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From peat swamp forest to oil palm plantations: The stability of tropical peatland carbon

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ABSTRACT

Accurate assessment of tropical peatland carbon dynamics is important to (a) determine the size of the active carbon pool, (b) estimate the scale of transfers of peat-derived greenhouse gases (GHGs) to the atmosphere resulting from land use change, and (c) support carbon emissions reduction policies. To date, information on the quality of tropical peatland organic matter and its sensitivity to increases in global temperatures is limited, particularly in the context of land conversion. The aim of this work is therefore to determine peat quality and temperature response of potential GHG emissions under flooded conditions from tropical peatland sites. Whilst reflecting the process of conversion from forest to oil palm plantation. Four land use types that represent the stages of conversion from peat swamp forest to oil palm were chosen: (i) secondary 'forest', (ii) recently 'drained' but not cleared forest (iii) cleared and recently planted 'young oil palm' plantation and (iv) 'mature oil palm' plantation. Overall, surface peat carbon was more labile than deeper peats. The largest labile pool was measured at forest sites. In the later stages of land conversion, the labile carbon had been lost and the relative abundance of recalcitrant organic material increased. Potential GHG fluxes were greatest in surface peats compared to deeper peats and declined as labile carbon was depleted following land conversion. Higher temperatures resulted in higher potential GHG emissions at all stages of conversion, but the magnitude of the temperature response depended on organic matter lability. For CO₂ fluxes, the temperature response was most pronounced at forest sites. This reflects the greater peat lability at this land use. In contrast, for CH₄ emissions, there were increased emissions both at forest and converted land types with higher temperatures. This suggests that increasing temperatures in response to climate warming may drive higher CH₄ emissions from sites dominated by degraded organic matter. Collectively, this study demonstrates that during conversion from peat swamp forest to oil palm plantation, the enhanced decomposition and reduced litter input rates is reflected eventually in reduced potential gross CO₂ emissions from peat. Nonetheless higher temperature resulting from climate warming may maintain high GHG emissions at plantation sites.

1. Introduction

Palm oil is one of the most widely used agricultural products in the world, with demand projected to increase in the future (Corley, 2009; Koh and Wilcove, 2008; Vijay et al., 2016). An estimate by Koh and Wilcove (2008) indicated that of all oil palm expansion between 1990 and 2005 in Malaysia, at least 50% has come at the expense of natural

rainforest, of which the natural vegetation is predominantly peat swamp forest (Davies et al., 2010). Peat swamp forests play an essential role in the global carbon cycle and are significant carbon sinks and stores, containing an estimated 15–19% of the global peat carbon stock (610 Gt C) (Dargie et al., 2017; Page et al., 2011).

Peat swamp forests are highly sensitive to disturbance by drainage or deforestation for conversion to oil palm plantations (Evers et al., 2017). Following conversion, the exchange of greenhouse gases (GHGs)

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between terrestrial ecosystems and the atmosphere is directly affected (IPCC, 2000) and carbon accumulated over centuries or millennia is rapidly released to the atmosphere, contributing to climate warming (Couwenberg et al., 2010; Hooijer et al., 2012; Davies et al., 2010; Moore et al., 2018). Since 1990, oil palm plantations have been linked to 2.5 GtC losses in carbon stock in tropical peatlands (Miettinen et al., 2017). There is, however, a lack of data regarding how rapidly carbon is lost to the atmosphere during the conversion process, and how changes to organic chemistry of remaining stored C determine its susceptibility to further release. A recent study in Malaysia suggests that organic matter content declines at least within the first one to 2 years following the start of conversion (Tonks et al., 2017). Furthermore, the conversion process altered surface peat functional organic chemistry as carbohydrates were preferentially depleted as a result of aerobic decay, suggesting that conversion will enhance peat recalcitrance but increase its aromaticity (Tonks et al., 2017; Yule et al., 2018).

In addition to land use conversion, tropical peatlands are also affected by climate change which is predicted to result in a 3–7 °C increase in temperature and increased seasonality of rainfall, resulting in more pronounced dry and wet seasons and, thus, longer periods of flooded conditions (IPCC, 2007, 2014). Recent work in pristine peatlands in the Neotropics has shown strong temperature responses of GHG emissions under high water-table conditions for both CO₂ and CH₄ (Sjögersten et al., 2018). However, temperature responses of GHG emissions from wetland soils differ considerably among land use types, likely in response to differences in organic matter lability (Dunfield et al., 1993; Duval and Radu, 2018; Gritsch et al., 2015; Inglett et al., 2012; Turetsky et al., 2015). As deforestation rates in Southeast Asia show no signs of slowing (Wijedasa et al., 2018), peat swamp forests are predicted to be extinct by 2050 if current rates of peatland deforestation continue unchecked (Miettinen et al., 2016). It is therefore critical that we quantify the climate feedback potentials from both peat swamp forests and also degraded peats in plantations. Indeed, it is plausible that high temperatures further increase the climate burden of GHG emissions from oil palm plantations, as the temperature sensitivity of organic matter decomposition is predicted to increase with recalcitrance, as higher activation energies are required for catabolism, in line with kinetic theory (Bosatta and Ågren, 1999; Davidson and Janssens, 2006).

GHG emissions from drained tropical peatland conversion are at present overlooked in GHG emission budgets as considered by the UN Framework Convention on Climate Change (IPCC, 2006; IPCC, 2014). However, given their important role in the global carbon cycle and the pressures they are exposed to from both land use and climate change, it is vital to develop a mechanistic understanding of the controls of GHG emissions from forested and converted peatlands to underpin the delivery of evidence based sustainable land use management and policy (Evers et al., 2017). Therefore, this study aims to improve our understanding of the impact of anthropogenic activities, e.g. drainage and deforestation, on soil organic matter stability and subsequent GHG fluxes from tropical peatlands. To achieve this, the study addresses three specific hypotheses linked to how land use and temperature changes alter peat lability and CO₂ and CH₄ fluxes: Our first hypothesis (1) “land conversion of drainage-based oil palm plantation results in depletion of labile substrates in surface peat affected by drainage, but not in deeper peat layers” is based on the notion that drainage promotes aerobic decomposition in surface peat but not in deeper peats below the water-table where anoxic conditions remain (Couwenberg et al., 2010; Jauhiainen et al., 2008). Because substrate lability is often a predictor of GHG emissions in tropical peatlands (Hoyos-Santillan et al., 2016; Wright et al., 2011), we hypothesise that (2) “ex situ anaerobic CO₂ and CH₄ production will be lower in the later stages of land conversion to oil palm plantation as a result of depletion of labile carbon”. In line with kinetic theory (Bosatta and Ågren, 1999; Davidson

and Janssens, 2006) we also hypothesise that (3) “the impact of substrate depletion on GHG production is exacerbated by higher temperatures, with the strongest impact in surface peat”.

2. Materials and methods

2.1. Study sites

Field data and sample collection was conducted in November–December 2014 in North Selangor Peat Swamp Forest, Malaysia. The North Selangor Peat Swamp Forest comprises Raja Musa Forest Reserve, Sungai Karang Forest Reserve, Sungai Dusun Wildlife Reserve and part of Bukit Belata Forest Reserve Extension, and overall covers an area of 81,304 ha. The central area of the reserve is secondary mixed forest; the majority of the area was selectively logged from the 19th century up until the 1980s, and a significant area of the northern edge of the reserve has already undergone oil palm conversion (Kumari, 1996). Four stages or classes of land conversion were identified (forest, drained forest, young oil palm plantation and mature oil palm plantation), and five replicate study sites were sampled in each class (Figs. 1 and 2). The forest sites chosen for this study had not been subject to logging for approximately 40 years; as a result the forest sites were in areas of high canopy density (trees >25 m, canopy coverage >80% (Global Environment Centre, 2014).

Drained sites comprised a similar forest structure but large drainage ditches (2–3 m wide and ca. 2 m deep) had been dug every few hundred meters, 6 months prior to field work, thus lowering the water-table. Secondary mixed forest and drained sites contained trees such as:

Macaranga pruinosa, *Camposperma coriaceum*, *Blumeodendron tokbrai*, *Shorea platycarpa*, *Parartocarpus venenosus*, *Ixora grandiflora*, *Pternandra galeata*; ferns: *Stenochlaena palustris*, *Asplenium longissimum*, *Nephrolepis biserrata*; palm: *Cyrtostachys* sp.; sedges: *Cyperus rotundus* and abundant stands of *Pandanus atrocarpus* (Yule and Gomez, 2009).

Recently planted young oil palm sites, where both artificial lowering of the water-table (drainage) and deforestation had occurred were chosen for sampling. Oil palm seedlings were planted 6 months prior to sampling. The final sites chosen were mature oil palm, where the oil palm trees were first generation and ca. 10–15 years old. Detailed site characteristics are summarised in Table 1.

2.2. Field sampling

In total, twenty 900 m² (30 m by 30 m) field plots were marked out (five plots in each of the four land conversion stages). Forest and mature oil palm areas were located widely around the North Selangor Peat Swamp Forest to maximise spatial distribution, though access constraints and challenging terrain also influenced final locations. Drained and young oil palm plantation sites were constrained to two main representative areas. Sample points were selected randomly within plots using random number tables to determine direction and distance from the south west corner of the plot. GPS coordinates were recorded for each corner and are provided in Tonks et al., 2017.

In each of the plots, we took three peat samples from depths 0–5 cm and 50–55 cm that covered mostly oxic and anoxic conditions respectively. We extracted samples using a side-filling Russian Peat Corer (Van Walt, UK), with a 50 cm long sampling chamber. Immediately following extraction, we bagged and sealed the peat samples to avoid moisture loss.

2.3. Laboratory incubations

Samples were transported from North Selangor, Malaysia to University of Nottingham, UK and frozen until analysis to avoid decay during storage. At time of incubation, we removed the samples from the



Fig. 1. Type of peatland habitats surveyed (a) forest with high water table, (b) drained forest with water table below the surface, (c) young oil palm and (d) mature oil palm plantation.

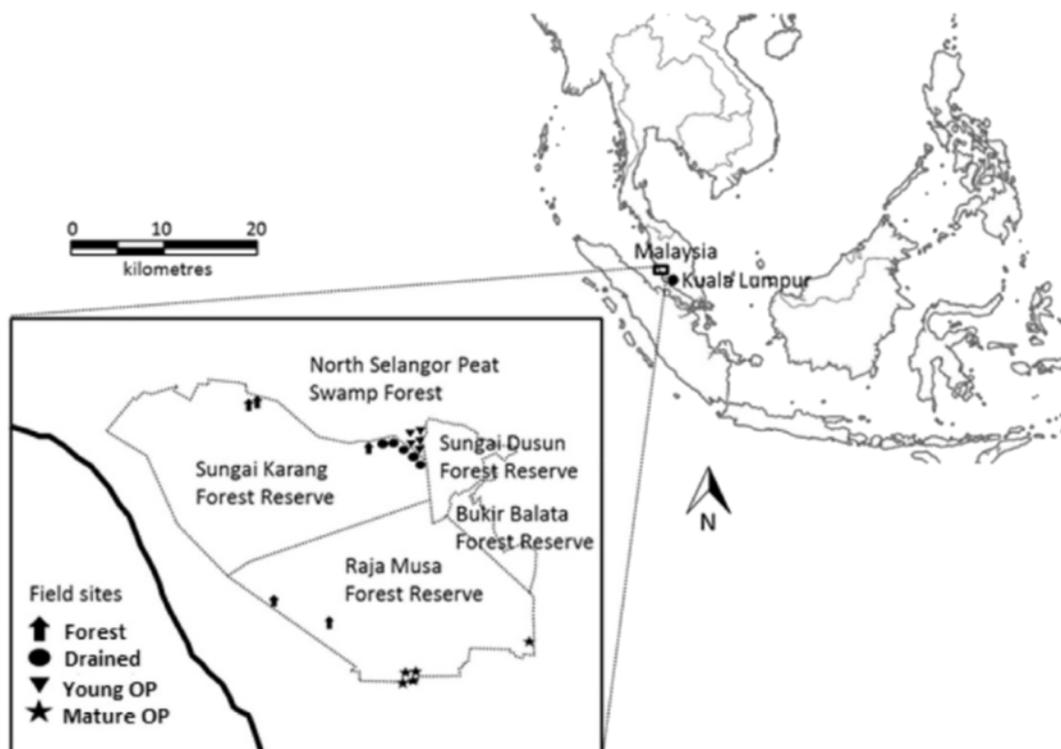


Fig. 2. Location of North Selangor Peat Swamp Forest and the sites belonging to the four different conversion stages. Forest, drained, young and mature oil palm plantation sites (Tonks et al., 2017).

freezer and left them to defrost in a cold room (4°C) before sub-sampling and subsequent incubation of the peat samples under anaerobic conditions (i.e. simulating flooded conditions) at two temperatures: 25 and 30°C. We acknowledge that the cold stage of the samples may have impacted on the original peat microbial community composition (Arnold et al., 2008; Lee et al., 2007; Verchot, 1999), however, we still expect the activity of the microbial community to be strongly controlled by the peat organic chemistry and incubation conditions.

Prior to incubation, 3 g of dry weight equivalent peat samples were placed in 125 ml serum bottles (80 in total) and flooded with 1 cm³ of water. We flushed the serum bottles with nitrogen for 2 min to displace oxygen and create anaerobic conditions before sealing with a rubber septa (13 × 19 × 12 mm; Rubber B.V., Hilversum, NL), and an aluminium crimp top. Serum bottles were placed in either 25°C or 30°C temperature control rooms to replicate ambient and elevated soil conditions.

Table 1
Soil and site characteristics for sampling locations in North Selangor. Annual precipitation from January 2015–December 2015 represents regional values. Means \pm one SEM.

Characteristics	Forest	Drained forest	Young oil palm	Mature oil palm
pH	3.4 \pm 0.06	3.7 \pm 0.06	3.7 \pm 0.08	3.9 \pm 0.08
OM %	94.1 \pm 1.5	88.8 \pm 2.5	86.1 \pm 5.93	77.3 \pm 5.9
Moisture content (%)	82.3 \pm 28	46.3 \pm 22	33.9 \pm 9	56.56 \pm 21
C/N ratio	34.5 \pm 2.7	28.2 \pm 1.2	37.9 \pm 4.0	29.1 \pm 3.5
Mean annual precipitation (mm)	209.5 \pm 34	209.5 \pm 34	209.5 \pm 34	209.5 \pm 34
Water table depth (cm)	6.0 \pm 22	-14 \pm 23	-39 \pm 15	-21 \pm 18
Shear strength (kPa)	8.4 \pm 0.6	6.8 \pm 0.9	7.8 \pm 0.6	9.7 \pm 0.6

To allow the microbial community time to recover from disturbances (freezing/thawing and handling during preparation of the microcosm) we left the samples for 7 days. After that the serum bottles were opened to the air to dissipate accumulated headspace gases and then flushed with nitrogen for 2 min and re-sealed. Following another 7 days of incubation, headspace gas samples (5 ml) were collected weekly by syringe from each serum bottle and analysed immediately by gas chromatography (GC-2014, Shimadzu UK LTD, Milton Keynes, UK) over 4 weeks.

We analysed CO₂ and CH₄ concentration using a single injection system, with a 1 ml sample loop that passed the gas sample using N₂ as a carrier. Thermal conductivity detectors (TCD) and flame ionization detectors (FID), were used to measure CO₂ and CH₄ respectively. The fluxes were calculated using linear regression of the gas concentration against time. The GHG data was converted to mass per volume and mass per weight by the use of the ideal gas equation and the molecular mass of each gas as shown in Eq. (1). From this, the gas flux from each incubation was calculated using Eq. (2).

$$PV = nRT \quad (1)$$

Where P is the atmospheric pressure (\approx 1 atm), V is the volume of headspace (dm⁻³), n is the number of moles of gas, R is the ideal gas constant (0.08205746 L atm K⁻¹ mol⁻¹), and T is temperature (273.15 + room temperature in °C).

$$E = \left(\frac{nm}{at} \right) \times 1000 \quad (2)$$

where E is the flux of each gas (mg m⁻² h⁻¹), n is the number of moles (CO₂ or CH₄), m is the molar weight (CO₂: 44.01 and CH₄: 16.04), a is the area of soil core used and t is the time in the hour.

2.4. Rock-Eval 6 pyrolysis

Rock-Eval pyrolysis is a technique which has been used recently to trace bulk changes in organic matter composition and degree of composition (Disnar et al., 2003; Newell et al., 2016). This technique predicts reliable soil C contents and is an appropriate and novel tool for assessing the vulnerability of SOC stocks (Saenger et al., 2013). For a more detailed description on Rock-Eval pyrolysis as applied to tropical peats see Upton et al. (2018) and Girkin et al. (2018).

Surface and subsurface peat samples were analysed using a Rock-Eval 6 analyser. Freeze-dried powdered peat samples (60 mg) were heated at 300 °C for 3 min before an increase in temperature to 650 °C at a rate of 25 °C per minute in an inert N₂ atmosphere. Residual carbon was subsequently oxidized from 300 °C to 850 °C at a rate of 20 °C per minute. The release of hydrocarbons during the two-stage pyrolysis process was detected by a flame ionization detector, with an infrared cell detecting the release of CO and CO₂ during the thermal cracking of

the organic matter. Rock-Eval analysis generated a range of standard parameters including:

- S1, a measure of free hydrocarbons released on heating to 300 °C.
- S2, hydrocarbons released on the thermal cracking of organic matter for temperatures up to 850 °C.
- TpkS2 corresponds to the temperature when the maximum amount of hydrocarbons was released during pyrolysis.
- Total organic carbon (TOC_{RE}) is calculated from the sum of the carbon moieties (HC, CO and CO₂).
- The Hydrogen Index (HI mg HC g⁻¹ TOC), a measure of hydrocarbons released relative to TOC, was calculated from $S2 \times 100 / TOC_{RE}$.
- The Oxygen Index (OI mg O₂ g⁻¹ TOC), corresponding to the amount of oxygen released as CO and CO₂ relative to TOC_{RE}, was calculated from $S3 \times 100 / TOC_{RE}$.
- The labile, intermediate and passive C pools (Cl, Ci, and Cp, respectively) which correspond to the deconvolution of S2 pyrograms into six Gaussian signals (F1–F6) based on maximising R² coefficient values. F1–F6 values have previously been attributed to organic compounds of increasing complexity and recalcitrance (Disnar et al., 2003; Sebag et al., 2006).
- F1–F2 signals represent high labile fresh plant material including simple polysaccharides, HC compounds are pyrolysed below 360 °C.
- F3 relates to increasingly humified macromolecules which are pyrolysed between 360 and 450 °C
- F4–F6 signals can be attributed to the presence of highly mature and recalcitrant soil organic matter, or charcoal, where HC are pyrolysed above 450 °C.
- C_l represents the highly labile hydrocarbon compounds (F1 and F2), C_i corresponds to the more stabilised soil carbon pool (F3), and C_p represents the highly recalcitrant passive pool (F4–F6) (Saenger et al., 2013).

2.5. Statistical analysis

Differences in Rock-Eval parameters and indices were assessed using linear mixed effects models fitted using Residual Maximum Likelihood (REML) to account for variable dependence between sampling plots. Conversion class and depth were selected as fixed effects and sites as random effects. Fluxes of CH₄ and CO₂, proportion of carbon in C_l, C_i and C_p, and total organic carbon were log-transformed to meet assumptions of normality and were also assessed using REML. Rock-Eval analysis provides multiple parameters, and to summarise these and to assess which were important in regulating GHG fluxes we used Principal Component Analysis (PCA), based on correlation matrices. All statistical analyses were conducted in GenStat (v17.07).

3. Results

Thermolabile hydrocarbons (S1 i.e. poorly stabilised SOC), which are released on heating at 300 °C, were significantly different between land uses in surface peats ($F_{3,32} = 7.79$, $P < 0.001$, Fig. 3a), with the highest concentrations measured at drained sites, followed by young oil palm, forest and mature oil palm. More recalcitrant hydrocarbons (S2 i.e. greater thermostable C) which are released between 300 and 650 °C (Johannes et al., 2006), also differed significantly in surface peats between land uses ($F_{3,32} = 5.45$, $p < 0.05$, Fig. 3b) and demonstrated a similar pattern as S1 values, with the highest values measured in drained sites and the lowest in mature oil palm plantations (Fig. 3a & b).

TpkS2 provides an overall assessment of the energy of the C bonds of molecules, and can be interpreted as the amount of energy required for microorganisms to decompose SOM. TpkS2 showed an increase with land conversion towards oil palm plantations ($F_{3,32} = 3.85$,

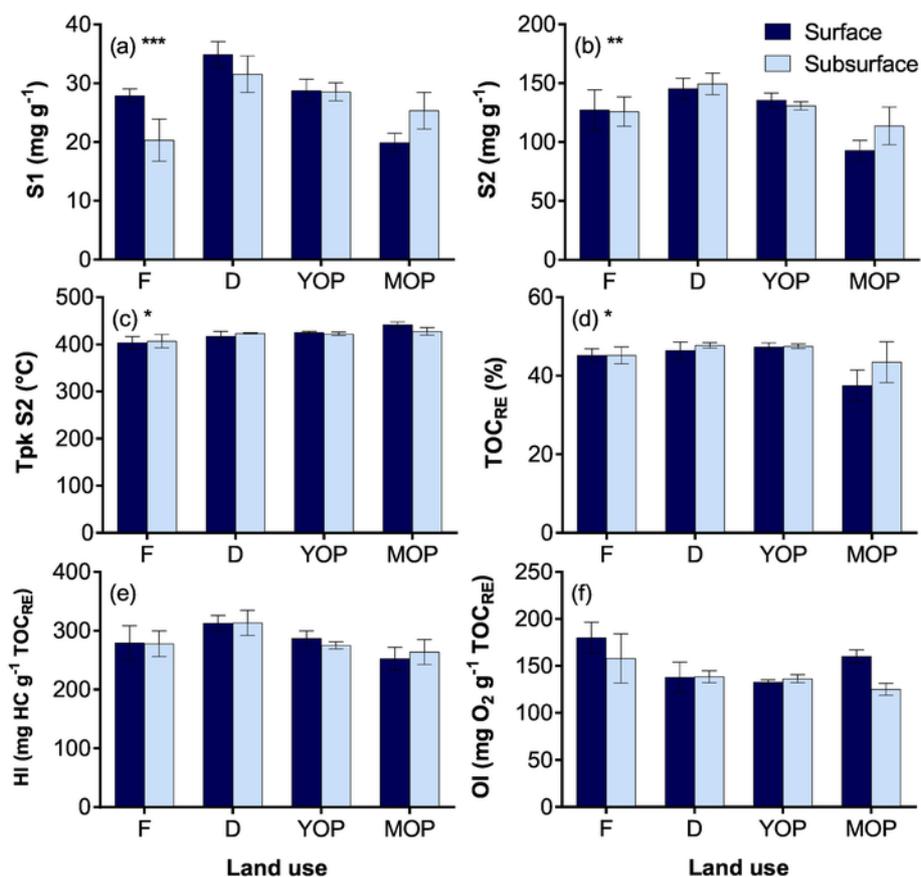


Fig. 3. Selected Rock-Eval 6 parameters across the different land uses in surface and subsurface peats. Where F is forest, D is drained, YOP is young oil palm and MOP is mature oil palm. * indicates land use significance at $p < 0.05$, ** at $p < 0.01$ and *** at $p < 0.001$. There were no significant differences with depths or interactions between land use and depth, $p > 0.05$.

$p < 0.05$, Fig. 3c). The lower TpkS2 values in forest and drained sites (403 and 416 °C respectively) are characteristic of the thermal breakdown of more labile polysaccharides and lignins. In contrast, values over 420 °C, as measured in young and mature oil palm sites (425 and 441 °C respectively), are typical of increasingly immature humic substances (Disnar et al., 2003). TOC was high and showed little variation between forest, drained and young oil palm sites (ranging from 45% to 47%); however, TOC was significantly lower in the mature oil palm sites with 37% ($F_{3,32} = 2.92$, $p < 0.05$, Fig. 3d).

In surface peats, HI (i.e. the amount of hydrogen relative to the amount of organic carbon) decreased from 312 mg HC g⁻¹ TOC_{RE6} at the drained sites to 252 mg HC g⁻¹ TOC_{RE6} in mature oil palm sites ($F_{3,32} = 2.73$, $p = 0.060$, Fig. 3e). OI (i.e. the amount of oxygen relative to the amount of organic carbon) increased from 180 O₂ g⁻¹ TOC_{RE6} in the forest sites to 132 mg O₂ g⁻¹ TOC_{RE6} in the recently

planted sites ($F_{3,32} = 2.73$, $p = 0.060$, Fig. 3f). In forest and drained sites, HI was higher in the subsurface compared to surface peats, and, similarly with OI, higher concentrations were measured in forest, drained and young oil palm sites in the subsurface peats (Fig. 3e & f).

In surface peats at forest, drained and recently planted sites, the labile carbon pool (C₁) was the largest of the three pools, accounting for 69%, 61% and 50% respectively (Fig. 4a). In contrast, C₁ differed significantly in mature oil palm sites from the other land uses ($F_{3,16} = 3.41$, $p < 0.05$, Fig. 4a) and accounted for only 15% of carbon. A similar trend was observed in subsurface peats in the C₁ pool, with a decrease in lability with conversion stages, although not significant ($F_{3,16} = 0.04$, $p = 0.84$, Fig. 4b). The intermediate carbon pool (C_i) varied significantly in surface peats ($F_{3,16} = 3.83$, $p < 0.05$, Fig. 4a) with mature oil palms sites having the largest contribution in this pool of 67%. The passive pool (C_p) differed significantly between sites in the

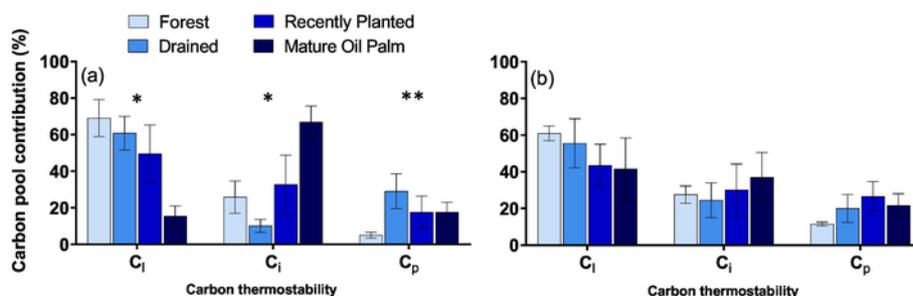


Fig. 4. Proportions of labile (C₁), intermediate (C_i) and passive (C_p) carbon pools for different sites in a) surface and b) subsurface peats (n = 5). Means ± one SE. * indicates land use significance at $p < 0.05$ and ** at $p < 0.01$. There were no significant differences with depth or interactions between land use and depth, $p > 0.05$.

surface peats ($F_{3,16} = 4.58$, $p < 0.05$, Fig. 4a) with the highest contribution at drained sites and the lowest in forest sites (29% and 5% respectively).

Peats incubated at 25 °C and 30 °C exhibited a significant declining trend in GHG fluxes with conversion in surface samples ($F_{3,16} = 9.4$, $p < 0.001$, Table 2, Fig. 5), with a similar pattern, although less pronounced, in subsurface peats (Fig. 5). Peats incubated at 30 °C had significantly higher CO₂ fluxes across all land uses ($F_{1,48} = 35.1$, $p < 0.001$, Table 2, Fig. 5a & b) when compared to peats incubated at 25 °C with the highest mean fluxes from forest peats, with an average of $5.2 \mu\text{g g}^{-1} \text{h}^{-1}$ from peats incubated at 25 °C and $9.1 \mu\text{g g}^{-1} \text{h}^{-1}$ from peats incubated at 30 °C.

CH₄ fluxes were significantly greater in forest and drained sites compared to both oil palm plantation ages in surface peats ($F_{3,16} = 9.4$, $p < 0.001$, Table 2, Fig. 5c & d), with diminishing difference in deeper peats from the young and mature oil palm sites.

The scores and loading of the first and second principal components accounted for most of the variance for surface and subsurface peats, 60% and 50% respectively. The surface peats (Fig. 6a & c) display clustering in each land use, demonstrating a difference in Rock-Eval parameters between sites, whereas in subsurface peats (Fig. 6b & d) there appears to be no clustering of parameters for each land use. In surface samples, mature oil palm sites are best described by TpkS2 and OI, whereas drained sites are predominantly separated by S1, S2 and C₁ pa-

rameters (Fig. 6c). CO₂ fluxes are regulated by TpkS2 in surface peat but by S2 and HI in subsurface peats; and in contrast, CH₄ fluxes are regulated by C_i pool in subsurface peats (Fig. 6d).

4. Discussion

4.1. Depletion of labile substrates with conversion to oil palm plantation

Land conversion resulted in a reduction in the labile carbon pool, which is highly available to the peat microbial community. Conversion from forest to mature oil palm resulted in a labile carbon pool reduction from ca. 70% to <20%, with an accompanying increase in the intermediate carbon pool (from ca. 20 to 70%) in surface peat (Fig. 4). This supports the first hypothesis, which predicted that losses of labile carbon with land conversion would be most pronounced in surface peat. Depletion of labile carbon pools and a relative build-up of more recalcitrant carbon in surface peat is in line with selective depletion of carbohydrates and decreasing carbohydrate to aromatics ratios and peat loss following land conversion demonstrated at these and other sites in Southeast Asia (Matysek et al., 2017; Tonks et al., 2017). This is further supported by the greater thermal stability of the surface peat at the mature oil palm sites than forested and drained forested sites (Fig. 6a and c), which previously have been linked to peat degradation in tropical peatlands in Panama (Upton et al., 2018).

Table 2

Gas flux statistics from different land uses and depths assessed by REML.

	CO ₂			CH ₄				
	F-statistic	d.f.	p	SED	F-statistic	d.f.	p	SED
Land use	9.4	3,16	<0.001	0.02	5.57	3,16	<0.05	0.02
Depth	63.7	1,48	<0.001	0.01	37.57	1,48	<0.001	0.01
Temp	35.1	1,48	<0.001	0.01	12.75	1,48	<0.001	0.02
Land use * Depth	8.28	3,48	<0.001	0.02	9.8	3,48	<0.001	0.02
Land use * Temp	0.18	3,48	0.909	0.02	0.33	3,48	0.806	0.02
Depth * Temp	3.05	1,48	0.087	0.01	6.53	1,48	<0.05	0.01
Land use * Depth * Temp	0.59	3,48	0.623	0.03	1.37	3,48	0.264	0.03

Significant differences in italics.

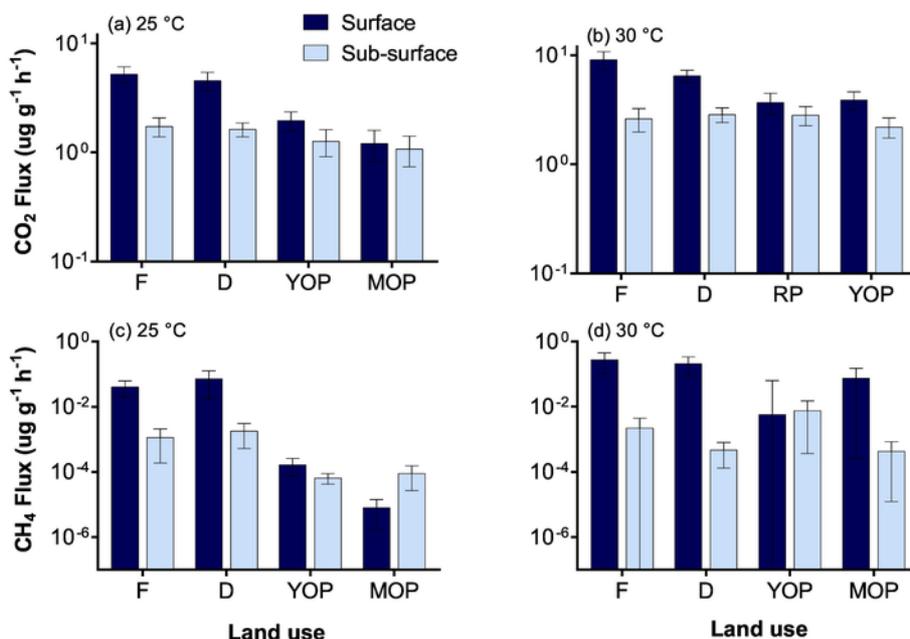


Fig. 5. Logged (Log₁₀) carbon dioxide (a & b) and methane fluxes (c & d) at 25 °C (a & c) and 30 °C (b & d) from surface (0–5 cm) and subsurface (50–55 cm) peats from forest (F), drained (D), young (YOP) and mature oil palm (MOP) sites in $\mu\text{g g}^{-1} \text{h}^{-1}$. Carbon dioxide fluxes are shown from time point one and methane from time point four where production was greatest. The pattern in the data was the same at the different time points ($n = 5$). Means \pm one SE.

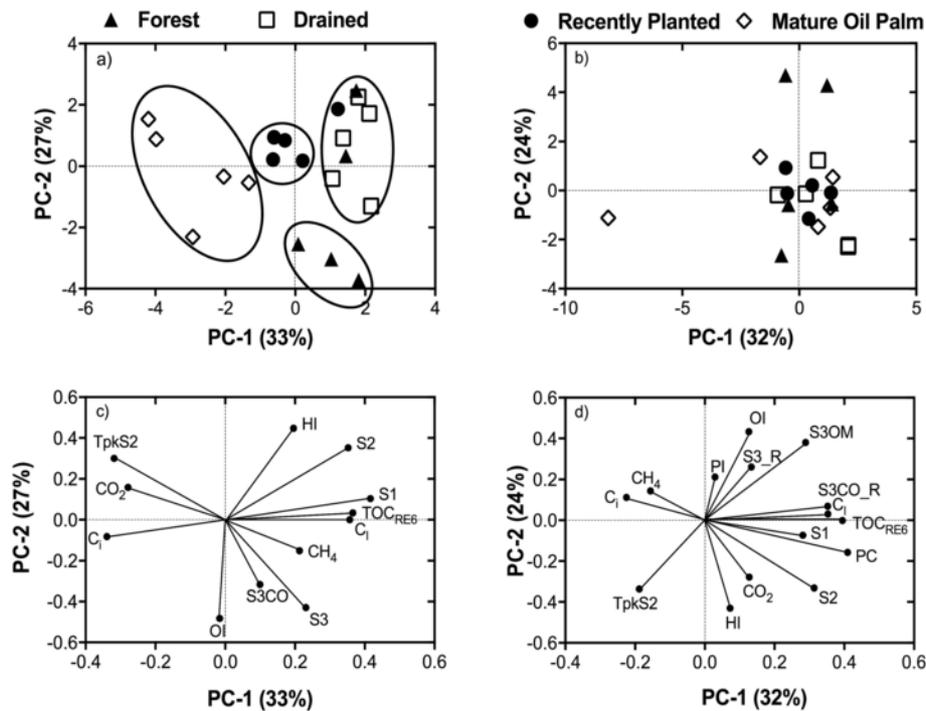


Fig. 6. Principal component scores (a & b) and loadings (c & d) for Rock-Eval parameters and carbon dioxide and methane fluxes from surface (a & c) and subsurface (b & d) peats. Combined PC1 and PC2 account for 60% and 56% of the variance respectively.

The changes in peat organic chemistry are linked to two main processes. First, lowered water-tables increase the oxygenation of the peat surface layer and enhance the degradation of organic polymers by bacteria and fungi (Couwenberg et al., 2010). The different responses between the surface and deeper peats to land use change in this study clearly demonstrate the impact of the long-term position of the water-table in peat, with the loss of labile carbon above the water-table and the preservation of significant quantities of labile organic material below the water-table.

Second, the shift in the vegetation litter inputs following conversion will also strongly impact on the relative abundance of the different carbon pools. In PSF, the vegetation adds carbon to the peat surface as litter and into the peat from the rhizosphere (Girkin et al., 2018b & 2018c), and thus contributes to maintenance of the peat carbon stores by compensating for carbon losses that result from concurrent decomposition (Jauhiainen et al., 2016). Little or no such inputs occur when sites are fully converted. Peat swamp forest litter is composed largely of coarse and fine roots, woody debris and leaf litter, and is rich in both cellulosic and more complex ligneous substrates (Hoyos-Santillan et al., 2016; Miyajima et al., 1997). However, as lignin is resistant to decomposition and ligninolytic microbes are obligate aerobes, the amount of cellulosic substrates decrease as peat decomposition advances even under anoxic condition, explaining the depletion of labile carbon with depth even at the forest sites (Hoyos-Santillan et al., 2016). Taken together it is clear that the lowered water tables and reduced quality and quantity of litter inputs associated with land conversion strongly alters the peat organic chemistry as labile organic matter are depleted through greater decomposition processes and not replenished through fresh litter inputs.

4.2. Linking CO_2 and CH_4 fluxes and organic matter properties

As expected, potential CO_2 production from flooded peat was several orders of magnitude higher than CH_4 production, as shown previously in both disturbed and natural tropical wetlands (IPCC, 2014; Hoyos-Santillan et al., 2016), with fluxes of similar magnitude but

slightly lower than those from pristine Neotropical peatlands (Sjögersten et al., 2018). Furthermore, emissions were consistently higher in surface peats suggesting these have greater production potential than degraded subsurface peats, likely reflecting substrate limitation of microbial decomposition processes with depth (Hoyos-Santillan et al., 2016; Sihi et al., 2018; Upton et al., 2018; Wright et al., 2011); though other factors may also play a role, e.g. shifts in the microbial community structure with depth in response to changes in peat properties (Jackson et al., 2009).

The successive reduction in ex situ CO_2 and CH_4 fluxes from waterlogged peat with progressively more advanced land conversion stages, together with the parallel depletion of labile carbon in surface peat (Fig. 5), suggests that the labile carbon pools strongly control GHG emissions in line with the second hypothesis which predicted that “ex situ anaerobic CO_2 and CH_4 production will be lower in the later stages of land conversion to oil palm plantation as a result of depletion of labile carbon”. Similar strong links between GHG fluxes from peats under anaerobic conditions and peat organic chemistry have previously been shown for undisturbed peatlands (Wright et al., 2011; Hoyos-Santillan et al., 2016), with greater fluxes found from peat with larger labile carbon pools. In contrast, no changes in GHG production were found with land conversion from the deeper peats, which is likely due to limited impacts of land conversion on decomposition in the peat that remained below the water-table even after drainage.

These findings clearly demonstrate that the loss of peat due to enhanced decomposition following conversion results in more recalcitrant peat which limits GHG emissions under waterlogged conditions. However, it is important to note that this substrate limitation of GHG emissions is most likely controlled by the anaerobic conditions which limit the microbial communities' capacity to utilise more complex organic molecules (e.g. lignin and humic substances). Under aerobic conditions, CO_2 fluxes would likely remain high across the conversion gradient as has been shown in situ in peatlands in South Selangor, Malaysia (Matysek et al., 2017), as the oxygen availability supports the activity of microbial communities capable of degradation of complex organic molecules (Hoyos-Santillan et al., 2016).

The relatively lower fluxes of both CO₂ and especially CH₄ from the mature oil palm sites suggest that although re-flooding of oil palm plantations may result in some CH₄ emissions in line with Jauhiainen et al. (2016), raising water-tables will not increase CH₄ emissions to the levels of those found in intact PSFs in the short term. Limited increases in CH₄ production following rewetting of peats that have been exposed to prolonged periods of oxic conditions has been reported previously from high latitude peatlands (Sjögersten et al., 2016) as well as tropical peatlands (Jauhiainen et al., 2008, 2016). This is likely linked to slow recovery of the methanogenic communities from oxic peat conditions. Indeed, functional shifts in microbial community composition, e.g. decline in macro fungi abundance, in response to conversion of PSF to oil palm plantations, as has been shown previously at these sites (Shuhada et al., 2017), suggests that strong impacts of land conversion should be expected on the microbially mediated decomposition processes. In the longer term, microbial communities and pools of labile substrates may recover if water-tables are raised and the native vegetation reintroduced (Jauhiainen et al., 2008; Jauhiainen et al., 2016). As peat swamp forests have higher percentage canopy cover, denser canopy closure (Yule and Gomez, 2009) and greater litter inputs than oil palm plantation (Guillaume et al., 2015), restoring peat swamp forests would likely increase pools of labile organic matter in surface peats which could shift microbial community functionality towards its original form (Nurulita et al., 2016). However, replacing the organic matter lost via rapid decomposition during the conversion would only recover slowly as the NPP of tropical peat swamp forests are low (ca. 1200 g C m⁻² yr⁻¹) when compared to the CO₂/C stock loss rates reported from recently drained oil palm plantations (Couwenberg et al., 2010; Matysek et al., 2017; Sjögersten et al., 2014).

4.3. Impact of temperature on surface and subsurface fluxes

The strong impact of temperature on both anaerobic CO₂ and CH₄ fluxes suggests that their production is highly sensitive to higher temperatures in line with findings from tropical peatlands in Panama (Sjögersten et al., 2018). The anaerobic CO₂ fluxes were consistently higher at 30 °C than 25 °C across depths and land conversion stages suggesting that the microbial community was temperature limited. The substantial increase in anaerobic CO₂ fluxes at the forest and drained sites at the 30 °C treatment indicate that the large labile C pool at these sites (Fig. 4.) supports high CO₂ emissions (Wright et al., 2011; Hoyos-Santillan et al., 2016; Duval and Radu, 2018) and that forested peatland sites may represent a substantial positive ecosystem feedback.

CH₄ production was more temperature sensitive at sites with degraded peat (oil palm sites) supporting kinetic theory that postulates greater energy demands for degradation of complex organic molecules (Bosatta and Ågren, 1999; Davidson and Janssens, 2006). Indeed, CH₄ emissions at 30 °C were comparable among land use classes, suggesting that high temperatures (30 °C in this study) overcome substrate limitation of CH₄ production supporting hypothesis three which predicted that the impact of substrate depletion on GHG production is exacerbated by higher temperatures, with the strongest impact in surface peat. This compares with anaerobic incubations studies of mineral subtropical wetland soils that also report comparable CH₄ emissions among land uses (ranging from agricultural to riparian forest) at 30 °C despite differences among land uses for anaerobic CO₂ fluxes (Moore et al., 2018). As only two temperatures were used in this study, results should be interpreted carefully, as in other tropical peat systems the response of greenhouse gas fluxes to warming is not always linear, meaning that small temperature changes can result in large increases in emissions (Sjögersten et al., 2018). However, the result indicates clearly that the climate burden from conversion of tropical peatlands to drainage-based agriculture/plantation will increase as regional temperatures continue to soar (IPCC, 2006). This adds further to the serious

concerns of the implications for the global climate of the ongoing rapid conversion of peat swamp forest to agriculture and oil palm plantations.

5. Conclusion

We have shown that high GHG emissions from surface peats are strongly controlled by labile substrate availability, suggesting a direct link between fresh litter inputs and microbial community GHG production, as well as depletion of labile carbon deeper in the peat profile. We also conclude that although higher temperatures generally increased GHG fluxes, the magnitude of the temperature response was dependent on organic matter lability, and, that the temperature response differed markedly between CO₂ and CH₄ fluxes. For CO₂ fluxes the greatest temperature response was found at forest sites, potentially reflecting high substrate availability, whilst for CH₄ fluxes higher temperatures increased emissions at both forest and converted sites, implying that climate warming are likely to drive higher CH₄ fluxes not only for sites with high labile carbon supplies (forest) but also from sites dominated by degraded organic matter (oil palm plantations) during periods of high water tables.

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