all agricultural plantations than at forest, with highest bulk density observed in 2nd generation mono-cropping ($F_{(5,118)}$=45.1, $p<0.001$; Fig. 2e).

There was significant difference between sites in terms of C content ($F_{(5,54)}$=39.0, $p<0.001$), N content ($F_{(5,54)}$=25.47, $p<0.001$) and C:N ratio ($F_{(5,54)}$=8.41, $p<0.001$).. The forest and first generation oil palm site had similar level of C content at *ca.* 50% (Table 3). The C content was highest at >60% in cleared and pineapple intercropping sites, while it was lowest at the 2nd generation oil palm at *ca.* 25%. The nitrogen content was highest in forest at 2.5%, which was reduced to *ca.* 2% at the first generation oil palm. In second generation agricultural

systems, cleared and pineapple intercropping systems had higher nitrogen content than the 1st generation oil palm, but the 2nd generation oil palm had lowest nitrogen content at 0.8%. . C:N was lowest at the forest, which was increased in 1st generation oil palm plantations, and the ratio was further increased in all the 2nd generation cropping systems with the 2nd generation oil palm containing the highest C:N ratio at 32.

3.2 Peat microbial communities

3.2.1 Variations between sites across the seasons

PC1 and 2 collectively accounted for 39% of the variation (Fig. 3). There were no interactions between site and season for either PC1 and 2 (Table 4). Hence main effects of the treatments were considered directly. Both PC1 and 2 showed significant discrimination between sites, while only PC1 showed significant discrimination between seasons. PC1 separated the two seasons, and also separated the forest site from the agricultural sites within each season. PC2 separated yam intercropping site in both seasons, 2nd generation oil palm mono-cropping and pineapple intercropping in wet season from the rest of the sites. The loading for individual PLFAs associated with each of the PCs were generally dispersed, with no particular dominance of any single PLFA (Fig. 3b). A notable characteristic of the loadings bi-plot was the association of saturated fatty acids with discrimination of wet season sites from the dry season sites (Fig. 3b).

Overall, the microbial community structure was different in agricultural plantations from the forest. Two of the 2nd generation systems; cleared and pineapple intercropping, had similar microbial structures as the 1st generation oil palm, while the other two 2nd generation systems; yam intercropping and 2nd generation oil palm, had different microbial community structures both between each other, and also from the 1st generation oil palm

338 3.2.2 Microbial phenotypic structure

339 All of the studied sites were dominated by bacteria, which constituted more than 50% of the
340 microbial relative abundance. Including actinomycetes (sub group that belongs to Gram-
341 positive bacteria) to general Gram-positive bacterial relative abundance, Gram-positive
342 bacteria were the most abundant microbial group at all sites and seasons. The fungal relative
343 abundance was *ca*. 7 times lower than the bacterial relative abundance for most sites (Fig.
344 4a,c).

345 All the studied microbial groups except Gram-negatives, varied significantly between sites
346 (Table 5). Actinomycetes showed increased relative abundance in 1st generation oil palm
347 compared to forest. In the 2nd generation plantations, the actinomycetes relative abundance
348 were lowest in both intercropping sites, (Fig. 4a). Gram-positive relative abundance which
349 was highest at the forest, was reduced in the first generation oil palm. The 2nd generation sites
350 (i.e. cleared and pineapple intercropping) had similar Gram-positive relative abundance as the
351 first generation oil palm, while the other two second generation plantations had lower Gram-
352 positive relative abundance, with yam intercropping having the lowest Gram-positive relative
353 abundance of all sites. The fungal relative abundance were at similar levels (<10%) at all sites
354 except the 2nd generation oil palm, and yam intercropping sites where fungi had higher
355 relative abundance, with yam intercropping sites containing the highest fungal relative
356 abundance of all sites.

357 At all sites, the relative abundance of all the individual microbial groups were higher in the
358 dry season than in the wet season, except non-specific fatty acid group. The interaction
359 between site and season were statistically significant only for Gram-positive microbial group
360 (Table 5), as the Gram-positive relative abundance increased for the forest , 1st generation oil
361 palm, and pineapple intercropping in the dry season from the wet season, stayed at the same
362 level for cleared and 2nd generation oil palm and decreased for yam intercropping.

363 The site and seasonal variations in the ratio between fungi and bacteria (F:B) was driven by
364 the yam intercropping sites, while all the other sites had similar F:B ratio with no seasonal
365 variations (Fig. 4b). The F:B ratio was highest at the yam intercropping site and the ratio was
366 higher in the dry season than in the wet season within that site.

367 The ratio between Gram-positive and Gram-negative (G+:G-) bacterial groups varied
368 significantly between sites, driven by the two intercropping sites that had lower ratios than
369 other sites (Fig. 4c), while variation between seasons and the interaction between site and
370 season were insignificant (Table 5).

371 3.2.3 Microbial communities and environmental controls

372 Both bacterial and fungal relatively abundance were significantly related to changes in
373 temperature, with Gram-positive and Gram-negative groups showing negative correlation
374 while fungal relative abundance was positively correlated with temperature (Fig. 5a,b . Gram
375 negative microbial group were also positively correlated to pH and organic matter content.
376 Actinomycetes exhibited negative correlation with moisture (Fig. 5c). Gram-negative relative
377 abundance also responded, positively to pH and organic matter content ($F_{(3,55)}$= 5.48,
378 p=0.002, R^2=0.188).

379 Among the ratios, F: B responded positively to temperature [Regression data: F:B=-
380 0.29+0.015(temperature); ($F_{(1,58)}$=6.52, p=0.013, R^2= 0.086)] While, G+:G- responded
381 negatively to moisture and pH ($F_{(2,56)}$=3.99, p=0.024, R^2=0.093)].

382 ## 3.4 Greenhouse gas emissions

383 3.5.1 Variations between sites across the seasons

384 The CO_2 emissions were highest at the forest site at both seasons (949 and 971 mg m^2 hr^{-1}).
385 The variations between seasons, within the sites, increased with increasing age of conversion
386 from forest (Fig. 6a, Table 2). During the wet season, 1st generation oil palm site had the

lowest emissions at 603 mg m^2 hr^{-1}. The cleared site and second generation intercropping sites maintained similar level of CO_2 emissions as 1st generation oil palm, while the 2nd generation oil palm mono-cropping had higher emissions closer to the emissions in forest. However, during the dry season the CO_2 emissions from the second generation oil palm mono-cropping reduced to less than half of the wet season CO_2 emissions and had the lowest value of all sites in the dry season. Reduction in CO_2 emissions during dry season was also observed in other 2nd generation agriculture sites, while forest and 1st generation oil palm maintained their respective CO_2 emissions in dry season. For dry season, the CO_2 emissions were significantly lower in the 2nd generation cropping systems.

CH_4 emissions were under 1 mg m^{-2} hr^{-1} in all sites during both seasons (Fig. 6b), nevertheless CH_4 emissions varied significantly between sites, between seasons, with significant interaction between site and season (Table 2). The forest site absorbed CH_4 during both seasons, while the first generation oil palm mono-cropping emitted similar low amount of CH_4. Among the 2nd generation agricultural systems, cleared and 2nd generation oil palm maintained similar lower level of CH_4 emissions as the 1st generation oil palm mono-cropping, while both yam and pineapple intercropping sites emitted higher amount of CH_4. Wet season CH_4 emissions were higher than dry season CH_4 emissions for all sites. The wet season emission for pineapple intercropping site at 497 µg m^{-2} hr^{-1} was considerably higher than the rest of the sites, which were all under 50 µg m^{-2} hr^{-1}. However, during the dry season, the CH_4 emissions were drastically reduced at pineapple intercropping, with emission values lower than the yam intercropping site at 11.4 µg m^{-2} hr^{-1}. The second generation oil palm mono-cropping had the least variations between seasons for CH_4 emissions.
No statistically significant relationship was identified between the changes in microbial community structure and GHG emissions.

411 3.4.1 GHG emissions and environmental controls

412 Overall, CO_2 emissions responded negatively to moisture and temperature, and responded
413 positively to pH and organic matter content ($F_{(4,799)}$= 11.45, $p<0.001$, R^2 =0.049). Linear
414 regression between CO_2 emissions and moisture for each individual site showed that moisture
415 was a significant predictor of logCO_2 in all sites except yam intercropping site (Fig. 7). While
416 for most sites, logCO_2 was negatively correlated with moisture, 2nd generation oil palm
417 plantations exhibited positive correlation between moisture and logCO_2.

418 CH_4 emissions responded positively to moisture and temperature ($F_{(2,32)}$=12.39, $p<0.001$,
419 R^2=0.401).Plotting of CH_4 against moisture showed exponential curve, with wet season
420 measurements in pineapple intercropping showing exponentially increased CH_4 emissions
421 with increased moisture (Fig. 8a). If the wet season pineapple site was removed from the
422 model, moisture was no more a significant predictor of CH_4, however CH_4 showed a positive
423 linear relationship to temperature (Fig. 8b).

424 # 4. Discussion

425 Agriculture in peatlands clearly had a significant impact on peat physico-chemical
426 characteristics and organic content, and the impacts were greatest in progressive generations
427 of oil palm mono-cropping with greatest loss of surface organic matter and C content. The
428 intercropping sites maintained similar surface organic matter content as the forest site and
429 total surface C content was higher in some 2nd generation agricultural sites, possibly due to
430 the use of fire to clear the previous generation plantations (Turetsky *et al.*, 2015). Higher
431 organic matter content and low bulk density are the most important and defining properties
432 for peat classification (FAO, 2018) and it should be noted that those properties were most
433 affected by prolonged oil palm mono-cropping, indicating potential declassification of these
434 ecosystems due to oil palm mono-cropping. However, intercropping systems appear to

ameliorate this damage by having more diverse litter input and greater vegetation cover throughout the agricultural land. This is in line with observations from other tropical soil systems where intercropping maintained improved soil physico-chemical characteristics compared to mono-culture (Zhigang *et al.*, 2015; Chen *et al.*, 2019).

These two crucial changes in peat properties directly and indirectly influenced other ecosystem properties and functions. One example of functional change was from the 2nd generation mono-cropping site that had severe changes in moisture content between seasons, and exhibited moisture limitation to CO_2 emissions (Fig. 7), which is common in dry mineral soil ecosystems (Chen *et al.*, 2002; Werner *et al.*, 2006) and unusual for tropical peatlands of any land-use (Jauhiainen *et al.*, 2005; Couwenberg *et al.*, 2010; Hergoualc'h *et al.*, 2017; Sangok *et al.*, 2017; Wakhid *et al.*, 2017). The surface peat were coarser in older generation plantations with greater bulk density, which may not retain as much water as light, fibrous and organic peat in forest during the times of low rainfall (Campos *et al.*, 2011). Increase in bulk density up to an intermediate level is expected to linearly increase the water retention capacity of soil, but further compression would result in linear reduction in moisture content (Archer and Smith, 1973). It is plausible that peat soil in the 2nd generation mono-cropping had reached the compression threshold and did not retain moisture in dry season that had very low rainfall. However the 2nd generation intercropping systems maintained relatively higher moisture in dry season, owing to lower bulk density and management practices that reduce the severity of drainage in agricultural systems such as less number of drainage ditches in the field. In addition, the intercropping systems are known to enhance soil water distribution and be more efficient in water usage (Wu *et al.*, 2016; Chen *et al.*, 2018), which might have also contributed to higher moisture level in intercropping relative to the mono-cropping systems. This confirms our first set of hypotheses that peat properties are altered in oil palm plantations compared to forest, and predict that peat properties such as organic matter

content, moisture content, bulk density, pH and temperature are progressively affected more from 1st to 2nd generation cropping systems, while intercropping ameliorated such damage to peat properties.

In spite of lower surface C content in forest than in some agricultural sites, C:N ratio was lowest in the forest. Increased N inputs possibly via biological N fixation in the forest may be associated with observed increased methane absorption at the site, as the two processes are biologically related in peatlands (Larmola *et al.*, 2014; Vile *et al.*, 2014). The higher N content in forest may be further aided by N addition through leaf litter in the forest site (Ong *et al.*, 2017). This C:N ratio also influenced the changes in microbial community structure. The difference in microbial phenotypic structure between forest and the agricultural plantations was characterised by decrease in Gram-positive relative abundance at all agricultural plantations, and increase in fungal relative abundance in some 2nd generation cropping systems. The increased Gram-positive relative abundance may be due to higher nitrogen content in the forest site (Balser, 2001; Liu *et al.*, 2015). Similarly lower N content also affected higher fungal relative abundance in yam and 2nd gen oil palm, as N limitation affects bacterial communities (Zhang *et al.*, 2016). The difference in C:N ratio also explains the distinction in microbial community structure shown by PCA (Fig. 2a), between the cluster containing 1st generation oil palm, cleared and pineapple intercropping (C:N =25-30, Table 3), and the other two 2nd generation agricultural sites such as yam intercropping and 2nd generation oil palm (C:N>30, Table 2).

The other peat characteristics such as pH and temperature also influenced the ecosystem functions, though intercropping had relatively lower amelioration effect on these peat properties. For example, the agricultural plantations had higher surface peat temperature due to open canopy in younger plantations and less complex canopy in mature oil palm plantations (Sheldon *et al.*, 2010). This increased temperature favoured fungal communities,

while reducing both the Gram-negative and Gram-positive bacterial PLFAs (Fig. 4). Higher temperature were also observed to favour fungi over bacteria in boreal peatlands (Thormann *et al.*, 2004). The combination of higher temperature, lower N content and relatively drier environment might be the cause behind higher F:B ratio in yam intercropping site than other sites, as bacteria are more dependent on N content and are less favourable to drier conditions (Bossuyt *et al.*, 2001; Fierer *et al.*, 2009; Zhang *et al.*, 2016). Higher pH generally tends to favour bacteria over fungi (Zhang *et al.*, 2016), though the pH was slightly higher in yam intercropping site than at other sites, it was still very acidic (ca. 3.5) and did not have major impact on the F:B ratio. The conversion of forest to oil palm plantations were known to increase pH in both peat and mineral soils (Tripathi *et al.*, 2012; Tonks *et al.*, 2017; Wood *et al.*, 2017), however the response of the soil microbial communities to this change in pH were different between these systems, as Gram-negative relative abundance increased with forest conversion and increasing pH in tropical peatlands (Fig. 5), while in tropical mineral soil system, Gram-negative relative abundance decreased with disturbance (Bossio *et al.*, 2005; Krashevska *et al.*, 2015). This validates part of our second hypothesis that the changes in peat properties correlates with changes in microbial community structure.

The changes in microbial community structure with land-use change has been observed before in different tropical and temperate systems (Bossio *et al.*, 2005; Krashevska *et al.*, 2015; Szoboszlay *et al.*, 2017), however a more intriguing novel finding in this study is that the effect of seasonality on tropical peat microbial community structure was greater than the effect of land-use change. This seasonal change was presumably driven by flooding and the response of microbial PLFAs with higher abundance of straight chain saturated fatty acids (Bossio and Scow, 1998), which are of non-specific origin (Wilkinson *et al.*, 2002). Mono unsaturated (*18:1n7, 18:1n9 & 16:1n9*) fatty acids that are associated with aerobic conditions (Li *et al.*, 2006) were abundant in dry season, adding further evidence to the contribution of

510 flooding to the seasonal variations in microbial community structure. Thus, validating part of
511 our third hypothesis that the microbial community structure were affected by seasonal
512 changes.

513 CH_4 emissions were very low and were under 1 mg m^{-2} hr^{-1} at all the studied sites, which is in
514 the range observed in previous studies showing similar low level emissions in SEA peatlands
515 (Inubushi *et al.*, 2003; Melling *et al.*, 2005; Couwenberg *et al.*, 2010). The forest site in
516 Malaysian peatlands absorbed CH_4, contradicting the results observed in neotropical
517 peatlands, where high productivity systems emitted higher amount of CH_4 (Winton *et al.*,
518 2017). However, previous studies have shown that CH_4 emissions in neotropics were
519 generally higher than that of SEA peatlands (Couwenberg *et al.*, 2010; Sjögersten *et al.*,
520 2014; Girkin *et al.*, 2018). This might be due to the differences between the neotropical and
521 SEA peatlands in microbial communities and above ground vegetation, that have influence
522 on GHG emissions through root exudation and substrate composition (Troxler *et al.*, 2012;
523 Girkin *et al.*, 2018), also the secondary forests in the site was historically drained for logging.
524 Higher CH_4 emissions in pineapple intercropping site during the wet season directly
525 coincides with the standing water at this site. The increase in CH_4 emissions with increasing
526 temperature in tropical peatlands was consistent with previous observations (Melling *et al.*,
527 2005; Aben *et al.*, 2017). This is reflected by higher CH_4 emissions in pineapple
528 intercropping site with higher temperature and wetter conditions. The changes in moisture in
529 other sites, where the water table were below surface, did not significantly alter or influence
530 CH_4 emissions. Methanogenic archaea were found to be abundant at 30-40 cm below water
531 level (Galand *et al.*, 2002; Lin *et al.*, 2014), leading to a plausible explanation that the water
532 table above surface, made the methanogenic communities become active and abundant closer
533 to the surface and rhizosphere in pineapple intercropping site during the wet season.
534 Conversely, higher methane oxidation in the forest site is in complement with Jackson *et al.*

(2009)'s finding that the methanogenic bacterial communities were completely absent at the top 50 cm of surface peat in North Selangor peat swamp forest. However the same study found phyla containing methanotrophs such as Proteobacteria and Verrucomicrobia in North Selangor peatlands, plausibly contributing to the methane oxidation in the forest site.

The results show that total CO_2 emissions were lower in the agricultural plantations irrespective of the generation of the plantations. However total CO_2 comprises both autotrophic root respiration and heterotrophic microbial respiration (Hergoualc'h and Verchot, 2011). The root respiration does not contribute to the C loss as it is part of the plants' photosynthetic cycle, while heterotrophic respiration decomposes peat that is stored over ages (Dariah *et al.*, 2014). The autotrophic contribution from a dense secondary peat forest was observed to be >50% of the total CO_2 emissions (Murdiyarso *et al.*, 2017), but the autotrophic component was almost non-existent at a cleared site and about half of the sampling points in other agricultural sites were away from vegetation. Therefore, it is highly likely that heterotrophic contribution from the forest is about 50% of the total emission while for 1st generation oil palm it is >70% and for all the 2nd generation plantations it is >80% of their respective total emissions, owing to the age of the oil palm in each plantations (Dariah *et al.*, 2014; Comeau *et al.*, 2016; Hergoualc'h *et al.*, 2017; Matysek *et al.*, 2017; Murdiyarso *et al.*, 2017). Considering this, C loss through CO_2 emissions were in the similar range (*ca.* 400-500 mg CO_2 m^{-2} hr^{-1}) for all the studied sites. However C addition to peatlands through aboveground vegetation is much higher in natural forest than in the agricultural landscapes like oil palm plantations (Guillaume *et al.*, 2016), which results in net C accumulation in forested peatlands (Page *et al.*, 2006). Additionally, it had been found that leaf litter from some natural peatland tree species are more resistant to microbial decomposition, resulting in organic matter accumulation and peat formation (Yule and Gomez, 2009). Whereas, homogenous litter in agricultural land uses are easily degradable (Kerdraon *et al.*, 2017) and

presumably lack the chemical and physical properties required for the formation of peat, and with low water levels, the already stored C is gradually decomposed and lost. The above postulation is supported by our observations and various other observations in oil palm mono-cropping, indicating the complete lack of humus or leaf litter layer (Bruhl and Eltz, 2010; Fayle *et al.*, 2010). This is also evident in our results showing that organic matter content through loss on ignition and total C, were reduced to half that of the other studied sites in 2nd generation mono-cropping.

5 Conclusions

Tropical peat characteristics are significantly altered by oil palm agriculture relative to forested forms. Such changes in peat characteristics were also significantly correlated with peat microbial community structure and GHG emissions. Defining peat properties such as organic matter content and bulk density were most affected by prolonged mono-cropping. Though intercropping systems had distinctively higher CH_4 emissions, they were very low and relatively insignificant in comparison to CO_2 emissions. Higher CO_2 emissions in forest is plausibly due to a higher proportion of root respiration to the total respiration in forest than in other scarcely-planted agricultural plantations, and thus does not imply higher carbon loss via gas emissions in forested peatlands. Overall the damage to peat properties and loss of C was greatest in the 2nd generation of mono-cropping, which also exhibited unusual moisture limitation to decomposition in peatlands, while the intercropping systems maintained most of the forest peat organic content and caused relatively lesser damage to other peat properties such as pH, moisture and bulk density, with relatively higher seasonal stability.

ACKNOWLEDGEMENTS

583 This work was supported by Crops For the Future (CFF), Malaysia [BioP1-011] and the
584 School of Biosciences, University of Nottingham, UK. We thank Dr Robert Linforth for
585 assistance with gas chromotography, and other lab technicians in Agriculture and
586 Environmental Sciences Division at the University of Nottingham. We are thankful to Dr Jim
587 Craigon for help with experimental design and statistics. We would also like to thank Dr
588 Mark Pawlett and lab technicians at Cranfield University for help with setting up PLFA lab
589 procedure. We are thankful to Selangor State Forestry Department, GEC Malaysia and the
590 local villagers in Kampung Raja Musa. Marshall Kana Samuel assisted with gas flux
591 calculations, and thanks to Din (forest ranger) and Martha Ledger for some in-field
592 assistance. Thanks to Chloe Brown for providing us with site map.

593

Figure Captions

Figure 1: Site location

Figure 2: Effect of site and season upon (a) organic matter content, (b) moisture, (c) pH, (d) temperature and (e) bulk density between different study sites during wet (black) and dry (grey) season. Bars denote mean values (1a-d: n<75; 1e: n=10) and whiskers denote standard errors. Note 1st gen OP denotes 1st generation oil palm monocropping, yam denotes, 2nd generation oil palm and yam intercropping, pineapple denotes 2nd generation oil palm and pineapple intercropping, 2nd gen OP denotes 2nd generation oil palm mono-cropping.

Figure 3: Effects of site and season upon phenotypic structure of soil microbial communities determined by PLFA analysis, as shown by principal component (PC) analysis. (a) ordination of PC1 and 2 and (b) associated loadings for individual PLFAs. For (a), points denote means (n=5), whiskers denote standard errors. Note F denotes forest site, 1st OP denotes 1st generation oil palm mono-cropping site, C denoted cleared site, yam denotes 2nd generation oil palm and yam intercropping site, PA denotes 2nd generation oil palm and pineapple intercropping sites, and 2nd OP denotes 2nd generation oil palm monocropping site.

Figure 4: Effects of site and season upon a) relative abundance of different microbial groups as determined by PLFA analysis, (b) the difference in ratio of the relative abundance of fungi to bacteria (F:B) between different study sites, (c) the difference in ratio of the realtive abundance of Gram-positive to Gram-negative bacteria (G+:G-) between different study sites. Bar denotes mean values (n=5), and whiskers denote standard errors. Note 1st gen OP denotes 1st generation oil palm mono-cropping, yam denotes, 2nd generation oil palm and yam intercropping, pineapple denotes 2nd generation oil palm and pineapple intercropping, 2nd gen OP denotes 2nd generation oil palm mono-cropping.

Figure 5: Relationship between (a) Gram-positive relative abundance (Mol%) and temperature, (b) Fungal relative abundance (Mol%) and temperature, (c) Actinomycetes relative abundance (Mol%) and moisture. Points denote all circmstances of site and season combinations. Significant regression lines and their equations, R^2, F and p values are reported in the figures.

Figure 6: Effects of site and season upon (a) CO_2 emissions, (b) CH_4 emissions between different study sites during wet (black) and dry (grey) season. Bars denote mean values (n<75) and whiskers denote standard errors.

Figure 7: Relationship between log CO_2 and moisture at (a) forest site, (b) 1st generation oil palm mono-cropping site (1st gen OP), (c) cleared site, (d) pineapple intercropping site, (e) 2nd generation oil palm mono-cropping site (2nd gen OP).

Figure 8: Relationship between CH_4 emissions and (a) moisture, (b) temperature. Points denote mean value of each sampling occasion (n=24-30). Note that for (b) wet season visits for pineapple intercropping site (PA-wet) was left out of the regression equation.

Tables

Table 1: Site description

Site	Co-ordinates	Oil palm age in Years	No. of drainage ditches	Notable characteristics (wet season)	Observable changes between sampling seasons (dry season)
1st generation oil palm monocropping (1st gen OP)	3°25'25.8"N 101°20'12.9" E	15	1	Abundant understorey vegetation, dead wood from previous land use, uneven surface with hollows and hammocks	None
Cleared	3°25'23.9"N 101°20'09.0" E	0	2	Lime trees were planted in the midst of wet season measurements. Cleared oil palm trees were stacked in rows and left along the site.	Lime trees were killed off and oil palm were planted before dry season measurement . Most of the surface was covered by grass.
2nd generation oil palm and yam intercropping (Yam intercropping)	3°25'22.7"N 101°18'46.7" E	1	0	Oil palms planted in rows with ample space in between, where four to six rows of yam were planted.	New pineapple crop in the open areas. New smaller yam saplings in place of the older harvested yam.
2nd generation oil palm and pineapple intercropping (Pineapple intercropping)	3°25'20.6"N 101°19'56.6" E	1-2	0	There were stagnant water on most part of the site during the wet season measurements. Some area without standing water were covered with grass	Pineapple plants were fully grown and provided full ground cover. No stagnant water at the surface.

2nd generation oil palm monocropping (2nd gen OP)	3°24'51.3"N 101°19'42.7" E	3-5	0	1st generation oil palm trees were killed off chemically and still standing on the site. Surface was covered with brown grass and green algae under the shades of young oil palm	No grass or algal cover in the surface

636

637

638

639 Table 2. Linear mixed model (REML) for environmental parameters, showing statistical

640 significance of the effects of site, season and the interactions between site and season.

641 Statistically significant figures are presented in bold.

642

	Site	**Season**	**Site*season**
Organic matter %	$F_{(5,835.3)}$=485,***p<0.001***	$F_{(1,4)}$=0.23,p=0.658	$F_{(5,835.9)}$=2.19,p=0.053
pH	$F_{(5,836.5)}$=35.4,***p<0.001***	$F_{(1,4)}$=1.26,p=0.325	$F_{(5,837)}$=15,***p<0.001***
Moisture	$F_{(5,887.2)}$=124,***p<0.001***	$F_{(1,4)}$=8.26,***P<0.05***	$F_{(5,887.2)}$=15.2,***p<0.001***
Temperature	$F_{(5,879.2)}$=180,***p<0.001***	$F_{(1,4)}$=0.20,p=0.681	$F_{(5,879.3)}$=9.2,***P<0.001***
CO_2	$F_{(5,845.1)}$=37.8,***p<0.001***	$F_{(1,3.9)}$=80.3,***p<0.001***	$F_{(5,843.2)}$=12.5,***p<0.001***
CH_4	$F_{(5,861.8)}$=27.5,***P<0.001***	$F_{(1,3.8)}$=37.5,***p<0.005***	$F_{(5,854.6)}$=6.7,***p<0.001***

643

644

Table 3. Total C, N and C:N under different sites at surface layers (n=10). Note 1st gen OP denotes 1st generation oil palm mono-cropping, yam denotes, 2nd generation oil palm and yam intercropping, pineapple denotes 2nd generation oil palm and pineapple intercropping, 2nd gen OP denotes 2nd generation oil palm mono-cropping.

Site	C %	N %	C:N
Forest	48.9 ±1.29	2.47 ±0.11	19.8 ±0.81
1st gen OP	51 ±1.4	1.97 ±0.06	26 ±1.01
Cleared	64.1 ±2.53	2.13 ±0.19	30 ±2.505
Yam	46.3 ±2.91	1.49 ±0.07	31 ±1.42
Pineapple	60.2 ±2.36	2.27 ±0.16	26.5 ±1.9
2nd gen OP	26.4 ±1.65	0.83 ±0.07	32 ±1.67

651 Table 4. Linear mixed model (REML) for principal component scores, showing statistical
652 significance of the effects of site, season and the interaction between site and season.
653 Statistically significant figures are presented in bold.

	PC1	**PC2**
Site	$F_{(5,48)}$= 7.53, p=0.138	$F_{(5,48)}$= 3.81, ***p<0.005***
Season	$F_{(1,48)}$= 65.64, ***P<0.001***	$F_{(1,48)}$= 3.91, p=0.054
Site*Season	$F_{(5,48)}$= 1.77, p=0.138	$F_{(5,48)}$= 0.53, p=0.753

654
655
656

Table 5. Linear mixed model (REML) for aggregated PLFA data with respect to microbial groups, showing statistical significance of the effects of site, season and the interactions between site and season. Statically significant figures are presented in bold.

	Site	**Season**	**Site*season**
Non-specific	$F_{(5,48)}$=5.34,***p<0.001***	$F_{(1,48)}$=55.08,***p<0.001***	$F_{(5,48)}$=2.23,p=0.066
Fungi	$F_{(5,48)}$=4.90,***p=0.001***	$F_{(1,48)}$=11.45,***p=0.001***	$F_{(5,48)}$=0.79,p=0.561
Gram-negative	$F_{(5,48)}$=1.65,p=0.165	$F_{(1,48)}$=2.90,p=0.095	$F_{(5,48)}$=1.45,p=0.222
Gram-positive	$F_{(5,48)}$=8.37,***p<0.001***	$F_{(1,48)}$=7.52,***p=0.009***	$F_{(5,48)}$=3.06,***p=0.018***
Actinomycetes	$F_{(5,48)}$=10.44,***p<0.001***	$F_{(1,48)}$=1.11,p=0.297	$F_{(5,48)}$=1.47,p=0.218
F:B	$F_{(5,48)}$=5.93,***p<0.001***	$F_{(1,48)}$=4.84,***p=0.033***	$F_{(5,48)}$=0.87,P=0.509
G+:G-	$F_{(5,48)}$=3.85,***p=0.005***	$F_{(1,48)}$=0.23,p=0.637	$F_{(5,48)}$=1.41,p=0.238

663 **REFERENCES:**

664 Aben, R.C.H., Barros, N., van Donk, E., Frenken, T., Hilt, S., Kazanjian, G., Lamers, L.P.M.,
665 Peeters, E., Roelofs, J.G.M., Domis, L.N.D., Stephan, S., Velthuis, M., Van de Waal, D.B.,
666 Wik, M., Thornton, B.F., Wilkinson, J., DelSontro, T., Kosten, S., 2017. Cross continental
667 increase in methane ebullition under climate change. Nat. Commun. 8, 8.

668 Andersen, R., Chapman, S.J., Artz, R.R.E., 2013. Microbial communities in natural and
669 disturbed peatlands: A review. Soil Biol. Biochem. 57, 979-994.

670 Aneja, M.K., Sharma, S., Fleischmann, F., Stich, S., Heller, W., Bahnweg, G., Munch, J.C.,
671 Schloter, M., 2006. Microbial Colonization of Beech and Spruce Litter—Influence of
672 Decomposition Site and Plant Litter Species on the Diversity of Microbial Community.
673 Microb. Ecol. 52, 127-135.

674 Archer, J.R., Smith, P.D., 1973. The relation between bulk density, available water capacity
675 and air capacity of soils. J. Soil Sci. 23, 475–480. J. Terramechan. 10, 61.

676 Azhar, B., Lindenmayer, D.B., Wood, J., Fischer, J., Manning, A., McElhinny, C., Zakaria,
677 M., 2011. The conservation value of oil palm plantation estates, smallholdings and logged peat
678 swamp forest for birds. Forest Ecol. Manag. 262, 2306-2315.

679 Azhar, B., Puan, C.L., Zakaria, M., Hassan, N., Arif, M., 2014. Effects of monoculture and
680 polyculture practices in oil palm smallholdings on tropical farmland birds. Basic Appl. Ecol.
681 15, 336-346.

682 Azhar, B., Saadun, N., Puan, C.L., Kamarudin, N., Aziz, N., Nurhidayu, S., Fischer, J., 2015.
683 Promoting landscape heterogeneity to improve the biodiversity benefits of certified palm oil
684 production: Evidence from Peninsular Malaysia. Glob. Ecol. Conserv. 3, 553-561.

685 Balser, T.C., 2001. The impact of long-term nitrogen addition on microbial community
686 composition in three Hawaiian forest soils. The Scientific World Journal 1, 500-504.

687 Bossio, D.A., Girvan, M.S., Verchot, L., Bullimore, J., Borelli, T., Albrecht, A., Scow, K.M.,
688 Ball, A.S., Pretty, J.N., Osborn, A.M., 2005. Soil microbial community response to land use
689 change in an agricultural landscape of Western Kenya. Microb. Ecol. 49, 50-62.

690 Bossio, D.A., Scow, K.M., 1998. Impacts of carbon and flooding on soil microbial
691 communities: Phospholipid fatty acid profiles and substrate utilization patterns. Microb. Ecol.
692 35, 265-278.

693 Bossuyt, H., Denef, K., Six, J., Frey, S.D., Merckx, R., Paustian, K., 2001. Influence of
694 microbial populations and residue quality on aggregate stability. App. Soil Ecol. 16, 195-208.

695 Bruhl, C.A., Eltz, T., 2010. Fuelling the biodiversity crisis: species loss of ground-dwelling
696 forest ants in oil palm plantations in Sabah, Malaysia (Borneo). Biodivers. Conserv. 19, 519-
697 529.

698 Campos, J.R.D., Silva, A.C., Fernandes, J.S.C., Ferreira, M.M., Silva, D.V., 2011. Water
699 retention in a peatland with organic matter in different decomposition stages. Rev. Bras. Cienc.
700 Solo 35, 1217-1227.

701 Chen, C., Liu, W., Wu, J., Jiang, X., Zhu, X., 2019. Can intercropping with the cash crop help
702 improve the soil physico-chemical properties of rubber plantations? Geoderma 335, 149-160.

703 Chen, G., Kong, X., Gan, Y., Zhang, R., Feng, F., Yu, A., Zhao, C., Wan, S., Chai, Q., 2018.
704 Enhancing the systems productivity and water use efficiency through coordinated soil water
705 sharing and compensation in strip-intercropping. Sci Rep 8, 10494.

706 Chen, X.Y., Eamus, D., Hutley, L.B., 2002. Seasonal patterns of soil carbon dioxide efflux
707 from a wet-dry tropical savanna of northern Australia. Aust. J. Bot. 50, 43-51.

708 Chung, A.Y.C., Eggleton, P., Speight, M.R., Hammond, P.M., Chey, V.K., 2000. The diversity
709 of beetle assemblages in different habitat types in Sabah, Malaysia. Bull. Entomol. Res. 90,
710 475-496.

711 Comeau, L.-P., Hergoualc'h, K., Hartill, J., Smith, J., Verchot, L.V., Peak, D., Salim, A.M.,
712 2016. How do the heterotrophic and the total soil respiration of an oil palm plantation on peat
713 respond to nitrogen fertilizer application? Geoderma 268, 41-51.

714 Couwenberg, J., Dommain, R., Joosten, H., 2010. Greenhouse gas fluxes from tropical
715 peatlands in south-east Asia. Global Change Biology 16, 1715-1732.

716 Cusack, J., 2011. Characterising small mammal responses to tropical forest loss and
717 degradation in northern Borneo using capture-mark-recapture methods. Imperial College
718 London, London, p. 81.

719 Dariah, A., Marwanto, S., Agus, F., 2014. Root- and peat-based CO2 emissions from oil palm
720 plantations. Mitig. Adap. Strat. Global Change 19, 831-843.

721 Davidson, E.A., Trumbore, S.E., Amundson, R., 2000. Biogeochemistry - Soil warming and
722 organic carbon content. Nature 408, 789-790.

723 Dislich, C., Keyel, A.C., Salecker, J., Kisel, Y., Meyer, K.M., Auliya, M., Barnes, A.D., Corre,
724 M.D., Darras, K., Faust, H., Hess, B., Klasen, S., Knohl, A., Kreft, H., Meijide, A.,
725 Nurdiansyah, F., Otten, F., Pe'er, G., Steinebach, S., Tarigan, S., Tolle, M.H., Tscharntke, T.,
726 Wiegand, K., 2017. A review of the ecosystem functions in oil palm plantations, using forests
727 as a reference system. Biol. Rev. 92, 1539-1569.

728 Dohong, A., Aziz, A.A., Dargusch, P., 2017. A review of the drivers of tropical peatland
729 degradation in South-East Asia. Land Use Pol. 69, 349-360.

730 Faruk, A., Belabut, D., Ahmad, N., Knell, R.J., Garner, T.W.J., 2013. Effects of Oil- Palm
731 Plantations on Diversity of Tropical Anurans. Conserv. Biol. 27, 615-624.

732 Fayle, T.M., Turner, E.C., Snaddon, J.L., Chey, V.K., Chung, A.Y.C., Eggleton, P., Foster,
733 W.A., 2010. Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy,
734 epiphytes and leaf-litter. Basic Appl. Ecol. 11, 337-345.

735 Fierer, N., Strickland, M.S., Liptzin, D., Bradford, M.A., Cleveland, C.C., 2009. Global
736 patterns in belowground communities. Ecol. Lett. 12, 1238-1249.

737 Galand, P.E., Saarnio, S., Fritze, H., Yrjala, K., 2002. Depth related diversity of methanogen
738 Archaea in Finnish oligotrophic fen. Fems Microbiol. Ecol. 42, 441-449.

739 Girkin, N.T., Turner, B.L., Ostle, N., Craigon, J., Sjögersten, S., 2018. Root exudate analogues
740 accelerate CO2 and CH4 production in tropical peat. Soil Biol. Biochem. 117, 48-55.

741 Global Environmental Centre, G., 2014. Integrated Management Plan for North Selangor Peat
742 Swamp Forest 2014-2023 for Selangor State Forestry Department. p. 183.

743 Guillaume, T., Holtkamp, A.M., Damris, M., Brümmer, B., Kuzyakov, Y., 2016. Soil
744 degradation in oil palm and rubber plantations under land resource scarcity. Agric. Ecosyst.
745 Environ. 232, 110-118.

746 Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A.,
747 Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L.,
748 Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest
749 cover change. Science 342, 850-853.

750 Hergoualc'h, K., Verchot, L.V., 2011. Stocks and fluxes of carbon associated with land use
751 change in Southeast Asian tropical peatlands: A review. Global Biogeochem. Cycles 25, 13.

752 Hergoualc'h, K., Verchot, L.V., 2014. Greenhouse gas emission factors for land use and land-
753 use change in Southeast Asian peatlands. Mitig. Adapt. Strat. Glob. Chang, 19, 789-807.

754 Hergoualc'h, K., Hendry, D.T., Murdiyarso, D., Verchot, L.V., 2017. Total and heterotrophic
755 soil respiration in a swamp forest and oil palm plantations on peat in Central Kalimantan,
756 Indonesia. Biogeochemistry 135, 203-220.

757 Inubushi, K., Furukawa, Y., Hadi, A., Purnomo, E., Tsuruta, H., 2003. Seasonal changes of
758 CO2, CH4 and N2O fluxes in relation to land-use change in tropical peatlands located in coastal
759 area of South Kalimantan. Chemosphere 52, 603-608.

760 Jackson, C.R., Liew, K.C., Yule, C.M., 2009. Structural and Functional Changes with Depth
761 in Microbial Communities in a Tropical Malaysian Peat Swamp Forest. Microb. Ecol. 57, 402-
762 412.

763 Jauhiainen, J., Takahashi, H., Heikkinen, J.E.P., Martikainen, P.J., Vasander, H., 2005. Carbon
764 fluxes from a tropical peat swamp forest floor. Glob. Chang. Biol. 11, 1788-1797.

765 Jin, H., Sun, O.J., Liu, J., 2010. Changes in soil microbial biomass and community structure
766 with addition of contrasting types of plant litter in a semiarid grassland ecosystem. J Plant Ecol
767 3, 209-217.

768 Kerdraon, D., Drewer, J., Slade, E., Sayer, E., 2017. From forest to oil palms, the effect of
769 forest on soil carbon dynamics in Borneo. Ecology Across Borders, Ghent, Belgium.

770 Krashevska, V., Klarner, B., Widyastuti, R., Maraun, M., Scheu, S., 2015. Impact of tropical
771 lowland rainforest conversion into rubber and oil palm plantations on soil microbial
772 communities. Biol. Fertil. Soils 51, 697-705.

773 Larmola, T., Leppänen, S.M., Tuittila, E.-S., Aarva, M., Merilä, P., Fritze, H., Tiirola, M.,
774 2014. Methanotrophy induces nitrogen fixation during peatland development. Proc. Natl.
775 Acad. Sci. 111, 734-739.

776 Li, W.H., Zhang, C.B., Jiang, H.B., Xin, G.R., Yang, Z.Y., 2006. Changes in Soil Microbial
777 Community Associated with Invasion of the Exotic Weed, Mikania micrantha H.B.K. Plant
778 and Soil 281, 309-324.

779 Lin, X.J., Tfaily, M.M., Steinweg, M., Chanton, P., Esson, K., Yang, Z.K., Chanton, J.P.,
780 Cooper, W., Schadt, C.W., Kostka, J.E., 2014. Microbial community stratification linked to
781 utilization of carbohydrates and phosphorus limitation in a boreal peatland at Marcell
782 experimental forest, Minnesota, USA. Appl. Environ. Microbiol. 80, 3518-3530.

783 Liu, L., Gundersen, P., Zhang, W., Zhang, T., Chen, H., Mo, J.M., 2015. Effects of nitrogen
784 and phosphorus additions on soil microbial biomass and community structure in two reforested
785 tropical forests. Sci Rep 5, 10.

786 Lo, J., Parish, F., 2013. Peatlands and Climate Change in Southeast Asia. Global Environment
787 Centre, Selangor, Malaysia.

788 Luskin, M.S., Potts, M.D., 2011. Microclimate and habitat heterogeneity through the oil palm
789 lifecycle. Basic Appl. Ecol. 12, 540-551.

790 Matysek, M., Evers, S., Samuel, M.K., Sjogersten, S., 2017. High heterotrophic CO2 emissions
791 from a Malaysian oil palm plantations during dry-season. Wetl. Ecol. Manag.

792 Melling, L., Hatano, R., Goh, K.J., 2005. Methane fluxes from three ecosystems in tropical
793 peatland of Sarawak, Malaysia. Soil Biol. Biochem. 37, 1445-1453.

794 Miettinen, J., Hooijer, A., Tollenaar, D., Malins, C., Vernimmen, R., Shi, C., Liew, S.C., 2012.
795 Historical Analysis and Projection of Oil Palm Plantation Expansion on Peatland in Southeast
796 Asia. International Council on Clean Transportation, Washington DC.

797 Miettinen, J., Liew, S.C., 2010. degradation and development of peatlands in peninsular
798 malaysia and in the islands of Sumatra and Borneo since 1990. Land Degrad. Dev. 21, 285-
799 296.

800 Miettinen, J., Shi, C.H., Liew, S.C., 2016. Land cover distribution in the peatlands of
801 Peninsular Malaysia, Sumatra and Borneo in 2015 with changes since 1990. Glob. Ecol.
802 Conserv. 6, 67-78.

803 Mohd Kusin, F., Akhir, N.I.M., Mohamat-Yusuff, F., Awang, M., 2015. The impact of nitrogen
804 fertilizer use on greenhouse gas emissions in an oil palm plantation associated with land use
805 change. Atmósfera 28, 243-250.

806 Murdiyarso, D., Saragi-Sasmito, M.F., Rustini, A., 2017. Greenhouse gas emissions in restored
807 secondary tropical peat swamp forests. Mitig. Adapt. Strateg. Glob. Chang.

808 Norwana, A.A.B.D., Kunjappan, R., Chin, M., Schoneveld, G., Potter, L., Andriani, R., 2011.
809 The local impacts of oil palm expansion in Malaysia; An assessment based on a case study in
810 Sabah state. CIFOR, Bogor, Indonesia.

811 Oertel, C., Matschullat, J., Zurba, K., Zimmermann, F., Erasmi, S., 2016. Greenhouse gas
812 emissions from soils—A review. Chemie der Erde - Geochemistry 76, 327-352.

813 Ong, C.S.P., Joon, C.J., Yule, C.M., 2017. The contribution of leaching to nutrient release from
814 leaf litter of two emergent tree species in a Malaysian tropical peat swamp forest.
815 Hydrobiologia 794, 125-137.

816 Page, S.E., Rieley, J.O., Banks, C.J., 2011. Global and regional importance of the tropical
817 peatland carbon pool. Glob. Chang. Biol. 17, 798-818.

818 Page, S.E., Rieley, J.O., Wüst, R., 2006. Chapter 7 Lowland tropical peatlands of Southeast
819 Asia. In: Martini, I.P., Martínez Cortizas, A., Chesworth, W. (Eds.), Developments in Earth
820 Surface Processes. Elsevier, pp. 145-172.

821 Parish, F., Sirin, A., Charman, D., Joosten, H., MInayeva, T., Silvius, M., Stringer, L., 2008.
822 Assessment on peatlands, biodiversity and climate change. Global Environment Centre and
823 Wetlands International, Selangor, Malaysia and Wageningen, The Netherlands.

824 Rashid, A.H.A.M., Hamzah, K.A., Joseph, K.T., 2013. Land use change in Malaysia. Reports
825 from the technical panels of the 2nd green house gas. Roundtable on Sustainable palm oil.

826 Samuel, M.k., Evers, S., 2016. Tropical peatland carbon emissions from oil palm plantations
827 microsites. 15th international peat congress, Kuching, Malaysia.

828 Sangok, F.E., Maie, N., Melling, L., Watanabe, A., 2017. Evaluation on the decomposability
829 of tropical forest peat soils after conversion to an oil palm plantation. Sci, Total Environ. 587-
830 588, 381-388.

831 Schrier-Uijl, A.P., Silvius, M., Parish, F., Lim, K., Rosediana, S., Anshari, G., 2013.
832 Environmental and social impacts of oil palm cultivation on tropical peat - a scientific review.
833 Roundtable on Sustainable Palm Oil.

834 Schrier-Uijl, A.P., Veraart, A.J., Leffelaar, P.A., Berendse, F., Veenendaal, E.M., 2011.
835 Release of CO2 and CH4 from lakes and drainage ditches in temperate wetlands.
836 Biogeochemistry 102, 265-279.

837 Sheldon, F.H., Styring, A., Hosner, P.A., 2010. Bird species richness in a Bornean exotic tree
838 plantation: A long- term perspective. Biol. Conserv. 143, 399-407.

839 Sjögersten, S., Black, C.R., Evers, S., Hoyos-Santillan, J., Wright, E.L., Turner, B.L., 2014.
840 Tropical wetlands: A missing link in the global carbon cycle? Glob. Biogeochem. Cycles 28,
841 1371-1386.

842 Sjögersten, S., Cheesman, A.W., Lopez, O., Turner, B.L., 2011. Biogeochemical processes
843 along a nutrient gradient in a tropical ombrotrophic peatland. Biogeochemistry 104, 147-163.

844 Szoboszlay, M., Dohrmann, A.B., Poeplau, C., Don, A., Tebbe, C.C., 2017. Impact of land-use
845 change and soil organic carbon quality on microbial diversity in soils across Europe. FEMS
846 Microbiol. Ecol. 93, fix146-fix146.

847 Tonks, A.J., Aplin, P., Beriro, D.J., Cooper, H., Evers, S., Vane, C.H., Sjogersten, S., 2017.
848 Impacts of conversion of tropical peat swamp forest to oil palm plantation on peat organic
849 chemistry, physical properties and carbon stocks. Geoderma 289, 36-45.

850 Tripathi, B.M., Kim, M., Singh, D., Lee-Cruz, L., Lai-Hoe, A., Ainuddin, A.N., Go, R., Rahim,
851 R.A., Husni, M.H.A., Chun, J., Adams, J.M., 2012. Tropical Soil Bacterial Communities in
852 Malaysia: pH Dominates in the Equatorial Tropics Too. Microb. Ecol. 64, 474-484.

853 Troxler, T.G., Ikenaga, M., Scinto, L., Boyer, J.N., Condit, R., Perez, R., Gann, G.D., Childers,
854 D.L., 2012. Patterns of soil bacteria and canopy community structure related to tropical
855 peatland development. Wetlands 32, 769-782.

856 Turetsky, M.R., Benscoter, B., Page, S., Rein, G., van der Werf, G.R., Watts, A., 2015. Global
857 vulnerability of peatlands to fire and carbon loss. Nat. Geosci. 8, 11-14.

858 Vile, M.A., Kelman Wieder, R., Živković, T., Scott, K.D., Vitt, D.H., Hartsock, J.A., Iosue,
859 C.L., Quinn, J.C., Petix, M., Fillingim, H.M., Popma, J.M.A., Dynarski, K.A., Jackman, T.R.,
860 Albright, C.M., Wykoff, D.D., 2014. N2-fixation by methanotrophs sustains carbon and
861 nitrogen accumulation in pristine peatlands. Biogeochemistry 121, 317-328.

Wakhid, N., Hirano, T., Okimoto, Y., Nurzakiah, S., Nursyamsi, D., 2017. Soil carbon dioxide emissions from a rubber plantation on tropical peat. Sci. Total Environ. 581-582, 857-865.

Werner, C., Zheng, X.H., Tang, J.W., Xie, B.H., Liu, C.Y., Kiese, R., Butterbach-Bahl, K., 2006. N2O, CH4 and CO2 emissions from seasonal tropical rainforests and a rubber plantation in Southwest China. Plant Soil 289, 335-353.

Wilkinson, S.C., Anderson, J.M., Scardelis, S.P., Tisiafouli, M., Taylor, A., Wolters, V., 2002. PLFA profiles of microbial communities in decomposing conifer litters subject to moisture stress. Soil Biol. Biochem. 34, 189-200.

Winton, R.S., Flanagan, N., Richardson, C.J., 2017. Neotropical peatland methane emissions along a vegetation and biogeochemical gradient. PLOS ONE 12, e0187019.

Wood, S.A., Gilbert, J.A., Leff, J.W., Fierer, N., D'Angelo, H., Bateman, C., Gedallovich, S.M., Gillikin, C.M., Gradoville, M.R., Mansor, P., Massmann, A., Yang, N., Turner, B.L., Brearley, F.Q., McGuire, K.L., 2017. Consequences of tropical forest conversion to oil palm on soil bacterial community and network structure. Soil Biol. Biochem. 112, 258-268.

World Weathers Online, 2018. Kuala Selangor Historical Weather. Accessed from https://www.worldweatheronline.com/kuala-selangor-weather-history/selangor/my.aspx.

Wu, J., Liu, W., Chen, C., 2016. Can intercropping with the world's three major beverage plants help improve the water use of rubber trees? J Appl. Ecol. 53, 1787-1799.

Xu, J.R., Morris, P.J., Liu, J.G., Holden, J., 2018. PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. Catena 160, 134-140.

Yule, C.M., 2010. Loss of biodiversity and ecosystem functioning in Indo-Malayan peat swamp forests. Biodivers. Conserv. 19, 393-409.

884 Yule, C.M., Gomez, L.N., 2009. Leaf litter decomposition in a tropical peat swamp forest in
885 Peninsular Malaysia. Wetl. Ecol. Manag. 17, 231-241.

886 Zhang, B., Deng, H., Wang, H.-l., Yin, R., Hallett, P.D., Griffiths, B.S., Daniell, T.J., 2010.
887 Does microbial habitat or community structure drive the functional stability of microbes to
888 stresses following re-vegetation of a severely degraded soil? Soil Biol. Biochem. 42, 850-859.

889 Zhang, Q., Wu, J.J., Yang, F., Lei, Y., Zhang, Q.F., Cheng, X.L., 2016. Alterations in soil
890 microbial community composition and biomass following agricultural land use change. Sci
891 Rep 6, 10.

892 Zhigang, W., Bao, X.-G., Li, X., Jin, X., Zhao, J., Sun, J.-H., Christie, P., Li, L., 2015.
893 Intercropping maintains soil fertility in terms of chemical properties and enzyme activities on
894 a timescale of one decade.

895

896

897