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Abstract

Oil palm is the fastest expanding equatorial crop, and is one of the biggest threats to carbon-rich tropical peatlands in Malaysia. Smallholder plantations cover a vast area of peatlands in Peninsular Malaysia and follow varied cropping systems. Here we analyse the impacts of specific crops and the effects of proximity to such crops, upon GHG emissions from the soil, and the soil microbial community phenotype. We found that only mature oil palm plants in 1st generation oil palm mono-cropping potentially had significant autotrophic contributions to total CO_2 emissions with 33.5% increase in locations closer to mature oil palm stems. The sampling locations closer to younger oil palms and other crops did not significantly increase total CO_2 emissions. CH_4 emissions were significantly greater for sampling locations near plants with adventitious root system such as yam and pineapple crops. However CH_4 emissions were very low in comparison to CO_2 emissions, and their contribution to carbon loss was limited in these sites. Surface peat microbial community structure was unaffected by proximity to different crops within each cropping system, possibly due to a lack of influence of rhizosphere in the surface peat layers (0-5 cm). The results suggest that most of the total CO_2 emissions from these agro-ecosystems contribute to C loss due to microbial decomposition of the peat soil, unlike greater autotrophic contributions to total emissions in forested peatlands reported in other studies. Hence without appropriate above-ground vegetation or hydrology conducive to peat formation, ancient carbon stored in these peatlands is gradually lost into the atmosphere via greater heterotrophic respiration under agricultural management on such peat-based ecosystems.

Keywords: Histosols, Microbial phenotypic community structure, GHG emissions, oil palm plantations, intercropping, tropical peatlands.

1. Introduction

Peatlands are formed because of primary production exceeding microbial decomposition of such produced material, resulting in accumulation of partially-decomposed plant organic matter (DAF, 2009; Miettinen et al., 2012; Parish et al., 2008). Peatlands cover about 2.85% of the global land surface area (Xu et al., 2018), yet store one third of the total global soil carbon pool (Hapsari et al., 2017). Though most peatlands are located in the northern hemisphere, there is a considerable cover of these carbon rich ecosystems in the tropics, which store 18% of total global peat carbon (Hapsari et al., 2017; Strack, 2008), most of which are in South East Asia (Dohong et al., 2017). Hydrology is a major driving factor in the formation of tropical peatlands, inhibiting aerobic decomposition by reducing oxygen availability (Parish et al., 2008; Wösten et al., 2008). Drainage of peatlands for agriculture and logging have severely affected the South East Asian peatlands and their functions in recent decades (Couwenberg et al., 2010).

Agricultural expansion, especially oil palm plantation, remains one of the biggest threats to Malaysian forests including peatlands (Lo and Parish, 2013; Tan et al., 2009). Oil palm is native to west Africa and was first introduced to Malaysia as an ornamental plant in 1875 (Abdullah et al., 2009). The commercial plantations started in the early 20th century on a smaller scale, and these have grown extensively at an industrial scale over recent decades, to the extent that Malaysia is currently the second largest producer of palm oil in the world, and has the greatest deforestation rate in the 21st century globally (Abdullah et al., 2009; Hansen et al., 2013; Strack, 2008). The peatlands are usually drained and completely cleared of forest vegetation to establish oil palm plantation, effecting carbon loss above-ground with loss of dense and large vegetation structures (Bruhl and Eltz, 2010; Luskin and Potts, 2011; ; Tonks et al., 2017; Dhandapani et al., 2019b). Though most of the rapid expansion in last few

decades has been via industrial plantations, there is also considerable cover of smallholder plantations in Malaysia (Miettinen et al., 2016), particularly in Peninsular Malaysia, where about half of the managed peatlands are smallholder scale (Miettinen et al., 2016). Smallholder plantations follow different cropping systems depending on local needs, and vary greatly in intensity compared to industrial plantations (Azhar et al., 2011). Furthermore, smallholders often practice intercropping and multiple cropping with oil palm. The functions of undisturbed peatlands are significantly altered by disturbance into secondary forested peatlands (Dhandapani et al., 2019b) .The conversion of secondary forest peatlands to oil palm plantations were known to further increase pH, reduce C stocks, and alter peat physico-chemical properties through increased decomposition, causing some irreversible damage to the ecosystem services provided by them (Tonks et al., 2017). Though intercropping systems were known to ameliorate such damage to peat properties (Dhandapani et al., 2019a), individual influence of the oil palm and intercrops on peat properties, peat microbial phenotypic structure and GHG emissions are virtually unknown.

Varied cropping systems result in an increased diversity in aboveground vegetation, which is known to impact temporal and spatial variations in soil respiration (Han et al., 2014; Johnson et al., 2008). Plants also induce rhizosphere microbial communities to a habitat, often with cell densities that are greater than the cell density of the root system itself (Mendes et al., 2013), which could possibly impact GHG emissions from soil. Increased diversity in vegetation aboveground can also diversify the carbon sources that are available for microbial decomposition, thus potentially affecting both microbial community composition and activity (Blagodatskaya and Anderson, 1998), which could in turn affect GHG emissions. Multiple cropping systems generate varied patches of microclimate, with high habitat heterogeneity that creates uncertainty in the estimation of GHG emissions from a habitat (Azhar et al., 2015; Han et al., 2014). Therefore, understanding the rhizosphere influence of different plants

on total GHG emissions is crucial to evaluate the environmental impacts of these different cropping systems followed in tropical peatlands.

Total soil respiration is composed of autotrophic root respiration, and microbial decomposition through heterotrophic activity (Hergoualc'h et al., 2017). Root respiration does not contribute to C loss, and often contributes to a larger portion of total emissions measured in ecosystems with dense and large trees such as tropical peat swamp forests (Hergoualc'h and Verchot, 2011; Murdiyarso et al., 2010). Oil palm has a fibrous root systems that is divided into primary, secondary, tertiary and quaternary roots (Dariah et al., 2014). The root density decreases with increasing distance from the stem (Dariah et al., 2014) and the majority of roots are present within the first 60 cm from the surface (Mutert, 1999). The contribution of the oil palm rhizosphere to total soil respiration was observed to be dependent on the age of the oil palm plants with increased autotrophic contribution with greater age of oil palm (Dariah et al., 2014). There are a few, albeit limited, number of studies on autotrophic and heterotrophic components of GHG emissions from oil palm plantations, but the microbial communities associated with the variability in GHG emissions between bulk soil and rhizosphere remain unexplored.

To address this knowledge gap, we studied two intercropping systems, and two mono-cropping systems of two different ages and generations to evaluate the influence of the proximity of plants on surface peat characteristics, GHG emissions and microbial community structure. We hypothesised that the environmental parameters, GHG emissions and surface peat microbial community structure are contingent on the nearby vegetation and its age within a cropping system, due to the influence of such vegetation on microclimate, carbon substrate supply, and associated rhizosphere microbial communities. We also hypothesised there would be increased GHG emissions near the crops due to increased contribution from root respiration.

2 Materials and Methods

2.1 Study sites

2.1.1 First generation oil palm mono-cropping site

The oil palm monocropping site (3°25'25.8"N 101°20'12.9"E) was located adjacent to Raja Musa forest reserve on the southern edge of the North Selangor peatlands. Indicative views of all sampled sites are shown in Supplementary information 1. The oil palm plantations were about 15 years old. The site borders other oil palm plantations which were abandoned for forest regeneration inside Raja Musa protected forest reserve. A drainage ditch, running down the middle, divided the site into two halves. The site had a sizeable cover of understorey vegetation, predominantly ferns. There was abundant decaying dead wood of non-oil palm plants on the site. There were some dead cut stems of other plants and trees of previous land use, visibly protruding from the surface. There was no observable change in the physical environment such as vegetation, surface flooding etc., at this site between wet season and dry season sampling periods. This site is denoted as '1st gen OP' hereafter.

2.1.2 Second generation oil palm mono-cropping site

This young oil palm site (3°24'51.3"N 101°19'42.7"E) was located in Kampung Raja Musa village. The plantation itself is second generation, 3-5 years old. The first generation oil palm trees were killed off chemically and were still standing on the site. Most of the site surface was covered with dead, dried and brown grass. During the wet season, there were green algal growths on the surface under the shade of young oil palm trees.

During the dry season measurements, most of the grass on surface was cleared and there was no algal growth on the surface. This site is denoted as '2nd gen OP' hereafter.

2.1.3 Second generation oil palm and pineapple intercropping

The oil palm and pineapple intercropping site (3°25'20.6"N 101°19'56.6"E) in Kampung Raja Musa consisted of *circa* one year-old oil palm plants in rows with pineapple planted densely

between the oil palm rows. There were two drainage ditches along the border on either side of the site, but none within the site. There was stagnant water over most of the site during the wet season measurements. Some open regions without any stagnant water were covered with grass. During dry season measurements, the pineapple plants were fully grown and covered any remaining open spaces between pineapple rows and there was no stagnant water at the surface. The site is denoted as ‘pineapple intercropping’ hereafter.

2.1.4 Second generation oil palm and yam intercropping site

The oil palm and yam intercropping site (3°25'22.7"N 101°18'46.7"E) was a site containing one year-old oil palms planted in rows with ample space in between, where four to six rows of yams were planted. There was a cleared open space between each of the paired yam and oil palm rows. The surface of the site was relatively dry and flat with numerous dead oil palm roots of the previous generation of plantation. The edge of the site was cropped with pineapple plants in the available spaces in between yam and oil palm rows.

During the dry season, yam crops were harvested and a new pineapple crop was planted in the open areas. The pineapple crop was newly planted and presumably the root structures were in their preliminary stage. There were smaller yam saplings in place of the older harvested yam. The site is denoted as ‘yam intercropping’ hereafter, for both wet and dry season results.

2.2 Sampling strategy

Sampling was carried out during both the wet and dry seasons, as described in Dhandapani et al. (2019a); Dhandapani et al. (2019b). The wet season sampling was carried out during November 2016 to January 2017 and the dry season sampling was done during July 2017. Each site was visited three times during each season. At each time, samples were collected from 25 random points distributed over the site, and proximity to neighbouring plants were

noted. At each sampling point, greenhouse gas measurements were taken and soil samples were collected for laboratory analyses.

The sampling locations within a site were represented depending on whether they were proximal or distant from a plant. The notation used here is 'P' for proximal with subscript explaining the neighbouring plant, followed by the distance from the plant, and 'D' for sampling location distant from plants. A sampling location was considered distant, when the location was >3 m away from mature oil palm for 1st generation oil palm monocropping, >2.5 m away from nearest oil palm in 2nd generation oil palm monocropping, and >1.5 m away from nearby crops for both the intercropping sites. Hence oil palm, yam and pineapple were denoted in subscripts as P_{OP}, P_{YA}, $P_{PA,}$ respectively. The proximal distances were prescribed as <1 m and <2.5 m for young and mature oil palm respectively, and <30 cm for yam and pineapple, the former concomitant with Matysek et al. (2017) and Dariah et al. (2014), and the latter we considered as an appropriate scale for these plants. For the second generation oil palm site, some of the measurements were taken proximal to dead standing oil palm tree trunks and hence were denoted '$P_{OPD<1m}$'. For phospholipid fatty acid (PLFA) analysis (see below), 3 random samples were chosen from the wet season sampling period for each sampling location within each site.

2.3 Greenhouse gas measurements

CO_2 and CH_4 emissions from soil surface were measured using a Los Gatos (San Jose, California, USA) ultraportable greenhouse gas analyser as described in Dhandapani et al (2019a, 2019b). The gas analyser works on the principle of laser absorption spectroscopy and gives readings of CH_4 and CO_2 ppm as well as gas temperature. The measurements were made using closed chamber method using a chamber with a height of 15 cm and the inner diameter of 13.5 cm. The chamber had an inlet and an outlet port that were connected to the gas analyser, using a 6.35 mm outer diameter polytetrafluoroethylene (PTFE) tube. During

each measurement about 1 cm of the chamber was carefully inserted into the ground until it was sealed to the ground surface, and gas measurements were taken for 5 minutes. There was no surface vegetation in any of the measurement points. The gas analyser was set to record gas flux every 20 seconds, 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 (8.314J. $K^{-1}mol^{-1}$) and T = temperature in kelvin (K), with conversion factor, 1 mol of CO_2 = 44.01g and 1 mol CH_4 = 16.02g.

2.4 Soil properties

Soil temperature and moisture were measured *in situ*, using a digital thermometer from Fischer Scientific® and a theta probe® digital volumetric moisture meter, respectively. 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 Mettler Toledo® pH meter. Oven dried peat samples 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 550^{o}C for 4 hours. The organic matter content was then determined by the loss on ignition as follows, organic matter content (%) = [(weight of oven dried soil – weight of ash) / weight of oven dried soil] ×100.

2.5. PLFA Analysis

2.5.1 PLFA extraction

Microbial community phenotypic structure was determined by phospholipid fatty acid (PLFA) analysis. The surface peat samples collected from the field using hand trowel, were stored in the Ziplock bags, transported to local university campus for freeze drying. PLFAs were extracted from replicate 1 g freeze-dried tropical peat samples using a modification of the method described by Frostegard et al. (1991). The lipids from peat were extracted using Bligh & Dyer extraction (Bligh and Dyer, 1959). The extracted lipids were then separated into neutral lipids, glycol lipids and polar lipids (containing phospholipids) fractions using Megabond Elut® silica gel column supplied by Agilent (Santa Clara, USA). The extracted polar lipids were then methylated by mild alkaline methanolysis and converted into fatty acid methyl esters, which were then analysed using gas chromatography.

2.5.2 Gas chromatography and peak identification

The dried fatty acid methyl esters were suspended in 200 µl of hexane, ready for GC injection. One µl of each sample was injected into the GC in split-less mode. The column used in the GC for phospholipid analysis was 'ZB-FFAP' column, supplied by Phenomenex (Torrance, USA). The column was 30 m length x 0.25 mm inner diameter x 0.25 µm film thickness. The carrier gas was helium with a constant pressure of 18 psi. The initial oven temperature in GC was 120°C; this was maintained for 1 min and then programmed to 250°C at the rate of 5°C min^{-1}. The constant temperature of 250ºC was maintained throughout the run. The results were displayed as a chromatogram of retention times of the compounds and the mass spectroscopy provides the ion profile of each compounds.

The fatty acids were represented by a fatty acid shorthand, showing the number of carbon atoms, followed by the number of double bonds separated by colon. The position of the double bond is defined by the letter 'n' followed by the number of carbons from the methyl

end of the fatty acid molecule. The prefixes ‘i’ and ‘a’ were used to represent isomers and anti-isomers. 10me indicates a methyl group on the 10th carbon atom from the carboxyl end of the molecule. The prefix cyc refers to cyclopropyl fatty acids. The fatty acids i15:0, a15:0, i16:0, i17:0, a17:0 were considered as Gram-positive biomarkers (Wilkinson et al., 2002). The fatty acids 10me16:0 and 10me18:0 were described as the biomarkers for actinomycetes (Wilkinson et al., 2002, Moore-Kucera & Dick, 2008), a group that belongs to Gram-positive bacteria. The relative abundances of Gram-negative bacteria were calculated using 16:1n9, 16:1n7, cyc17:0, 18:1n7 and cyc19:0 as biomarkers (Kaiser et al., 2010; Wilkinson et al., 2002). 18:2n6 and 18:1n9 were used as fungal biomarkers (Kaiser et al., 2010; Vestal and White, 1989; Wilkinson et al., 2002). 14:0, 16:0, 18:0, a17:1 and 20:0 were non-specific fatty acids (Wilkinson et al., 2002). The fatty acids with similar mass spectra 18:1n9 and 18:1n7 were differentiated with the help of neutral lipid fatty acid analysis, by the findings that fungal biomarker 18:1n9 should have much greater NLFA/PLFA ratio that the Gram-negative biomarker 18:1n7 (Baath, 2003). The ratio of cyclopropane fatty acids (cyc17:0& cyc19:0) to their monoeionic precursors (16:1n7 & 18:1n7) and the ratio of total saturated fatty acids (14:0, 16:0, 18:0, 20:0) to mono-unsaturated fatty acids (16:1n9, 16:1n7, a17:1n, 18:1n9, 18:1n7) were used indicators of stress and other ecological conditions (Bossio and Scow, 1998).

2.6 Statistical analyses

All the statistical analyses were carried out using Genstat 17th edition. The significance of differences between sites for greenhouse gas emissions, other environmental parameters, microbial relative abundance and PLFA ratios were evaluated using linear mixed models with restricted maximum likelihood (REML). To meet normality assumptions for the data that were not normally distributed, log transformation was used. If the log transformed data was not normally distributed, Boxcox transformation was used. 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).

3. Results

3.1 CO_2 emissions

With respect to the difference between CO_2 emissions with respect to distance from the plants, sampling location within each site was significant only at the 1st generation oil palm mono-cropping and yam intercropping sites. In the 1st generation oil palm site, CO_2 emissions at $P_{OP<2.5m}$ were greater than the CO_2 emissions further away at D (Fig. 1 & Table 1). In the yam intercropping site, CO_2 emission were greatest in $P_{YA<30cm}$ and lowest in $P_{PA<30cm}$, while the CO_2 emissions did not significantly vary between $P_{OP<1m}$ and D in that site.

3.2 CH_4 emissions

CH_4 emissions differed with respect to proximity to crop plants within each site sampling location except for 1st generation oil palm site (Fig. 2 and Table 1). For 2nd generation oil palm site, $P_{OP<1m}$ absorbed CH_4 during both seasons, while the other sampling locations emitted similar smaller amounts of CH_4. CH_4 emissions within pineapple intercropping was greatest at $P_{PA<30cm}$ followed by $P_{OP<1m,}$ while CH_4 emissions at D were near zero. CH_4 emissions within the yam intercropping site was greatest at $P_{YA<30cm}$, and the variations between other Sampling locations were insignificant. As for CO_2 emissions, planting of a new pineapple crop during the dry season did not affect CH_4 emissions over the short term.

3.3 Peat characteristics

Organic matter contents varied only slightly, albeit statistically significantly, between the sampling locations in all studied sites (Table 1 & 2). For 1st generation oil palm $P_{OP<2.5m}$ had lower organic matter content than D. For 2nd generation oil palm, organic matter content was

greatest at $P_{OPD<1m,}$ followed by $P_{OP<2m}$ and then D. For pineapple intercropping, organic matter content lower in $P_{PA<30cm}$ than at other sampling locations. For yam intercropping, organic matter content was greatest at $P_{OP<1m}$ and lowest at $P_{YA<30cm}$.

The changes in moisture between the sampling locations was significant only for the 1st generation oil palm mono-cropping, here $P_{OP<2.5m}$ had lower moisture than D.

The variations in pH between the sampling locations were significant for all sites except the pineapple intercropping site, where pH was about 3 for all sampling locations. For 1st generation oil palm, pH was greater in $P_{OP<2.5m}$ than D. For 2nd generation oil palm, pH was greater near the dead oil palm at $P_{OPD<1m}$, while the other sampling locations had a similar pH. For the yam intercropping site, the significant difference was because of greater pH at $P_{YA<30}$ cm, while all the other sampling locations had a similar pH. Temperature was significantly different between the sampling locations only for yam intercropping site, due to greater temperature in D and $P_{PA<30cm}$ region.

3.4 Microbial phenotypic community structure

In the PCA of the PLFA profiles, PC1 and 2 collectively accounted 44% of the total variance (Fig. 3). PC1 showed significant discrimination between sampling locations ($F_{(10,32)} = 3.13$, $p=0.012$), while PC2 did not significantly discriminate sampling locations ($F_{(10,32)}= 1.21$, $p=0.335$). However the discrimination by PC1 was predominantly associated with sampling locations from one site i.e., 1st gen OP, which contained higher proportion of actinomycete biomarkers (10me18:0 and 10me16:0) along with the bacterial fatty acids i16:0 and cyc19:0. The rest of the PLFAs were generally dispersed near zero or on the positive side of the PC1 graph. Other than the above with respect to sampling locations from 1st gen OP, there were no other distinct groupings or discrimination of sampling locations and related PLFAs. However, PCA for different sites strongly reinstated the significant discrimination between

1st gen OP and the rest of the second generation cropping systems (Supplementary information 2).

The relative abundance of PLFAs did not significantly differ between sampling locations within each site for all the identified microbial groups, fungal: bacterial or stress ratios (cyc:pre, sat:mono) (Table 3). All of the studied sites were dominated by Gram-positive bacterial PLFAs, with very high total relative abundance of bacterial PLFAs to fungal PLFAs (Fig. 4). The fungi:bacteria ratio were around 0.1 for all the sampling locations in all sites (Fig. 5), while the Gram+:Gram- ratio was between 1.5 and 2 for all the 2nd generation cropping systems, and around 2.5 for 1st gen OP (Fig. 5).

4. Discussion

4.1 Effect of plant proximity on CO_2 emissions

CO_2 emissions were significantly influenced by proximity to oil palms only for the cropping system that had mature oil palm trees. The CO_2 emissions at $P_{OP<2.5m}$ was 33.5% greater than the CO_2 emission at D, which is in the similar range to the 32.5% autotrophic contribution reported in 14 year old 1st generation oil palm plantations in Peninsular Malaysia (Matysek et al., 2017). However, it was slightly greater than the 29% autotrophic contribution reported by Dariah et al. (2014) under 15 year-old oil palm plantations in Indonesia. It should be noted that there was no difference in CO_2 emissions between the measurements made near the recently dead oil palm trees, $P_{OPD<2m}$ and other areas in the 2nd generation oil palm mono-cropping site, potentially showing the significant contribution of autotrophic root respiration from mature oil palm trees is instantaneously reduced after the death of mature oil palms. Nonetheless, the second generation mono-cropping site also had oil palm plants about 5 years old, and their possible autotrophic contribution to the total soil respiration was not significant enough to make a difference in total CO_2 emissions near the young palm trees. Indeed,

Dariah et al. (2014) concluded that autotrophic respiration from 6 year-old oil palm plants contributed only about 14% of the total respiration. This is strikingly different from the results of Hergoualc'h et al. (2017) which showed autotrophic emissions from a 6 year old plantation contributed 39% to the total CO_2 emissions.

Yam is tuber crop with an adventitious rooting system preceded by a temporary seminal or tubercular rooting system (Charles-Dominique et al., 2009). The yam plants in our study were mature during wet season measurements, and the dry season measurements were made when the older yam plants were harvested and replaced with new younger plants, possibly containing the temporary seminal or tubercular rooting system. The root length density of yam plants are usually low with a maximum of 0.25 cm cm^{-3}. The root system can grow as far as 5 m horizontally and up to 40 cm depth (O'Sullivan, 2008), however Hgaza et al. (2012) did not find any roots at 15-30 cm depth at a distance of 50 cm from yam plant. The contribution of yam root respiration to total soil respiration has not been studied before, but our study has demonstrated that they make a significant contribution to total CO_2 emissions, with about 23.4% increase in CO_2 emissions than what is observed in sampling locations further than 1.5 m away from the crops at 'D'.

Pineapple root systems are adventitious and shallow and can grow well beyond the length of the associated canopy (DHA, 2008). A single plant can produce about 450 main roots, which do not regenerate if damaged (DAF, 2009). The shallow root system can grow up to 1- 2 m long and about 0.85 m deep (DHA, 2008). The pineapple intercropping system in our study was densely planted and none of the $P_{OP<1m}$ and D, measurements were more than 1 m distant from a mature pineapple plant. It is possible that all the measuring points had some influence of pineapple root respiration. The oil palm plants in the pineapple intercropping were less than a year old and possible contribution of their root respiration was presumably minimal.

Though the CO_2 emissions from $P_{OP<1m}$ and distant sampling locations 'D' did not significantly differ between each other.

4.2 Effect of plant proximity on CH_4 emissions

A high ground water level is essential to create anoxic conditions, required for anaerobic decomposition that produces CH_4 (Page and Hooijer, 2016). This was clearly reflected by distinctly high CH_4 emissions in the pineapple intercropping site, which had a water table above the surface during the wet season measurements. All the other sites were drained with relatively dry surface peat layers, and water tables below the surface. Nonetheless, CH_4 emissions were very low and well under 1 mg m^{-2} hr^{-1} at all the sampling locations in the studied sites including the pineapple intercropping site.

Another distinct trend was greater CH_4 emissions near the plants with adventitious root systems such as yam ($P_{YA<30cm}$) and pineapple ($P_{PA<30cm}$), even when the moisture level did not spatially vary between different sampling locations within their respective sites (Tables 1&2). Ground vegetation composition could significantly influence methane emissions from soil through root exudates, along with other environmental conditions such as moisture, temperature, pH and organic content (Bhullar et al., 2014; Micallef et al., 2009). It is plausible that root exudation and rhizosphere communities from yam and pineapple root systems support methanogenic communities contributing to the CH_4 emissions. Conversely, regions near mature live ($P_{OP<2.5m}$) and dead oil palm trees ($P_{OPD<1m}$) oxidised CH4, this might be due to the mature trees rhizosphere communities containing methanotrophs, which also stayed after the death of the mature palm plants. However, the regions near young oil palm plants ($P_{OP<1m)}$ and $P_{OP<2m}$) emitted CH_4. Rhizosphere communities are known to change with different development stage of the plants (Chaparro et al., 2014; Micallef et al., 2009). It is possible that oil palm rhizosphere communities changed from greater abundance of methanogens to greater abundance of methanotrophs with increasing age. This also explains

significantly greater CO_2 emissions observed at $P_{OP<2.5\ m.}$ Another factor that possibly influenced greater methane oxidation and increased CO_2 emissions near the mature oil palm in the first generation mono-cropping, was the observed significantly lower moisture level at $P_{OP<2.5m}$ than at D, as CO_2 emissions in tropical peatlands are known to increase with decreasing moisture (Jauhiainen et al., 2005; Couwenberg et al., 2010; Hergoualc'h et al., 2017; Sangok et al., 2017; Wakhid et al., 2017).

4.3 Effect of plant proximity on surface peat microbial community structure

It is evident that the rhizosphere of proximal plants did not significantly influence the surface peat microbial community structure irrespective of the age, generation or the management practice of oil palm plantations in this study, however the difference is clear between the 1st generation and the 2nd generation plantations (Supplementary information 2). The only notable distinction was the greater relative abundance of actinomycetes in the 1st gen OP for both proximal and distant sampling locations (Fig. 4). Actinomycetes are filamentous prokaryotes with fungi-like characteristics and functions (Barka et al., 2016), and are capable of degrading recalcitrant forms of cellulose in plant remains (Bhatti et al., 2017), thus explaining greater relative abundance in the 1st gen OP that contained numerous dead forest wood from previous generation. However it is surprising that the microbial phenotypic community structures were unchanged by the sampling proximity to different plants, this might be because the sampling was carried at the surface peat (0-5 cm), not in the deeper layers at the actual rhizosphere root zone of each plant. This might also explain the observed significant change in CH_4 emission but not in CO_2 emissions between the proximal and distant sampling locations in most sites, as most CO_2 is produced by greater activity in the surface (Jackson et al., 2013), and CH_4 is produced from anaerobic conditions in deeper layers that have greater influence of rhizosphere communities.

5. Conclusions

The lack of variations in CO_2 emissions in relation to proximity to plants in most of the young cropping systems except for mature oil palm and yam crops demonstrate that our hypotheses are context dependent, and possibly contingent on the duration the plants or cropping system has been established. It is also clear that surface peat microbial phenotypic community structure is unchanged by the proximal plant type or age. In addition, without appropriate above ground vegetation or hydrology for peat formation, ancient carbon stored on these agricultural peatlands are gradually lost into the atmosphere due to potentially high heterotrophic respiration under agricultural systems on peat. Although CH_4 emissions exhibited significant variations depending on the sampling proximity to different plants, the emissions were actually very low and their contribution to carbon loss and climate change is limited at these sites.

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Tables

Table 1: Environmental parameters at different sampling locations under different sites. Note 1st gen OP denotes 1st generation oil palm mono-cropping, 2nd gen OP denotes 2nd generation oil palm mono-cropping, pineapple denotes 2nd generation oil palm and pineapple intercropping yam denotes, 2nd generation oil palm and yam intercropping, pineapple denotes 2nd generation oil palm and pineapple intercropping

Site	Position	Loss on ignition	pH	Moisture	Temperature
1st gen OP	$P_{op<2.5m}$	81.5 ±0.88	3.29 ±0.07	22.7 ±2.03	29.6 ±0.18
	D	83.5 ±0.53	3.16 ±0.04	30.4 ±1.74	29.3 ±0.12
2nd gen OP	$P_{OP<2m}$	53.9 ±1.83	3.5 ±0.09	28.4 ±2.88	27.8 ±0.17
	$P_{OPD<1m}$	59.1 ±2.76	3.8 ±0.1	32.4 ±4.63	28.3 ±0.28
	D	49.7 ±1.25	3.47 ±0.05	34.7 ±1.47	28.2 ±0.12
Pineapple	$P_{OP<1m}$	88.6 ±1.36	2.94 ±0.07	59.7 ±9.47	28.0 ±0.28
	$P_{PA<30cm}$	86.6 ±0.84	3.08 ±0.04	64.1 ±2.16	28.1 ±0.10
	D	90.4 ±0.85	3.05 ±0.07	61.9 ±4.06	28.3 ±0.17
Yam	$P_{op<1m}$	83.8 ±2.37	3.25 ±0.12	34.7 ±7.27	28.5 ±0.33
	$P_{YA<30cm}$	74.2 ±2.08	4.07 ±0.10	39.6 ±2.41	28.8 ±0.23
	D	79.3 ±1.38	3.24 ±0.08	36.4 ±1.39	29.3 ±0.22
	$P_{PA<30cm}$	81.2 ±1.80	3.4 ±0.08	35.3 ±1.88	29.7 ±0.07

Table 2: Linear mixed model (REML) for GHG emissions and environmental parameters, showing statistical significance of the effects of sampling location.

	1st gen OP	2nd gen OP	Pineapple	Yam
CO_2	$F_{(1,88)}$=16.4, ***P<0.001***	$F_{(2,107)}$=0.40, p=0.670	$F_{(2,103)}$=1.11, p=0.333	$F_{(3,146)}$=5.93, ***p<0.001***
CH_4	$F_{(1,88)}$=0.85, p=0.358	$F_{(2,107)}$=3.47, **p=0.035**	$F_{(2,103)}$=5.17, **p=0.007**	$F_{(3,146)}$=3.52, **p=0.017**
Organic matter %	$F_{(1,86)}$=4.19, ***p=0.044***	$F_{(2,107)}$=6.29, **p=0.003**	$F_{(2,104)}$=3.71, ***p=0.028***	$F_{(3,145)}$=3.25, ***p=0.024***
Moisture	$F_{(1,88)}$=6.76, ***p=0.011***	$F_{(2,107)}$=2, p=0.141	$F_{(2,104)}$=0.26, p=0.775	$F_{(3,146)}$=0.80, p=0.495
pH	$F_{(1,86)}$=3.15, p=0.079	$F_{(2,107)}$=4.13, **p=0.019**	$F_{(2,104)}$=0.72, p=0.489	$F_{(3,145)}$=16.30, ***p<0.001***
Temperature	$F_{(1,88)}$=2.13, p=0.148	$F_{(2,107)}$=2.24. p=0.111	$F_{(2,100)}$=0.88, p=0.419	$F_{(3,146)}$=4.04, ***p=0.009***

Table 3: Linear mixed model (REML) for relative abundance of microbial groups and ratios, showing statistical significance of the effects of sampling location.

	1st gen OP	2nd gen OP	Pineapple	Yam
Actinomycetes	$F_{(1,4)}$=1.20, P=0.335	$F_{(2,6)}$=0.21, p=0.819	$F_{(2,6)}$=1.11, p=0.388	$F_{(2,6)}$=0.12, p=0.891
Gram-positive	$F_{(1,4)}$=2.27, p=0.206	$F_{(2,6)}$=1.94, p=0.223	$F_{(2,6)}$=0.39, p=0.695	$F_{(2,6)}$=0.54, p=0.607
Gram-negative	$F_{(1,4)}$=0.10, p=0.763	$F_{(2,6)}$=1.35, p=0.328	$F_{(2,6)}$=0.11, p=0.898	$F_{(2,6)}$=0.69, p=0.535
Fungi	$F_{(1,4)}$=o.11, p=0.758	$F_{(2,6)}$=0.19, p=0.832	$F_{(2,6)}$=0.70, p=0.533	$F_{(2,6)}$=0.47, p=0.645
Non-specific	$F_{(1,4)}$=0, p=0.961	$F_{(2,6)}$=1.22, p=0.832	$F_{(2,6)}$=0.76, p=0.508	$F_{(2,6)}$=0.48, p=0.640
F:B	$F_{(1,4)}$=0.12, p=0.745	$F_{(2,6)}$=0.38, p=0.697	$F_{(2,6)}$=0.73, p=0.519	$F_{(2,6)}$=0.46, p=0.651
G+:G-	$F_{(1,4)}$=0.29, p=0.619	$F_{(2,6)}$=0.09, p=0.919	$F_{(2,6)}$=0.23, p=0.803	$F_{(2,6)}$=0.67, p=0.547
Cyc:pre	$F_{(1,4)}$=0.13, p=0.741	$F_{(2,6)}$=0.60, p=0.580	$F_{(2,6)}$=2.16, p=0.197	$F_{(2,6)}$=0.44, p=0.662
Sat:mono	$F_{(1,4)}$=0, p=0.951	$F_{(2,6)}$=0.67, p=0.544	$F_{(2,6)}$=1.16, p=0.375	$F_{(2,6)}$=1.59, p=0.279

Figure captions:

Figure 1: Effect of sampling location upon CO_2 emissions under different oil palm cropping systems. Bars denote mean values and whiskers denote standard errors. Note 1st gen OP denotes 1st generation oil palm mono-cropping, 2nd gen OP denotes 2nd generation oil palm mono-cropping, pineapple denotes 2nd generation oil palm and pineapple intercropping, yam intercropping denotes 2nd generation oil palm and yam intercropping.

Figure 2: Effect of proximity to crop plantssampling location upon CH_4 emissions under different oil palm cropping systems. Bars denote mean values and whiskers denote standard errors. Note 1st gen OP denotes 1st generation oil palm mono-cropping, 2nd gen OP denotes 2nd generation oil palm mono-cropping, pineapple intercropping denotes 2nd generation oil palm and pineapple intercropping, yam denotes 2nd generation oil palm and yam intercropping.

Figure 3: Effects of proximity to cropsampling location 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=3), whiskers denote standard errors. The description for sampling locations are given in the section 2.2. Additionally note 1^{st} OP in brackets denotes 1^{st} generation oil palm mono-cropping, 2^{nd} OP in brackets denotes 2^{nd} generation oil palm mono-cropping, PA in brackets denotes oil palm and pineapple intercropping, YA in brackets denotes yam and oil palm intercropping.

Figure 4: Relative abundance of different microbial groups as determined by PLFA analysis. Mean values are presented (n=3). Mol% is calculated by dividing the individual PLFA's peak area by the sum of the peak areas of all PLFAs and multiplying it by 100. The description for sampling locations is given in the section 2.2.

Figure 5: Ratios between different microbial groups and PLFA ratios used as stress indicators, as determined by PLFA analysis. Mean values are presented (n=3). Mol% is calculated by dividing the individual PLFA's peak area by the sum of the peak areas of all PLFAs. The description for sampling locations is given in the section 2.2.

Supplementary information 1: Indicative views of the sampled sites.

Supplementary information 2: Effects of site 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= 6 for 1st gen OP and n= 9 for all other sites), whiskers denote standard errors. Note 1st gen OP denotes 1st generation oil palm mono-cropping, 2nd gen OP denotes 2nd generation oil palm mono-cropping, pineapple denotes 2nd generation oil palm and pineapple intercropping, yam denotes 2nd generation oil palm and yam intercropping, pineapple denotes 2nd generation oil palm and pineapple intercropping.

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