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

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30

31 **Abstract**

32 Accurate inventory of tropical peatland carbon dynamics is important to (a) determine the size
33 of the active carbon pool; (b) estimate the scale of transfers of peat-derived greenhouse gases
34 to the atmosphere resulting from land use change; and (c) support carbon emissions reduction
35 policies. To date, information on the quality of tropical peatland organic matter and its
36 sensitivity to increases in global temperatures is limited, particularly in the context of land
37 conversion. The aim of this work is therefore to determine peat quality and the temperature
38 response of potential greenhouse gas (GHG) emissions under flooded conditions from tropical
39 peatland sites reflecting the process of conversion from forest to oil palm plantation. Overall,
40 surface peat carbon was more labile than deeper peats, with the largest labile pool at forest
41 sites. In the later stages of land conversion, the relative abundance of recalcitrant organic
42 material increased. Potential GHG fluxes were greatest in surface peats and declined as labile
43 carbon was depleted following land conversion. Higher temperatures resulted in higher
44 potential GHG emissions at all sites but the magnitude of the temperature response depended
45 on organic matter lability. For CO₂ fluxes, the temperature response was most pronounced at
46 forest sites reflecting the greater peat lability at these sites. In contrast, higher temperatures
47 resulted in increased CH₄ emissions both at forest and converted sites. This suggests that
48 increasing temperatures in response to climate warming may drive higher CH₄ emissions from
49 sites dominated by degraded organic matter. Collectively, this study demonstrates that the
50 enhanced decomposition and reduced litter input rates, is reflected in reduced potential CO₂
51 emissions but that higher temperature resulting from climate warming may maintain high GHG
52 emissions at plantation sites.

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55 1. Introduction

56 Palm oil is one of the most widely used agricultural products in the world, with demand
57 projected to increase in the future (Corley, 2009; Koh and Wilcove, 2008; Vijay et al., 2016).
58 Globally, the total land area of mature oil palm plantations increased from 3.5 Mha in 1975 to
59 18.7 Mha in 2014, and a large proportion of this increase occurred in Malaysia (rising from 0.4
60 Mha to 4.7 Mha) (FAOSTAT, 2014). An estimate by Koh and Wilcove (2008) indicated that
61 of all oil palm expansion between 1990 and 2005 in Malaysia, at least 50% has come at the
62 expense of natural rainforest, of which the natural vegetation is predominantly peat swamp
63 forest (PSF) (Davies et al., 2010). The most recent estimates indicate that 1.8 Mha of PSF were
64 converted to oil palm plantation between 2007 and 2015, corresponding to a yearly average
65 deforestation rate of 4.1% in Southeast Asia (Miettinen et al., 2016).

66 PSFs play an essential role in the global carbon cycle and are significant carbon sinks and
67 stores, containing an estimated 15-19% of the global peat carbon stock (610 Gt C) (Dargie et
68 al., 2017; Page, S.E., et al., 2011). The peats are formed in tropical humid zones where water-
69 saturated soil inhibits shoot and root decomposition resulting in organic matter content of 65%
70 or more (Comeau et al., 2013). Peats located in Southeast Asia often contain more than 90%
71 organic matter (Davies et al., 2010). However, PSFs are highly sensitive to disturbance by
72 drainage or deforestation for conversion to oil palm plantations (Evers et al., 2017), and
73 following conversion carbon accumulated over centuries or millennia is rapidly released to the
74 atmosphere contributing to climate warming (Davies et al., 2010; Couwenberg et al., 2010;
75 Hooijer et al., 2013; Moore et al., 2018).

76 It is well known that land use and land use change directly affects the exchange of greenhouse
77 gases between terrestrial ecosystems and the atmosphere (IPCC, 2000). Within tropical

78 peatlands, water-table height is a key regulator of litter decomposition, with water-logged,
79 anoxic conditions driving formation of methane (CH₄) and aerobic environments driving the
80 release of CO₂ (Jauhiainen et al., 2005 and 2016; Couwenberg et al., 2010; Hoyos-Santillan et
81 al., 2016). The high net primary production of the PSF itself is also important for maintaining
82 high carbon accumulation rates (Sjogersten et al., 2014), as it provides inputs of root exudates,
83 decaying roots, wood and leaf material into the peatland system (Hoyos-Santillan et al., 2015,
84 Girkin et al., 2018), which is frequently halted through land conversion and deforestation, with
85 direct implications for carbon storage and organic matter composition.

86 Since 1990, oil palm plantations have been linked to 2.5 Gt C losses in carbon stock in tropical
87 peatlands (Miettinen et al., 2017). There is, however, a lack of data regarding how rapidly
88 carbon is lost to the atmosphere during the conversion process, although a recent study in
89 Malaysia suggests that organic matter content declines within the first one to two years
90 following the start of conversion (Tonks et al., 2017). Furthermore, the conversion altered the
91 surface peat functional organic chemistry as carbohydrates were preferentially depleted as a
92 result of aerobic decay suggesting that conversion will enhance peat recalcitrance but increase
93 its aromaticity (Tonks et al., 2017; Yule et al., 2018).

94 In addition to land use conversion, tropical peatlands are also affected by climate change which
95 is predicted to result in a 3-7 °C increase in temperature and increased seasonality of rainfall,
96 resulting in more pronounced dry and wet seasons (add reference). The impacts of this include
97 increasing length of periods of flooded conditions and above the surface water-tables (IPCC,
98 2007). Recent work in pristine peatlands in the Neotropics has shown strong temperature
99 responses of GHGs emissions under high water-table conditions for both CO₂ and CH₄
100 (Sjogersten et al., 2018). However, both aerobic and anaerobic temperature responses of GHG
101 emissions from wetland soils differ considerably among land use types, likely in response to

102 differences in organic matter lability (Dunfield et al., 1993; Inglett et al., 2012; Turetsky et al.,
103 2014; Gritsch et al., 2015; Duval and Radu 2018). As deforestation rates in Southeast Asia
104 show no signs of slowing, PSFs are predicted to be extinct by 2050, if current rates of
105 deforestation of peatlands continue unchecked (Miettinen et al., 2016). It is therefore critical
106 that we quantify the climate feedback potentials from bothPSF and also degraded peats in
107 plantations. Indeed, it is plausible that high temperatures may further increase the climate
108 burden of GHG emissions from oil palm plantations as the temperature sensitivity of organic
109 matter decomposition is predicted to increase with recalcitrance according to kinetic theory
110 (Bosatta and Ågren, 1999; Davidson and Janssens, 2006).

111 As a result of knowledge gaps outlined above, GHG emissions from drained tropical peatland
112 conversion are at present overlooked in GHG emission budgets as considered by the UN
113 Framework Convention on Climate Change (Climate Change 2014 Synthesis Report for
114 Policymakers, 2014; IPCC, 2006). However, given their important role in the global carbon
115 cycle and the pressures they are exposed to from both land use and climate change it is vital to
116 develop mechanistic understanding of the controls of GHG emissions from forested and
117 converted peatlands to underpin the delivery of evidence based sustainable land use
118 management and policy (Evers et al., 2017). Therefore, this study aims to improve our
119 understanding of the impact of anthropogenic activities e.g. drainage and deforestation on soil
120 organic matter stability and subsequent GHG fluxes from tropical peatlands. To achieve this
121 the study addresses the three specific hypothesis linked to how land use change and temperature
122 alter peat lability and CO₂ and CH₄ fluxes: Our first hypothesis (1) “land conversion of drainage
123 based oil palm plantation result in depletion of labile substrates in surface peat affected by
124 drainage but not in deeper peat layers” is based on the notion that drainage promotes aerobic
125 decomposition in surface peat but not in deeper peats below the water-table where anoxic

126 conditions remain (Jauhiainen et al., 2005; Couwenberg et al., 2010). Because substrate lability
127 often is a predictor of GHG emissions in tropical peatlands (Wright et al., 2011; Hoyos-
128 Santillan et al., 2016) we hypothesised that (2) “ex situ anaerobic CO₂ and CH₄ production will
129 be lower in the later stages of land conversion to oil palm plantation as a result of depletion of
130 labile carbon”. In line with kinetic theory (Bosatta and Agern 1999; Davidson and Janssens
131 2006) we also hypothesised that (3) “the impact of substrate depletion on GHG production is
132 exacerbated by higher temperatures with the strongest impact in surface peat”.

133

134 **2. Methods**

135 *2.1 Study Sites*

136 This study was conducted in November-December 2014 in North Selangor Peat Swamp Forest
137 (NSPSF), Malaysia. The NSPSF comprises of Raja Musa Forest Reserve, Sungai Karang
138 Forest Reserve, Sungai Dusun Wildlife Reserve and part of Bukit Belata Forest Reserve
139 Extension and covers an area of 81, 304 ha. The central area of the reserve is secondary mixed
140 forest; the majority of the area was logged from the 19th century up until the 1980’s, and a
141 significant area of the northern edge of the reserve has already undergone oil palm conversion
142 (Kumari, 1996). Four land conversion classes were selected, with five replicate sites for each,
143 to represent the stages involved in the process of conversion (ranging from secondary forest to
144 mature oil palm), shown in figure 1. The forest sites chosen for this study had not been targeted
145 for logging for approximately 40 years, as a result the forest sites were in areas of high canopy
146 density (trees > 25 m, canopy coverage > 80% (Global Environment Centre, 2014).

147 Drained sites comprised a similar forest structure but large drainage ditches (2-3 m wide and
148 ca. 2 m deep) had been dug every few hundred meters, six months prior to sampling, to lower

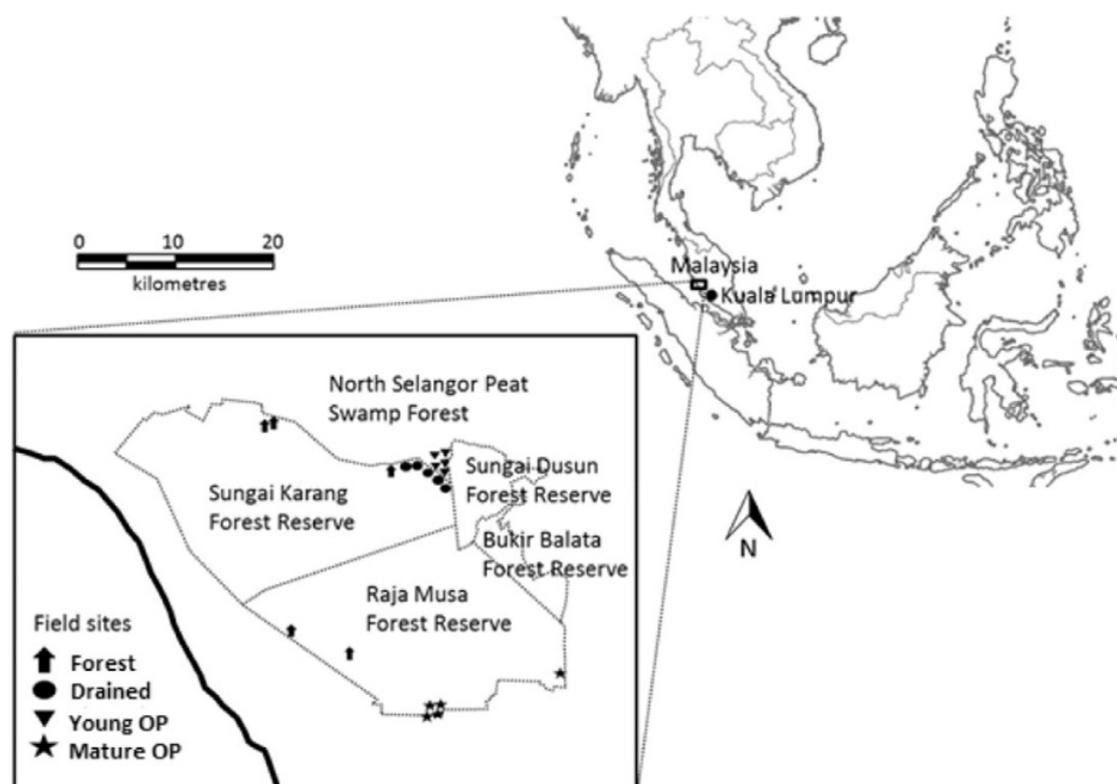
149 the water-table. Secondary mixed forest and drained sites contained trees such as: *Macaranga*
150 *pruinosa*, *Camposperma coriaceum*, *Blumeodendron tokbrai*, *Shorea platy-* *carpa*,
151 *Parartocarpus venenosus*, *Ixora grandiflora*, *Pternandra galeata*; ferns: *Stenoclaena*
152 *palustris*, *Asplenium longissimum*, *Nephrolepis biserrata*; palm: *Crytostachys sp.*; sedges:
153 *Cyperus rotundus* and abundant stands of *Pandanus atrocarpus* (Yule and Gomez, 2009).

154 Recently planted young oil palm sites, where both deforestation and artificial lowering of the
155 water-table had occurred were chosen for sampling. Oil palm seedlings were planted six
156 months prior to sampling.

157 The final sites chosen were mature oil palm, where the oil palm trees were first generation and
158 ca. 10-15 years old. Mature oil palm sites had been subject to deforestation of the PSF and
159 drained before seedlings were planted.



169 Figure 1. Type of peatland habitats surveyed (a) secondary PSF, (b) drained secondary PSF,
170 (c) six-month oil palm plantation and (d) mature oil palm plantation.



180 Figure 2. Location of North Selangor Peat Swamp Forest and the sites belonging to the four
181 different conversion stages. Forest, drained, recently planted and mature oil palm plantation
182 sites.

183

184 2.2 Field sampling

185 In total, four land conversion stages and five plots with an area of 900 m² were marked out.

186 Forest and mature oil palm areas were chosen to maximise spatial distribution, taking into
187 account access, and based on areal images and maps. Drained and recently planted oil palm
188 plantation sites were constrained to two areas due to land management.

189 At all sites, random number tables were used to determine the direction and distance from the
190 south west corner of the plot to ensure random sampling within each plot. GPS coordinates
191 were recorded for each corner and provided in Supplementary Information 1.

192 In each of the plots, peat samples were taken from depths 0-5 cm and 50-55 cm that covered
193 mostly oxic, waterlogged and anoxic conditions respectively. Samples were extracted using a
194 side-filling Russian Peat Corer (Van Walt, UK), with a 50 cm long sampling chamber.
195 Immediately following extraction, peat samples were bagged and sealed to avoid moisture loss.

196

197 *2.3 Peat physical properties*

198 Peat water content, bulk density and organic matter content were determined for all samples.
199 Volumetric water content was estimated from the field using a Delta-T Theta Probe.
200 Measurements were recorded three times per plot to provide an average. Gravimetric water
201 content was assessed by oven drying the peat at 105 °C for 48 hours. Organic matter content
202 was determined as the mass lost after ignition for 7 h at 550 °C and bulk density was determined
203 using oven dried mass methods and known volumes.

204

205 *2.4 Laboratory Incubations*

206 Samples were transported from North Selangor to University of Nottingham and frozen
207 immediately until analysis. At time of incubation, samples were taken from the freezer and left
208 to defrost in a cold room (4 °C) before sub-sampling and subsequent incubation at two
209 temperatures, i) 25 °C and anaerobic and ii) 30 °C and anaerobic.

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

216 After seven days to allow the microbial community to establish, serum bottles were opened to
217 the air to dissipate accumulated headspace gases and then flushed with nitrogen for two minutes
218 and re-sealed. Following an additional seven days of incubation, headspace gas samples (5 ml)
219 were collected weekly by syringe from each serum bottle and analysed immediately by gas
220 chromatography (GC-2014, Shimadzu UK LTD, Milton Keynes, UK) over four weeks.

221 CO₂ and CH₄ concentration were analysed using a single injection system, with a 1 ml sample
222 loop that passed the gas sample using N₂ as a carrier. Thermal conductivity detectors (TCD)
223 and a flame ionization detectors (FID), were used to measure CO₂ and CH₄ respectively.

224 The fluxes were calculated using linear regression of the gas concentration against time. The
225 greenhouse gas data was converted to mass per volume and mass per weight basis by the use
226 of the ideal gas equation and the molecular mass of each gas as shown in Eq. (1). From this,
227 the gas flux from each incubation was calculated using Eq. (2).

$$228 \quad PV = nRT \quad (1)$$

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

232

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

234 Where E is the flux of each gas ($\text{mg m}^{-2} \text{h}^{-1}$), n is the number of moles (CO_2 or CH_4), m is the
235 molar weight (CO_2 : 44.01 and CH_4 : 16.04), a is the area of soil core used and t is the time in
236 the hour.

237 *Rock-Eval 6 Pyrolysis*

238 Surface and subsurface peat samples were analysed using a Rock-Eval 6 analyser. Freeze-dried
239 powdered peat samples (60 mg) were heated at 300 °C for three minutes before an increase in
240 temperature to 650 °C at a rate of 25 °C per minute in an inert N_2 atmosphere. Residual carbon
241 was subsequently oxidized from 300 °C to 850 °C at a rate of 20 °C per minute. The release of
242 hydrocarbons during the two-stage pyrolysis process was detected by a flame ionisation
243 detector, with an infrared cell detecting the release of CO and CO_2 during the thermal cracking
244 of the organic matter. Rock-Eval analysis generated a range of standard parameters including
245 S1 (a measure of free hydrocarbons released on heating to 300 °C), S2 (hydrocarbons released
246 on the thermal cracking of organic matter for temperatures up to 850 °C), S3 CO and S3 CO_2
247 (the CO and CO_2 yielded from the breakdown of kerogen), TpkS2 (the temperature associated
248 with the highest yield of bound hydrocarbons) and total organic carbon (TOC_{RE}).

249 The Hydrogen Index (HI), a measure of hydrocarbons released relative to TOC was calculated
250 from $\text{S2} \times 100 / \text{TOC}_{\text{RE}}$. The Oxygen Index (OI), corresponding to the amount of oxygen
251 released as CO and CO_2 relative to TOC_{RE} was calculated from $\text{S3} \times 100 / \text{TOC}_{\text{RE}}$.

252 Additional parameters were calculated from the deconvolution of S2 pyrograms using Fityk
253 v0.9.7, a curve fitting and data analysis program. S2 pyrograms were deconvoluted into six
254 Gaussian signals (F1 – F6) based on maximising R^2 coefficient values. F1 – F6 values have
255 previously been attributed to organic compounds of increasing complexity and recalcitrance

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256 (Disnar et al., 2003; Sebag et al., 2006). F1 signals represent high labile fresh plant material
257 including simple polysaccharides. F2 signals correspond to lignin and cellulose derived
258 compounds, and F3 and F4 relate to increasingly humified macromolecules. F5 and F6 signals
259 can be attributed to the presence of highly mature and recalcitrant soil organic matter, or
260 charcoal. These signals were used to develop an additional sets of indices. Saenger et al. (2013)

261 proposed combining these signals into three categories representing different phases of carbon
262 thermal stability. C_1 represents the highly labile hydrocarbon compounds (F1 and F2), C_i
263 (corresponding to the more stabilised soil carbon pool, F3), and the highly recalcitrant passive
264 pool, C_p (F4 – F6) (Saenger et al., 2013).

265

266 *2.5 Statistical Analysis*

267 Differences in Rock-Eval parameters and indices were assessed using linear mixed effects
268 model fitted using Residual Maximum Likelihood (REML) to account for variable dependence
269 between sampling plots. Conversion class and depth were selected as fixed effects and sites as
270 random effects. Rates of CH_4 and CO_2 , proportion of carbon in C_1 , C_i and C_p , and total organic
271 carbon were log-transformed to meet assumptions of normality and were also assessed using
272 REML. Relationships between Rock-Eval parameters and CH_4 and CO_2 fluxes from different
273 land uses and depths were assessed using Principal Component Analysis (PCA), based on
274 correlation matrices. All statistical analyses were conducted in GenStat (v17.07)

275

276 **3. Results**

277 *3.1 Rock-Eval Pyrolysis*

278 Thermolabile hydrocarbons (S1), which are released on heating at 300 °C were significantly
279 different between land uses in surface peats ($F_{3,32} = 7.79$, $P < 0.001$, Table 2), with the highest
280 concentrations measured at drained sites, followed by recently planted, forest and mature oil
281 palm plantations (Table 1). More recalcitrant hydrocarbons (S2) which are released between
282 300-650 °C (Johannes et al., 2006), also significantly differed in surface peats between land
283 uses ($F_{3,32} = 5.45$, $p < 0.05$, Table 2) and demonstrated a similar pattern as S1 values, with the

highest values measured in drained sites and the lowest in mature oil palm plantations (Table 1).

TpkS2, which corresponds to the temperature at which hydrocarbon compound release is maximised (Disnar, 1994; Espitalié et al., 1985), showed an increase with land conversion towards oil palm plantations. 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 recently planted 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 recently planted sites (ranging from 45 % to 47 %), however TOC was significantly lower in the mature oil palm sites with 37 % (Table 1) ($F_{3,32} = 2.92$, $p < 0.05$, Table 2).

Table 1. Selected Rock-Eval 6 parameters in surface and subsurface peats. Means \pm one SEM.

Parameter	Peat Depth	Forest	Drained	Recently Planted	Mature Oil Palm
S1 (mg g⁻¹)	Surface	27.87 \pm 1.17	34.89 \pm 2.23	28.76 \pm 1.91	19.91 \pm 1.58
	Subsurface	20.33 \pm 3.59	31.54 \pm 3.1	28.55 \pm 1.52	25.34 \pm 3.12
S2 (mg g⁻¹)	Surface	127.26 \pm 17.04	145.26 \pm 9.04	135.68 \pm 5.98	92.88 \pm 8.53
	Subsurface	125.95 \pm 12.52	149.44 \pm 9.25	130.71 \pm 3.54	113.68 \pm 16.00
TpkS2 (°C)	Surface	403.8 \pm 13.06	416.8 \pm 10.81	425.4 \pm 2.46	441.6 \pm 6.12
	Subsurface	406.8 \pm 14.12	423.6 \pm 1.25	422.4 \pm 3.52	427.6 \pm 8.00
TOC_{RE} (%)	Surface	45.21 \pm 1.64	46.48 \pm 2.13	47.37 \pm 1.05	37.51 \pm 3.96
	Subsurface	45.21 \pm 2.15	47.77 \pm 0.71	47.54 \pm 0.61	43.45 \pm 5.20
HI (mg HC g⁻¹ TOC_{RE6})	Surface	279.2 \pm 29.38	312.4 \pm 13.43	286.8 \pm 12.75	252.6 \pm 19.3
	Subsurface	277.8 \pm 21.66	313.4 \pm 21.35	275.2 \pm 6.09	263.8 \pm 21.15
OI (mg O₂ g⁻¹ TOC_{RE6})	Surface	180 \pm 16.37	138.6 \pm 16.00	132.8 \pm 2.52	160.2 \pm 6.94

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Subsurface	158±26.32	138.6±6.35	136±4.30	125.2±6.29
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Table 2: Rock-Eval 6 statistics assessed via linear mixed effects model (REML). Significant differences in italics.

	Land use				Depth				Land use*Depth			
	F-statistic	d.f.	p	SED	F-statistic	d.f.	p	SED	F-statistic	d.f.	p	SED
S1 (mg g⁻¹)	7.79	3,32	<0.001	3.43	0.68	1,32	0.41	3.43	2.53	3,32	0.074	4.86
S2 (mg g⁻¹)	5.45	3,32	0.004	15.7	0.33	1,32	0.557	15.7	0.52	3,32	0.669	22.3
S3CO (mg g⁻¹)	1.47	3,32	0.242	4.48	1.35	1,32	0.254	4.48	0.35	3,32	0.791	6.34
S3CO₂ (mg g⁻¹)	0.46	3,32	0.712	2.62	1.54	1,32	0.223	2.62	0.07	3,32	0.976	3.7
T_{peak} (°C)	3.85	3,32	0.018	12.34	0.09	1,32	0.772	12.34	0.54	3,32	0.658	17.46
TOC_{RE} (%)	2.92	3,32	0.049	3.7	0.91	1,32	0.332	3.7	0.55	3,32	0.653	5.3
HI	2.73	3,32	0.060	27.38	0.0	1,32	0.988	27.38	0.12	3,32	0.950	38.72
OI	2.73	3,32	0.060	18.1	3.13	1,32	0.087	18.1	0.81	3,32	0.496	25.60

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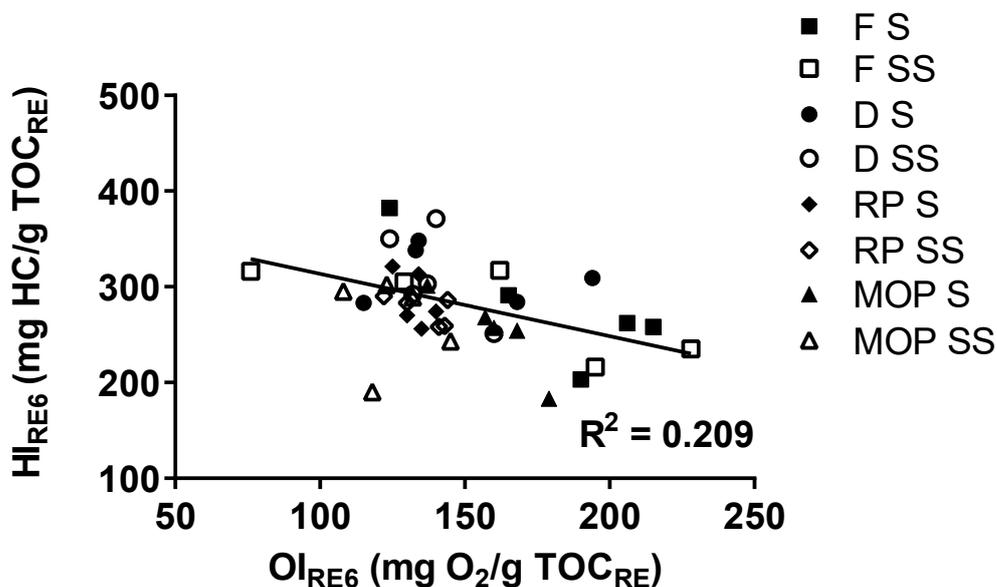


Figure 3. Pseudo-Van Krevelen linking changes against HI and OI for all land uses in surface (S) and subsurface samples (SS) showing trends in humification.

In surface peats, HI 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, while OI 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 (Table 2). 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 recently planted sites in the subsurface peats.

There was large variation ($F_{3,32} = 2.73$, $p=0.06$, Table 2), in HI and OI in surface peats at forest and drained sites compared to later conversion stages in recently planted and mature oil palm plantations which clustered closer together (Fig. 3).

3.2 SOM Thermostability

In surface peats at forest, drained and recently planted sites, the labile carbon pool (C_l) was the largest of the three pools, accounting for 69%, 61% and 50% respectively (Fig. 4). In contrast, C_l significantly differed in mature oil palm sites from the other land uses ($F_{3,16} = 3.41$, $P < 0.05$, Table 3) and accounted for only 15% of carbon. A similar trend was observed in sub surface peats in the C_l pool, with a decrease in lability with conversion stages, although not significant peats ($F_{3,16} = 0.04$, $P = 0.84$, Table 3). The intermediate carbon pool (C_i) varied significantly in surface peats ($F_{3,16} = 3.83$, $P < 0.05$, Table 3) with mature oil palms sites having the largest contribution in this pool of 67% (Fig. 4). The passive pool (C_p) differed significantly between sites in the surface peats ($F_{3,16} = 4.58$, $P < 0.05$, Table 3) with the highest contribution at drained sites and the lowest in forest sites (29% and 5% respectively).

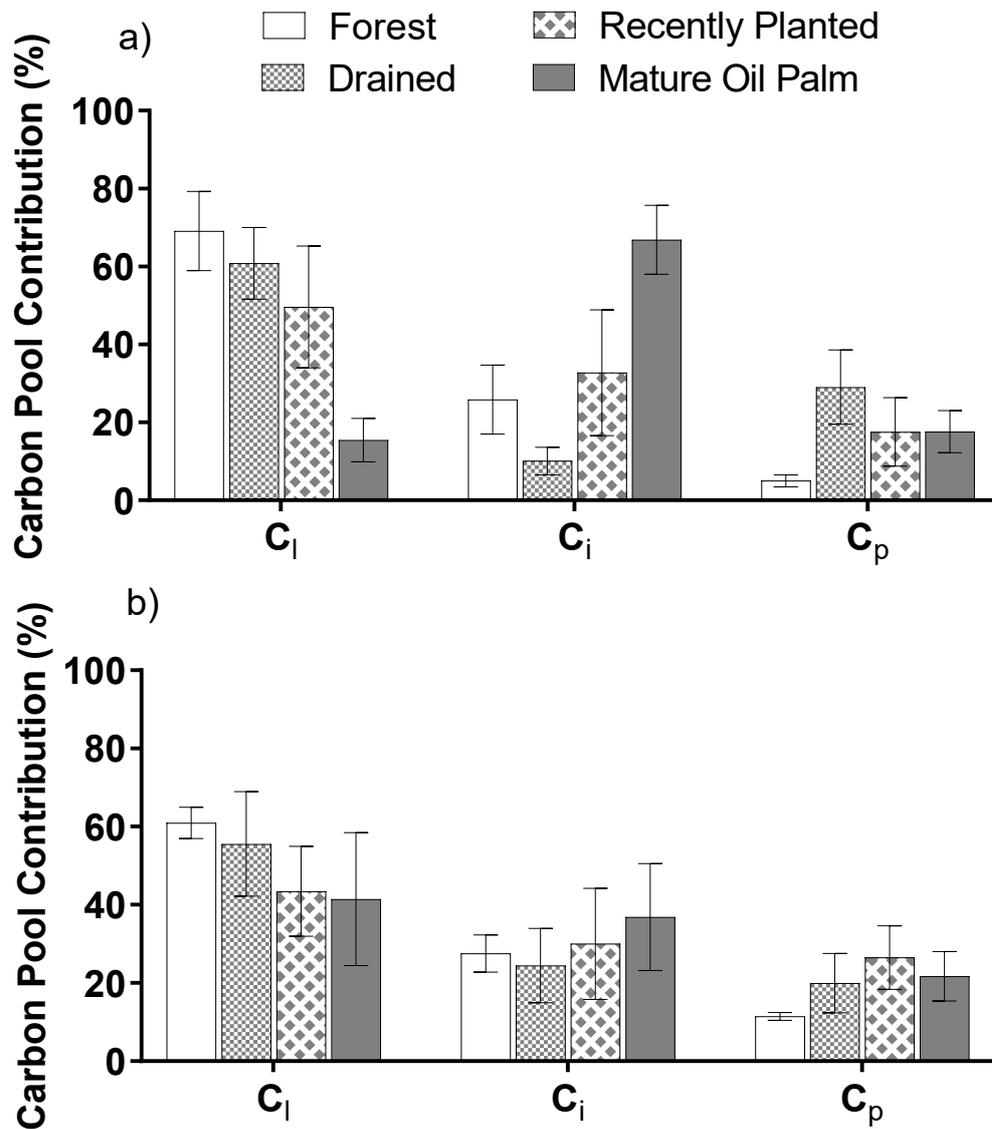


Figure 4. Proportions of labile (C_l), intermediate (C_i) and passive (C_p) carbon pools for different sites in a) surface and b) subsurface peats. Means \pm one SEM. n = 5.

Table 3: Carbon pools, measured through deconvolution of pyrograms produced by Rock-Eval 6, statistics assessed via linear mixed effects model (REML). Significant differences in italics.

	Land use				Depth				Land use*Depth			
	F-statistic	d.f.	p	SED	F-statistic	d.f.	p	SED	F-statistic	d.f.	p	SED
C ₁	<i>3.41</i>	<i>3,16</i>	<i>0.04</i>	<i>16.4</i>	0.04	1,16	0.84	15.4	1.11	3,16	0.34	21.9
C _i	<i>3.83</i>	<i>3,16</i>	<i>0.03</i>	<i>15.3</i>	0.29	1,16	0.6	15.6	1.44	3,16	0.27	22.1
C _p	<i>4.58</i>	<i>3,16</i>	<i>0.017</i>	<i>9.6</i>	0.19	1,16	0.67	11.8	0.47	3,16	0.71	16.6

3.3 CO₂ and CH₄ Incubations

Peats incubated at 25°C and 30°C exhibited a significant declining trend with conversion in surface samples ($F_{3,16} = 9.4$, $p < 0.001$, Table 4), 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 4) when compared to peats incubated at 25°C with the highest mean fluxes from forest peats, with an average of 5.2 ug g⁻¹ h⁻¹ from peats incubated at 25°C and 9.1 ug g⁻¹ h⁻¹ from peats incubated at 30 °C.

CH₄ fluxes were significantly higher in forest and drained sites compared to recently planted and mature oil palm plantations in surface peats ($F_{3,16} = 9.4$, $p < 0.001$, Table 4), with a less pronounced difference with depth from the recently planted and mature oil palm sites.

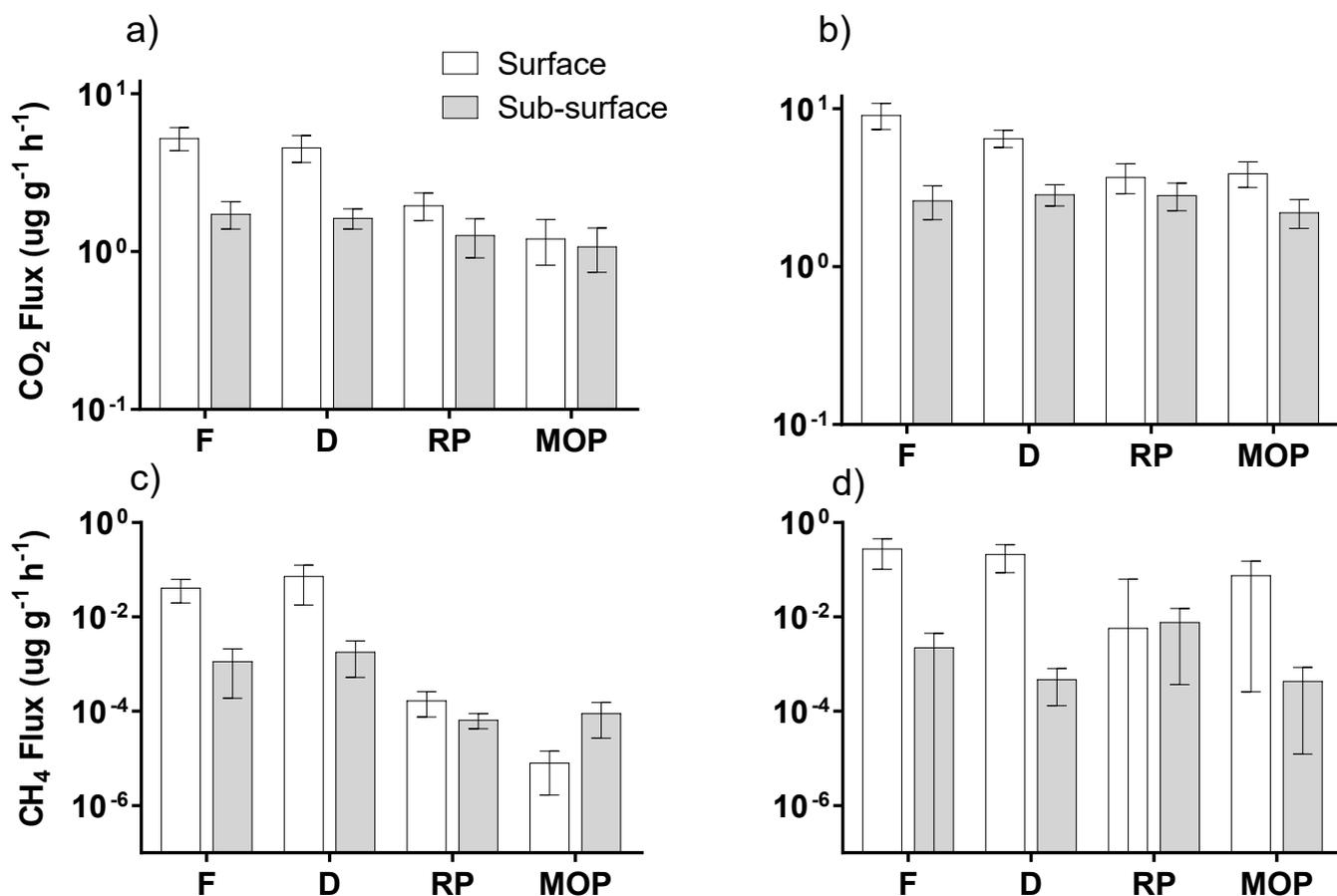


Figure 5. Logged carbon dioxide (a&b) and logged methane fluxes (c&d) at 25°C (a&c) and 30°C (b&d) from surface (0-5 cm) and subsurface (50-55 cm) peats from forest (F), drained (D), recently planted (RP) and mature oil palm (MOP) sites. Carbon dioxide fluxes are shown from time point one and methane from time point four. The pattern in the data was the same at the different time points. Means \pm one SEM. n=5.

Table 4. Gas flux statistics from different land uses and depths assessed by REML. Significant differences in italics.

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

3.4 Relationships between Organic Matter Properties and CO₂ and CH₄ Fluxes

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 C_i parameters (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).

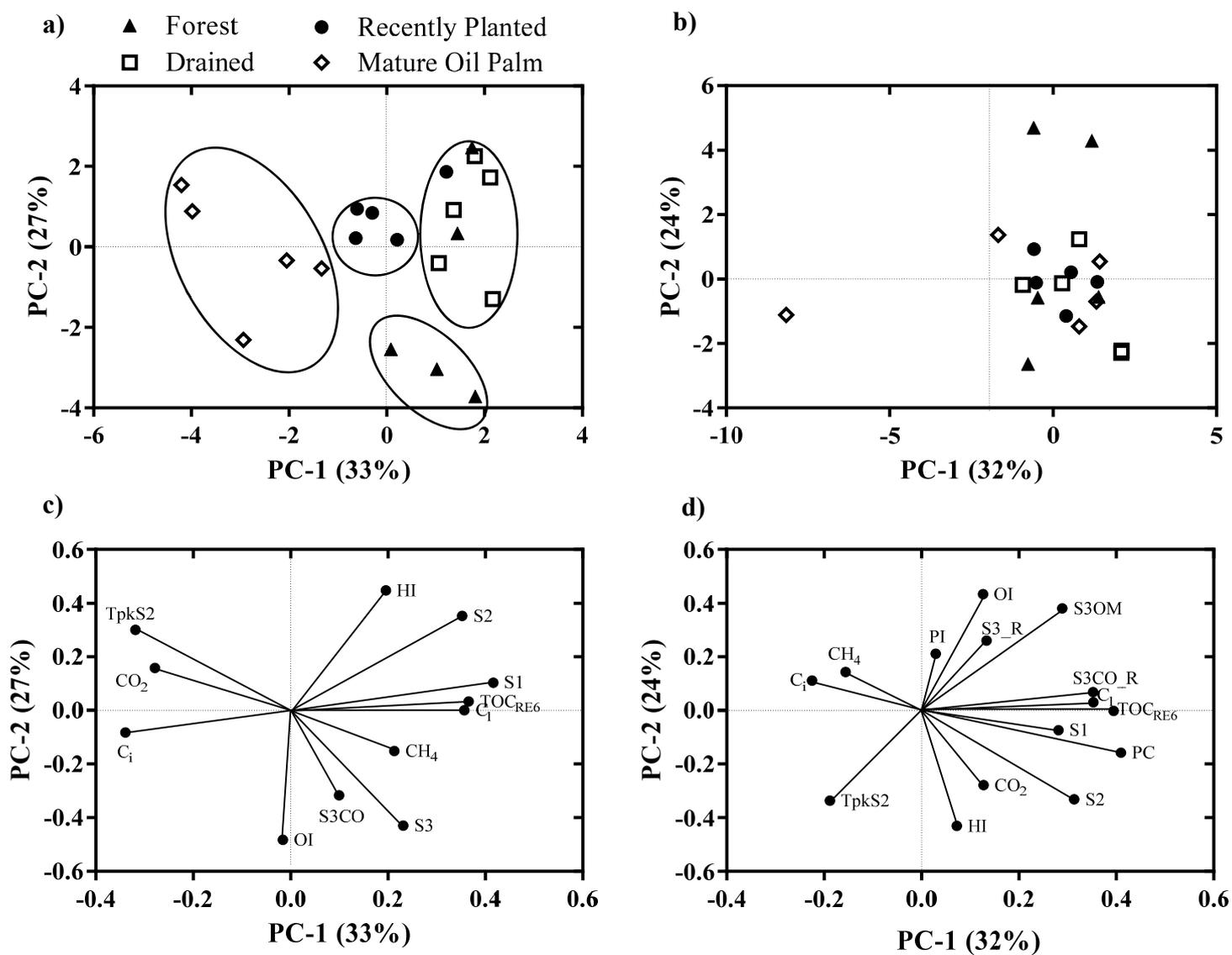


Figure 6. Principal component scores (a&b) and loadings (c&d) for Rock-Eval parameters and carbon dioxide and methane fluxes from surface (a&c) and subsurface (b&d) peats. Combined PC1 and PC2 account for 60% and 56% of the variance respectively.

4. Discussion

4.1 Depletion of labile substrates with conversion to oil palm plantation

The clear decrease in the size of the labile carbon with land conversion (from ca 70 to less than 20% when comparing forest and mature oil palm), together with an increasing intermediate carbon pool (from ca 20 to 70 % when comparing forest and mature oil palm) in surface peat but not in deeper peats (Fig. 4), supported 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 (Tonks et al., 2017; Matysek et al., 2017; Kononen et al., 2017). This is further supported by the greater thermostability 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).

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 enhances the degradation of organic polymers by bacteria and fungi (Couwenberg et al., 2010; Kononen et al 2016). The different responses between the surface and deeper peats to land use change in this study clearly demonstrates 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 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

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the peat surface as litter and into the peat from the rhizosphere, and thus contributes to maintenance of the peat carbon stores by compensating for carbon losses that result from concurrent decomposition (Jauhiainen et al., 2016). PSF 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 (Miyajima et al., 1997; Hoyos-Santillan et al., 2015). However, as lignin is resistant to decomposition and ligninolytic microbes are obligate aerobes (Zeikus, 1981), the amount of cellulosic substrates decreases 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., 2015).

4.2 Linking CO₂ and CH₄ fluxes and organic matter properties

As expected, potential CO₂ production from flooded peat was several orders of magnitude higher than CH₄ 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 (Sjogersten 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 (Wright et al., 2011; Hoyos-Santillan et al., 2016; Sihi et al., 2018; Upton et al., 2018) but 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* CO₂ and CH₄ fluxes from waterlogged peat with progressively more advanced land conversion stage, 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. Similar strong links between GHG fluxes (from water logged peat) and peat organic chemistry has 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 was found with land conversion from the deeper peats which is likely due to limited impacts of land conversion on decomposition deeper in the peat profile which remained below the water-table also after drainage.

These findings clearly demonstrate that the loss of peat due to enhanced decomposition following conversion result 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 limits the microbial communities' capacity to utilise more complex organic molecules. Under aerobic conditions, CO₂ 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 support 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 (Sjogersten et al., 2016) as well as tropical peatlands (Jauhianen et al., 2008). This is likely linked to slow recovery of the methanogenic communities from oxic peat conditions. Indeed, functional shifts in microbial

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community composition e.g. decline in macro fungi abundance, in response to conversion of PSF to oil palm plantations at has been shown previously at these sites (Rajihan et al., 2017; Shuhada et al., 2017) suggesting 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 (Jauhianen et al., 2008; 2016). As PSFs have higher percentage of canopy cover and denser canopy closure (Yule and Gomez, 2009) and greater litter inputs than oil palm plantation (Guillaume et al., 2015), restoring PSF would likely increase pools of labile organic matter in surface peats which could shift microbial community functionality towards its original form, restoration of microbial community functionality has been shown to be limited 3.5 years after forest restoration (Nurulita et al., 2016).

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 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.

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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 Agren 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. 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).

4.4 Conclusion

Surface peat carbon was consistently higher in surface than deeper peats and was greatest in forest sites, with relative decreases following land conversion. GHG fluxes were also greatest from surface peats and declined alongside labile carbon. Higher temperatures also drove higher GHG fluxes but the magnitude of the temperature response was dependent on organic matter lability. While the increase in CO₂ fluxes was greatest at forest sites, higher temperatures increases CH₄ emissions at both forest and converted sites, implying that increasing temperature due to climate warming may drive higher CH₄ fluxes from sites dominated by degraded organic matter. This study demonstrates that the enhanced decomposition and reduced litter input rates is reflected in reduced potential CO₂ emissions but that higher temperature resulting from climate warming may maintain high GHG emissions at plantation sites.

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