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Will CO₂ Emissions from Drained Tropical Peatlands Decline Over Time? Links Between Soil Organic Matter Quality, Nutrients, and C Mineralization Rates

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1 **Will CO₂ emissions from drained tropical peatlands decline over time? Links between soil**
2 **organic matter quality, nutrients, and C mineralization rates**

3 *Shortened version:* CO₂ production from tropical peat decomposition

4 Swails, E¹, Jaye, D¹, Verchot, L², Hergoualc'h, K³, Schirrmann, M⁴, Borchard, N^{3,5}, Wahyuni,
5 N³, Lawrence, D¹

6

7 ¹*Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903,*

8 ²*International Center for Tropical Agriculture, Km 17 Recta Cali-Palmira, Apartado Aereo*

9 *6713, Cali 763537, Colombia, ³Center for International Forestry Research, Jalan CIFOR, Situ*

10 *Gede, Sindang Barang, Bogor 16115, Indonesia, ⁴Leibniz Institute for Agricultural Engineering*

11 *and Bioeconomy, Max-Eyth-Allee 100, 14469 Potsdam, Germany, ⁵Ruhr-University Bochum,*

12 *Institute of Geography, Soil Science/Soil Ecology, Universitätsstrasse 150, 44801 Bochum,*

13 *Germany*

14

15 Correspondence: Erin Swails, tel. +1 434 924 7761, e-mail: ees8rg@virginia.edu

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17 *Keywords:* tropical peat swamp forest, oil palm plantation, land use change, incubation,

18 microbial respiration, Indonesia

19

20 **Abstract**

21 **Conversion, drainage, and cultivation of tropical peatlands can change soil conditions, shifting**

22 **the C balance of these systems, which is important for the global C cycle.** We examined the

23 effect of soil organic matter (SOM) quality and nutrients on CO₂ production from peat

24 decomposition using laboratory incubations of Indonesian peat soils from undrained forest in
25 Kalimantan and drained oil palm plantations in Kalimantan and Sumatra. We found that oil palm
26 soils had higher C:N and lower SOM quality than forest soils. Higher substrate quality and
27 nutrient availability, particularly lower ratios of aromatic:aliphatic carbon and C:N, rather than
28 total soil organic matter or carbon, explained the higher rate of CO₂ production by forest soils
29 ($10.80 \pm 0.23 \mu\text{g CO}_2\text{-C g C hr}^{-1}$) compared to oil palm soils ($5.34 \pm 0.26 \mu\text{g CO}_2\text{-C g C hr}^{-1}$)
30 from Kalimantan. These factors also explained lower rates in Sumatran oil palm ($3.90 \pm 0.25 \mu\text{g}$
31 $\text{CO}_2\text{-C g C hr}^{-1}$). We amended peat with nitrogen (N), phosphorus (P), and glucose to further
32 investigate observed substrate and nutrient constraints across the range of observed peat quality.
33 Available N limited CO₂ production, in unamended and amended soils. P addition raised CO₂
34 production when substrate quality was high and initial P state was low. Glucose addition raised
35 CO₂ production in the presence of added N and P. Our results suggest that decline in SOM
36 quality and nutrients associated with conversion may decrease substrate driven rates of CO₂
37 production from peat decomposition over time.

38

39 **Introduction**

40 With estimated C stocks of 88.6 Pg C (Page *et al.*, 2011), tropical peat soils comprise 19% of
41 global tropical forest C stocks in an area that is roughly 1% of total tropical forest extent (Pan *et*
42 *al.*, 2011a). Indonesian peatlands hold an estimated one third of tropical peat soil carbon stocks
43 (Gumbricht *et al.*, 2017), but are a major and growing source of greenhouse gas emissions due to
44 increasing pressure from agricultural uses, particularly the expansion of oil palm plantations
45 (Hooijer *et al.*, 2010; Koh *et al.*, 2011; Miettinen *et al.*, 2012). Conversion of tropical peat
46 swamp forests to oil palm plantations usually entails emissions of CO₂, CH₄, and N₂O from

47 clearing and burning, while peat drainage generates additional and sustained CO₂ emissions from
48 the decomposition of soil organic matter (SOM). By one estimate, development of existing
49 government leases for oil palm in Kalimantan peatlands alone may contribute 18% (0.44-0.55 Gt
50 CO₂-equivalent yr⁻¹) of Indonesia's 2020 projected greenhouse gas emissions (Carlson et al.,
51 2012).

52 Enhanced understanding of controls on peat decomposition is needed to reduce
53 uncertainty in estimates of CO₂ emissions from tropical peat. Though CO₂ fluxes from peat soils
54 are highly heterogeneous over space and time (Jauhiainen *et al.*, 2005; Hirano *et al.*, 2009,
55 2012), existing regional analyses rely on extrapolation of point-based flux measurements using
56 land cover as a proxy for CO₂ emissions, applying for example IPCC emission factors (Drösler *et*
57 *al.*, 2014). These analyses do not directly consider the biogeophysical parameters influencing
58 temporal and spatial variation in carbon emissions from peat. Among biogeophysical factors,
59 water table depth is considered the dominant control on decomposition of tropical peat soils
60 (Couwenberg et al., 2009). However, empirical evidence indicates that soil temperature and
61 moisture influence mineralization of SOM in tropical peatlands (Hirano *et al.*, 2007, 2009, 2012;
62 Jauhiainen *et al.*, 2008, 2014). The influence of SOM quality on decomposition as well as
63 nutrients, specifically N and P, has been well documented in mineral soils (e.g. Haynes 1986;
64 Hobbie and Vitousek 2000; Prescott 1995). These factors also affect spatial and temporal
65 variability in decomposition of peat soils in boreal regions (Turetsky *et al.*, 2000; Minkinen *et*
66 *al.*, 2007; Sjögersten *et al.*, 2016), temperate regions (Scanlon 2000; Schrier-Uijl *et al.*, 2011;
67 Juszczak *et al.*, 2013), and tropical regions (Wright *et al.*, 2011; Hoyos-Santillan *et al.*, 2016),
68 including Southeast Asia (Jauhiainen *et al.*, 2016; Comeau *et al.*, 2016).

69 In undrained mature tropical forests, peat SOM quality and nutrient content are
70 determined by original bedrock material, climate, hydrological regime, and peat forming
71 vegetation (Page *et al.*, 1999; Wust & Bustin 2004; Dommain *et al.*, 2011). Conversion of peat
72 swamp forest to agricultural use alters peat SOM quality and nutrient content as a consequence
73 of drainage, burning, and changes in litter and nutrient inputs in temperate (Heller *et al.*, 2015)
74 and tropical peatlands (Hirano *et al.*, 2012; Jauhiainen *et al.*, 2014; Könönen *et al.*, 2015) (Figure
75 1). Increasing levels of disturbance in peatlands result in the loss of labile carbon and an
76 increasing proportion of recalcitrant compounds in peat surface layers as well as depletion of N,
77 P, and K (Könönen *et al.*, 2016). Thus conversion of tropical peatlands to oil palm plantations
78 may influence *in situ* rates of CO₂ production from microbial decomposition of peat by altering
79 the quality of peat substrate available for decomposition.

80 Field based studies (e.g. Comeau *et al.*, 2016) cannot easily separate physical drivers
81 from chemical and biological controls on peat decomposition. To date, *ex situ* studies of CO₂
82 production by tropical peats have largely focused on forested peatlands (e.g. Wright *et al.*, 2011;
83 Jauhiainen *et al.*, 2016; Hoyos-Santillan *et al.*, 2016) and disregarded oil palm plantations. This
84 *ex situ* study addresses gaps in knowledge of controls on microbial decomposition in undrained
85 and drained tropical peat soils. Specifically, we investigated the influence of variation in SOM
86 quality and nutrient availability on CO₂ production in peat from forests and oil palm plantations.
87 Our study included soils from undrained peat forest and drained smallholder oil palm plantations
88 on shallow peat (< 3 m) in Kalimantan and industrial oil palm plantations on deep peat (> 7 m) in
89 Sumatra. Smallholder plantations are an important and growing source of palm oil production in
90 Indonesia, **accounting for 40% of total oil palm area (BPS 2015)**, and roughly a third of national
91 production (Obidzinski *et al.*, 2012). The geographic range and management variability in our

92 study allowed us to investigate a wide range of peat quality comparable to that observed in
93 forested peatlands and oil palm plantations across Indonesia (Table 1).

94 We designed our experiments to test the hypothesis that CO₂ production from microbial
95 decomposition of peat decreases with decreasing substrate quality (as measured by SOM quality
96 and C:N ratio) and nutrient availability. In the course of the study, we asked three questions: (1)
97 How do peat substrate quality and nutrient availability vary among our sites? (2) Does variation
98 in substrate quality and nutrient availability explain variation in CO₂ production? And (3) does
99 CO₂ production respond to the addition of labile carbon and nutrients?

100 To investigate the influence of variation in substrate quality and nutrients on CO₂
101 production, we conducted laboratory incubations. Observing significant relationships in
102 unamended soils, we also conducted incubations of peat treated with N, P, and glucose to further
103 explore relationships among SOM quality, nutrient availability, and CO₂ production. Given the
104 stoichiometry of microbial biomass, N and P addition should increase C mineralization over the
105 short term, though increased N availability may decrease mineralization of recalcitrant C over
106 the long term (Moorehead and Sinsabaugh 2006; Craine *et al.*, 2007). With short incubations, we
107 address effects on the more labile C pool in soil samples.

108 **Materials and methods**

109 *Site description*

110 We collected peat samples at two sites in Kalimantan (S 02° 49,410', E 111° 48.785') and one
111 site in Jambi, Sumatra (S 01°38.456', E 103°54.335', Figure 2). We sampled undrained peat
112 forest and smallholder oil palm plantations in Central Kalimantan Province, approximately 10
113 km from the city of Pangkalan Bun, in and around Tanjung Puting National Park. Sumatra peat
114 samples were collected from an industrial oil palm plantation near Berbak National Park,

115 approximately 20 km from the city of Jambi. The climate of the region is humid tropical, with
116 little variation in temperature throughout the year and high annual rainfall. We used monthly
117 mean weather observations from Iskandar airport in Pangkalan Bun and Sultan Thaha airport in
118 Jambi during 2005-2014 to describe climate at the sampling sites. Mean annual temperature in
119 Pangkalan Bun is 27.4°C. Mean annual rainfall is 1808 mm and September is typically the driest
120 month (85 mm). In Jambi, mean annual temperature is 27.1°C. Mean annual rainfall is 1846 mm
121 with the driest month (115 mm) typically occurring in June.

122 At each site, we collected samples from three plots that were 1-10 km apart. The plots
123 represent a range of land use history and peat depth, as summarized in Table 2. Oil palm
124 plantation age ranged from four to eight years at the Kalimantan site and from five to ten years at
125 the Sumatra site. Kalimantan forest plots were situated at varying distances from the edge of the
126 main stem of the river surrounding the peat dome and thus differed in peat depth (Table 2).

127 Information on land use history at the Kalimantan sites was based on interviews with
128 smallholder plantation owners. The plot closest to the river (K-FOR-1) was a 30 year old
129 secondary forest, likely formerly used as an agroforestry garden at the time Tanjung Puting
130 National Park was established (Novita 2016), whereas the other two forest plots (K-FOR-2, K-
131 FOR-3) were mature forest. Vegetation height and basal area was similar among the three sites,
132 but K-FOR-1 had lower species diversity and evenness than K-FOR-2 and K-FOR-3, indicative
133 of forest succession at K-FOR-1 (Novita 2016).

134 Smallholders began planting oil palm on their lands in the late 2000s, following the
135 establishment of an industrial oil palm plantation adjacent to smallholder properties in the late
136 1990s. Part of the smallholder properties had been deforested, burned, and drained in 1989,
137 undergoing several cycles of burning, cropping with rice and vegetables, and fallow before the

138 establishment of oil palm. To maintain drained conditions smallholders excavated small canals in
139 the cultivated area of peat. In this area cleared in 1989, we installed one plot in a plantation
140 established in 2011 (K-OP-2011). Another area was cleared in 2005 and also underwent
141 cropping with rice and vegetables, likely experiencing multiple fires prior to the establishment of
142 oil palm. We installed a second plot in this area where palm was planted in 2009 (K-OP-2009)
143 and a third plot where palm had been established in 2007 (K-OP-2007). Information on land use
144 history at the Sumatra sampling site was obtained from company authorities. The area included
145 in our study was cleared in 2004 by the company and planted with oil palm in 2005 (S-OP-
146 2005), 2007 (S-OP-2007), and 2010 (S-OP-2010).

147 Kalimantan smallholders implemented plantation management practices comparable to
148 those implemented in the Sumatran industrial plantations. Smallholders worked at the nearby oil
149 palm company and followed the company's management practices. At both Kalimantan and
150 Sumatra sites, palms were planted in a triangular design with inter-palm distance of 7-9 m
151 (averaged 8m) for a density of 150 palms ha⁻¹. Smallholders concentrated fertilizer application
152 within a 200 cm radius of palms, applying controlled release fertilizer at a rate of 150 kg ha⁻¹ yr⁻¹
153 of N, 84 kg ha⁻¹ yr⁻¹ P, and 124 kg ha⁻¹ yr⁻¹ K in the youngest plantation (K-OP-2011) decreasing
154 to 120 kg ha⁻¹ yr⁻¹ of N, 67 kg ha⁻¹ yr⁻¹ P, and 100 kg ha⁻¹ yr⁻¹ K in the oldest plantation (K-OP-
155 2007). Fertilization rates for K-OP-2009 were not provided by smallholders. Fertilizer was
156 usually applied four times per year in smallholder plantations, but the actual frequency of
157 fertilization depended on available funds. In Sumatran industrial plantation with older vegetation
158 straight fertilizers were applied two times per year (urea, muriate of potash, rock phosphate,
159 CuSO₄, ZnSO₄, CaCO₃, borate) which is standard practice for mature plantations Southeast Asia
160 (Lim *et al.*, 2012). Average drainage depth at the Sumatra site (-60 cm, Oktarita *et al.*, 2017) was

161 greater than at the Kalimantan site (-50 cm, Swails *et al.*, in preparation). Oil palm plots
162 underwent single or multiple fires at both sites (Table 2).

163 *Soil sample collection*

164 We sampled the peat surface layer to assess the region of the soil column with maximum rates of
165 C mineralization. Active carbon cycling in undisturbed tropical peat swamp forests is largely
166 confined to the upper layer of peat soils. Sporadic aerobic conditions occur there and litterfall
167 and roots transfer fresh organic material to the soil (Moore *et al.*, 2013). Though drainage for oil
168 palm is typically around 40 cm or deeper (Lim *et al.*, 2012), root density and microbial activity is
169 usually highest closer to the soil surface (Khalid *et al.*, 1999, Goodrick *et al.*, 2016).

170 In June of 2015, we collected the samples for incubations and chemical analysis from the
171 peat surface layer (0-5 cm) using stainless steel bulk density rings (8 cm in diameter). Samples
172 from each plot were taken at three within plot locations separated by 10-20 m. In oil palm plots,
173 samples for incubation were collected along four transects emanating from one oil palm per
174 location (Figure 2c). The transects ran in randomly determined directions between 0° – 90°, 90° –
175 180°, 180° – 270°, and 270° – 360°. Four samples were collected from each transect at randomly
176 determined distances 1 – 2 m, 2 – 3 m, 3 – 4 m, and 4 – 5 m from the base of the palm. Total
177 transect length covered roughly half the distance between the palm and its nearest neighbors.
178 Similarly, in forest plots, transects originated from one tree per location at three within plot
179 locations. Due to lower bulk density and higher water content of forest soil, two soil samples
180 were drawn from each distance interval to yield an adequate dry mass of soil. Soil sampled along
181 the four transects at each location were composited to yield one soil sample per location (n = 3
182 per plot). The samples were transported in plastic bags to the laboratory then air dried for 72
183 hours followed by manual root removal and storage at 4°C. A subsample of each composite was

184 retained for chemical analysis. These subsamples were air dried for an additional 4 days,
185 followed by sieving to < 2 mm, manual removal of remaining small roots, and storage in sealed
186 plastic bags. Finally, bulk density was determined from replicate samples taken alongside
187 samples for incubation and soil chemistry. Samples were weighed in the field, transported in
188 plastic bags, and oven dried to constant mass at 60°C (Warren *et al.*, 2012). Soil collection was
189 completed within three weeks, under dry climatic conditions.

190 *Analysis of soil chemical properties*

191 Analysis of total C and N content was conducted at the University of Virginia by dry combustion
192 using a Thermo Scientific Flash 2000 CHNS/O analyzer. We also measured SOM content by
193 loss on ignition at 500°C for 180 minutes. Analysis of available N (NO_3^- and NH_4^+) (1 N KCl
194 cadmium reduction) and available P (Bray II) was carried out by Brookside Laboratories, New
195 Bremen, Ohio. Brookside also conducted measurement of pH (1:1 in H_2O) on samples collected
196 from plots in July of 2014 (Swails *et al.*, *unpublished data*). All analysis was conducted on air-
197 dry soils except for total C and N determination for which soils were oven dried at 60°C to
198 constant weight. All results are presented on an oven-dry basis.

199 *Collection of Vis-NIR spectra*

200 Visible to near infrared (Vis-NIR) spectroscopy detects absorbance of incident radiation at
201 wavelengths corresponding to specific functional groups present in SOM, enabling rapid and
202 cost-effective analysis of SOM quality compared to conventional soil analysis (Stenberg *et al.*,
203 2010; Gholizadeh *et al.*, 2013). This approach has successfully been used to detect levels of
204 aromatic and aliphatic carbon compounds in soils and litter material (Terhoeven-Urselmans *et*
205 *al.*, 2006). We collected Vis-NIR spectra within the wavelength range 350 – 2500 nm on air-
206 dried peat samples spread on petri dishes with a FieldSpec FR post dispersive spectrometer at the

207 Center for International Forestry Research in Bogor, Indonesia. Samples were illuminated by a
208 DC lamp adjusted to 24° beam angle (Rodionov *et al.*, 2014). A fiber optic probe placed 5 cm
209 above the surface gave an optical scanning field with 3.8 cm diameter (Rodionov *et al.*, 2014). In
210 order to increase signal to noise ratio, we averaged three repeated measurements on each peat
211 sample to generate one spectrum per sample. Absorbance spectra were obtained for all peat
212 samples (three locations for each of three plots at three sites, n = 27). We removed baselines
213 from the 27 absorbance spectra with the asymmetric least squares method implemented in the R
214 package ‘baseline’ (Eilers & Boelens, 2005). Using the baseline corrected spectra, we quantified
215 peak height at wavelengths associated with specific functional groups of interest. To facilitate
216 visual inspection of the spectra absorption peaks that were indicative of soil matter composition
217 and chemical structure, the spectra of the three plot locations were averaged to yield one
218 representative baseline corrected spectra per plot (n=9). To distinguish specific wavelengths
219 associated with functional groups of interest, we computed 1st derivatives of the spectra using the
220 Savitsky-Golay filter (Savitsky & Golay, 1964).

221 While humic acids (600 nm), phenols (990 nm), lignin (2270 nm), cellulose (2270, 2330
222 nm), starches and sugars (2100nm), and clays (2200 nm) can be detected from Vis-NIR spectra
223 (Shenk *et al.*, 1992, Workman & Weyer 2008, Wight *et al.*, 2016), we focused on aromatic and
224 aliphatic hydrocarbons. The ratio of the two is indicative of the state of decomposition of the soil
225 organic matter. A higher aromatic:aliphatic ratio is indicative of a higher proportion of
226 recalcitrant SOM, which Haberhauer *et al.* (1998) and Ernakovich (2014) related to a more
227 advanced state of decomposition in boreal peats. The absorption peak around 1730 nm is
228 indicative of aromatic functional groups, while the adjacent peak around 1760 nm is associated
229 with aliphatic carbohydrates as is the peak around 1200 nm (Workman & Weyer 2008). We

230 derived indices by dividing peak height at 1730 nm by peak height at 1760 nm
231 (aromatic:aliphatic I) and 1200 (aromatic:aliphatic II). We expected higher ratios in more highly
232 decomposed soils, and we expected lower rates of CO₂ production from those soils.

233 *Incubation without amendment*

234 The purpose of the first incubation was to determine the effect of differences in peat properties
235 on CO₂ production across the range of land history and management conditions represented by
236 oil palm and forest plots at the three sites. Both soil moisture and temperature were uniform
237 across treatments, however, soil moisture was fixed while air temperature was allowed to vary
238 with ambient temperature in the laboratory. Prior to incubation, the moisture content of air dried
239 composited soil samples was determined by weighing subsamples before and after oven drying
240 at 60°C for 48 hours (constant mass). Soils were brought to the target moisture level by adding
241 deionized (DI) H₂O and maintained at that level with further additions throughout the
242 experiment. The target gravimetric soil moisture level was 2 g DI H₂O / g oven dry soil. This
243 value falls within the typical range of soil moisture measured from Jan 2014 to Jun 2015 in the
244 oil palm plantations in Kalimantan (1.5 - 3.8 g DI H₂O g oven dry soil⁻¹, Swails *et al.*, *in*
245 *preparation*).

246 Following initial soil moisture adjustment, we placed subsamples of approximately 20 g
247 oven dry equivalent mass in 500 ml jars fitted with two one-way stopcock valves. Jars (3 sites *
248 3 plots * 3 locations * 3 reps = 81) were capped and soils allowed to equilibrate for 24 hours
249 prior to the first measurement. The concentration of CO₂ and atmospheric pressure in each jar
250 was measured with a PP Systems brand Infrared Gas Analyzer (IRGA) at 0, 1, 2, and 3 hours
251 after capping. We followed this 4-hour sampling procedure again after 8, 24, 48, 96 and 168
252 hours (day 7). Jars were uncapped at the beginning of each measurement period to allow mixing

253 of headspace with ambient air to draw down headspace CO₂ concentration. Jars remained closed
254 between measurement periods.

255 Air temperature was recorded with a Weatherhawk mini-station placed in the same room
256 with the incubation jars; it varied from 27.5 to 31.7°C when measurements were being taken.
257 Soil moisture was monitored by measuring the combined weight of each jar and subsample at the
258 beginning of the incubation and at each measurement period. Mean moisture over the experiment
259 (1.90 ± 0.12 g H₂O g d.m.⁻¹) remained close to the target of 2 g H₂O g d.m.⁻¹ with small but
260 significant differences among jars from different locations within plots. After the last CO₂
261 measurement period, the final weights of jars and subsamples were recorded. Subsamples were
262 oven dried to determine final soil moisture content and jar headspace volume was measured.

263 *Incubation with N, P and glucose amendment*

264 To further explore constraints on CO₂ production observed in the incubation of native soils, we
265 next amended soils with N and P (NP experiment) and with glucose with and without N and P
266 (NPG experiment). Physical limitations of our measurement approach prevented us from
267 including all nine plots in the experiments with nutrient and labile carbon additions. The number
268 of samples would have been too large to complete the first and second set of measurements in a
269 timely manner so as to capture transient effects of amendment on CO₂ production. Therefore we
270 used a subset of plots which included the 8-year old plantations in Sumatra and Kalimantan (S-
271 OP-2007 and K-OP-2007) and one of the mature peat swamp forest plots in Kalimantan (K-
272 FOR-3). By using one plot from each site, we were able to include the range of variation in soil
273 substrate quality and nutrient availability represented by our three sites. We followed the same
274 protocol used previously with some modifications. We incubated an equivalent of 15 g oven dry
275 mass in the NP experiment and 20 g oven dry mass in the NPG experiment. Samples were

276 allowed to equilibrate for 48 hours prior to treatment. Treatments were added in 1 ml solution in
277 the NP experiment and 3 ml solution in the NPG experiment. Controls received a volume of DI
278 H₂O equal to treatments in both experiments. Target gravimetric soil moisture for both
279 experiments was 2 g DI H₂O g d.m.⁻¹.

280 For the NP experiment, two subsamples from each location in each plot were randomly
281 assigned as replicates to one of five treatments (3 plots * 3 locations * 5 treatments * 2 replicates
282 = 90 samples): high N, low N, high P, low P, and control (DI H₂O). Low N treatment received
283 0.5 mg ammonium nitrate (NH₄NO₃) per g d.m. peat, a level equivalent to a single dose of 50 kg
284 N ha⁻¹ to the top 10 cm of soil within a 2 m radius of a palm. This level is representative of N
285 fertilization in Sarawak for adult oil palms growing on peat applied twice a year at a rate of 100
286 kg N ha⁻¹ year (Melling *et al.* 2007). N fertilizer application rates are comparable in Indonesia
287 (102 – 170 kg N ha⁻¹ year⁻¹, Darmosarkoro *et al.*, 2003) though lower rates of N application of 60
288 – 70 kg ha⁻¹ yr⁻¹ have also been reported (Marwanto & Agus, 2014; Comeau *et al.*, 2016). In
289 mature industrial plantations, the fertilization rates are typically based on leaf analysis (Lim *et*
290 *al.*, 2012). Low P treatment received 0.7 mg disodium phosphate (Na₂HPO₄) per g d.m. peat,
291 equivalent to a single application of 75 kg rock phosphate ha⁻¹ to the top 10 cm of soil (or 0.5 kg
292 rock phosphate per palm considering a palm density of 150 palms ha⁻¹). This dose is
293 representative of P fertilization for plantations in Southeast Asia (Lim *et al.*, 2012). High N and
294 high P treatments received rates 10 times higher than low N and P treatments.

295 In the NPG experiment, glucose was added with and without N and P. Two subsamples
296 from each location in each plot were randomly assigned as replicates in one of four treatments (3
297 plots * 3 locations * 4 treatments * 2 replicates = 72 samples): N + P, glucose, N + P + glucose,
298 and control (DI H₂O). Application rates of N and P were the same as low N and P treatments in

299 the NP experiment. Glucose was applied at a rate of 0.5 mg per g d.m. (0.2 mg of C per g d.m.),
300 approximately 0.04% of the total carbon pool in each jar. Glucose addition as low as 0.05 mg per
301 g d.m. has been shown to satisfy labile C requirements for microbial respiration in soil
302 incubations (Blagodaskaya *et al.*, 2007). We selected a higher rate of glucose addition to ensure
303 detection of enhanced CO₂ production with our measurement approach.

304 CO₂ measurements were taken (as described above) at 0, 8, 24, 48, 144 and 240 hours
305 (day 10). An additional measurement was collected at 96 hr (day 4) in the NPG experiment.
306 During measurements for the NP experiment, air temperature ranged between 25.9°C and 32.9°C
307 and during the NPG experiment, it varied between 27.5°C and 32.6°C. Daily air temperature
308 increased steadily over the course of the NP experiment ($p < 0.001$), but did not vary
309 systematically during the NPG experiment. Mean soil moisture was 1.93 ± 0.01 g H₂O g d.m.⁻¹
310 and 2.13 ± 0.02 g H₂O g d.m.⁻¹ in the NP and NPG experiments, respectively.

311 *Calculations and statistical analysis*

312 All statistical analyses were completed using R (v 3.2.5) except for repeated measures ANOVA,
313 conducted with SPSS (v 23). We used Bartlett's test of equal variance and then Student's t-test
314 or Welch's t-test as appropriate to detect differences in soil properties between forest and oil
315 palm soils from Kalimantan and between Kalimantan and Sumatran oil palm soils.

316 The rate of CO₂ production ($\mu\text{g CO}_2\text{-C}$ over time) was determined by linear regression of
317 the concentration measured at each hour of the measurement period. We derived cumulative
318 CO₂-C production over the experiment, assuming the rate between adjacent time points was the
319 average of the rate at the two time points. We report on per g dry mass (d.m.) and per g C basis.

320 We assessed treatment effects on cumulative CO₂ production with one-way and two-way
321 ANOVAs. To assess the effect of time on treatment response, we used one-way and two-way

322 repeated measures ANOVA. Despite efforts to keep soil moisture constant across treatments, it
323 varied somewhat, as determined by one-way ANOVA with Tukey's method for multiple
324 pairwise comparisons. Therefore we treated soil moisture as a covariate in our ANOVA models
325 to control for variation due to small differences in soil moisture. Though temperature in the
326 laboratory varied with time, all jars were incubated under the same temperature conditions, and
327 thus we did not treat temperature as a covariate. We used probability plots to assess normality of
328 residuals and a Brown-Forsythe test for homogeneity of variance in CO₂ production among
329 treatment groups.

330 For the incubation of unamended soils, we used one-way ANOVA with planned
331 comparisons to compare total cumulative CO₂ production between sites. In the repeated
332 measures ANOVA of rates through time, the data violated the assumption of sphericity
333 (Mauchly's $W = 0.080$, $p < 0.001$). Therefore, we applied the Greenhouse-Geisser correction for
334 tests of within-subjects effects. We also used this experiment to assess relationships among
335 measured soil parameters and indices of SOM quality and cumulative evolved CO₂-C. We used
336 simple univariate regression and backwards stepwise multiple linear regression using Aikake's
337 Information Criterion (AIC) for model selection. Only soil chemical properties significantly
338 related to CO₂ production in univariate regression were included in model selection.

339 In NP and NPG experiments, we used two-way ANOVA with planned comparisons to
340 compare rates of CO₂ production among treatments. As in the incubation on unamended soils,
341 data violated the assumption of sphericity for repeated measures ANOVA in NP (Mauchly's $W =$
342 0.035 , $p < 0.001$) and NPG (Mauchly's $W = 0.007$, $p < 0.001$) experiments. Therefore, we again
343 applied the Greenhouse-Geisser correction for test of within-subjects effects.

344

345 **Results**

346 *Soil chemical properties*

347 Peat substrate quality and nutrient content varied substantially among land uses and geographic
348 location (Table 3). C:N ratio, at 27.4 ± 0.7 , was 15% higher in Kalimantan oil palm than in
349 Kalimantan forest soil ($p = 0.004$). Available P concentration was three times higher in oil palm
350 soils ($12.9 \pm 3.2 \text{ mg kg}^{-1}$) than forest soils ($3.9 \pm 2.0 \text{ mg kg}^{-1}$, $p = 0.029$). Available N
351 concentration (sum of NO_3^- and NH_4^+) was $84.0 \pm 6.6 \text{ mg kg}^{-1}$ in oil palm and $114.9 \pm 23.8 \text{ mg}$
352 kg^{-1} for forest soils. NO_3^- was three times higher in oil palm soils ($p = 0.010$) despite NH_4^+ being
353 over two times higher in forest soils ($p = 0.004$). NH_4^+ was also quite variable among forest
354 plots, therefore total available N did not differ significantly between forest and oil palm in
355 Kalimantan. Other properties, including the concentration of C and OM, did not differ
356 significantly between the oil palm and forest soils in Kalimantan.

357 Sumatran oil palm soils were 39% higher than Kalimantan oil palm soils in total organic
358 matter ($p < 0.001$), 25% higher in total C ($p = 0.003$) and 20% higher in total N ($p = 0.009$).
359 Available N was more than two times higher in Kalimantan oil palm soils than in Sumatran oil
360 palm soils. Significantly higher NO_3^- concentration in Kalimantan soils than Sumatran oil palm
361 soils ($p = 0.001$) contributed substantially to the difference in available N, while NH_4^+
362 concentration at the two sites was similar.

363 Baseline corrected Vis-NIR spectra displayed peaks in absorbance typical of soils with
364 high organic matter content (Shenk *et al.*, 1992, Figure 3). For the Kalimantan forest soils, the
365 aliphatic peak at 1762 nm was higher than the aromatic peak at 1736 nm, with the exception of
366 shallow peat soils from K-FOR-1 that had experienced fire 30 or more years ago. In contrast, for
367 Sumatran oil palm soils the aliphatic peak was lower than the aromatic peak. The aliphatic and

368 aromatic peaks were roughly the same height for the Kalimantan oil palm soils, with the
369 exception of soils from the six year old plantation (K-OP-2009), where the aromatic peak was
370 higher than the aliphatic peak. Absorbance by aliphatics at 1200 nm was similar for Kalimantan
371 and Sumatran oil palm soils, and K-FOR-1. K-FOR-2 and K-FOR-3 spectra displayed much
372 higher absorbance at 1200 nm than other plots. The aromatic:aliphatic I ratio was higher in
373 Sumatran oil palm than in Kalimantan oil palm, based on absorbance by aliphatics at 1760 nm (p
374 = 0.002, Table 3). The opposite was true for the aromatic:aliphatic II ratio based on aliphatic
375 compounds at 1200 nm (p = 0.0001). Aromatic:aliphatic II was higher in Kalimantan oil palm
376 than Kalimantan forest peat (p = 0.005), but aromatic:aliphatic I was not significantly different.

377 *Variability in basal respiration without amendment*

378 Cumulative CO₂ production by Kalimantan forest soils ($1636.1 \pm 37.6 \mu\text{g CO}_2\text{-C g C}^{-1}$, $663.3 \pm$
379 $16.4 \mu\text{g CO}_2\text{-C g d.m.}^{-1}$) was roughly two times higher than production by Kalimantan oil palm
380 soils ($871.0 \pm 46.1 \mu\text{g CO}_2\text{-C g C}^{-1}$, $339.0 \pm 16.4 \mu\text{g CO}_2\text{-C g d.m.}^{-1}$) during the 7-day incubation
381 ($p < 0.001$, Figure 4). Cumulative CO₂ production by Kalimantan oil palm soils was
382 significantly higher than that of Sumatran oil palm soils ($600.1 \pm 23.7 \mu\text{g CO}_2\text{-C g C}^{-1}$) on a per
383 g C ($p < 0.0001$) but not per g d.m. basis ($320.7 \pm 16.4 \mu\text{g CO}_2\text{-C g d.m.}^{-1}$).

384 Throughout the experiment, on a per g C basis, the hourly rate of CO₂ production by
385 Kalimantan forest soils ($10.80 \pm 0.23 \mu\text{g CO}_2\text{-C g C hr}^{-1}$) was higher than that of Kalimantan oil
386 palm soils ($5.34 \pm 0.26 \mu\text{g CO}_2\text{-C g C hr}^{-1}$), and the rate of Kalimantan oil palm soils was higher
387 than that of Sumatran oil palm soils ($3.90 \pm 0.25 \mu\text{g CO}_2\text{-C g C hr}^{-1}$) (for both $p < 0.001$, Figure
388 5a). CO₂ production was higher at the beginning of experiment (p = 0.004), declining about 20%
389 to a fairly steady state after 24 hours.

390 Cumulative CO₂ production increased significantly with available N (Figure 6f). It
391 declined significantly with increasing C:N ratio, available P, and aromatic:aliphatic ratios
392 (Figure 6d, 6e, 6g, 6h). Aromatic:aliphatic ratio II and available N individually explained the
393 most variation in cumulative CO₂ production. Other significant relationships were weaker ($R^2 <$
394 0.50). CO₂ production was not significantly related to total C or OM concentration, on a per g
395 d.m or per g C basis. Considered together, C:N and aromatic:aliphatic ratios, available N and
396 available P accounted for 69% of variance (multiple linear regression, $p < 0.0001$). However,
397 only C:N ratio and aromatic:aliphatic ratio II were significant parameters in the model. The more
398 parsimonious model generated with backwards stepwise selection also accounted for 69% of
399 variance ($p < 0.0001$), and included C:N ratio, aromatic:aliphatic ratio II and available N.
400 Aromatic:aliphatic ratio II was the most important parameter in the model (standard partial
401 regression coefficient (sprc) = -0.42), followed by available N (sprc = 0.37) and C:N (sprc = -
402 0.33).

403 *Respiration in response to nutrient and labile carbon amendment*

404 In the NP experiment, only the high N and high P treatments - those ten times the typical
405 application rate in the field - significantly increased cumulative CO₂ production (Figure 7a). CO₂
406 production by high N treated soils ($2196.3 \pm 58.2 \mu\text{g CO}_2\text{-C g C}^{-1}$) was 28% higher than controls
407 ($1722.1 \pm 58.2 \mu\text{g CO}_2\text{-C g C}^{-1}$) ($p < 0.001$), while CO₂ production by high P treated soils
408 ($1911.2 \pm 58.2 \mu\text{g CO}_2\text{-C g C}^{-1}$) was only 12% higher ($p = 0.001$). The N effect was driven by
409 strong responses in Kalimantan forest and oil palm soils (Figure 7a). The effect of added P on
410 cumulative CO₂ production was driven by a strong response in Kalimantan forest soils (Figure
411 7a). The temporal patterns of CO₂ production among treatments differed ($p < 0.001$, Figure 5b).
412 Rates in the high N treatment were higher than controls through day 6, with differences peaking

413 at 8 hours. Rates were significantly enhanced under high P at 8 hours and 24 hours; differences
414 peaked at 24 hours and rates were similar to controls again after 48 hours.

415 Glucose increased cumulative CO₂ production compared to controls, but significantly so
416 only when N and P were also added ($p < 0.001$, Figure 7b). Cumulative CO₂ production in
417 glucose plus NP treated (NPG) soils ($1998.5 \pm 55.0 \mu\text{g CO}_2\text{-C g C}^{-1}$) was 21% higher than
418 controls ($1654.0 \pm 54.7 \mu\text{g CO}_2\text{-C g C}^{-1}$). Rates varied significantly with time ($p = 0.004$, Figure
419 5c), and temporal patterns differed among treatments ($p < 0.001$). During the first 24 hours,
420 glucose alone and glucose with NP significantly enhanced CO₂ production rate compared to
421 controls. Differences peaked at 8 hours, when glucose treated soils ($17.4 \pm 0.5 \mu\text{g CO}_2\text{-C g C}^{-1}$
422 hr^{-1}) and NPG soils ($18.0 \pm .8 \mu\text{g CO}_2\text{-C g C}^{-1} \text{hr}^{-1}$) both had rates two times higher than controls
423 ($7.4 \pm 0.5 \mu\text{g CO}_2\text{-C g C}^{-1} \text{hr}^{-1}$). Glucose treated soils returned to control levels after the first 24
424 hours, while rates in GNP soils remained higher than controls through day 4.

425 **Discussion**

426 *Soil chemical properties influenced by geography and land use*

427 At the plot level (within site), the organic matter, total C and N, available N and C:N ratio of our
428 soils were representative of the range observed to date in Indonesian peatlands (Table 1). The
429 high available N content we observed is characteristic of tropical peat swamp forest soils in
430 Southeast Asia (van Lent *et al.*, 2015). The peats are high in organic matter content prior to
431 conversion, and oil palm is typically fertilized with 60 - 100 kg N ha⁻¹ yr⁻¹ (Melling *et al.*, 2007;
432 Marwanto & Agus, 2014; Comeau *et al.*, 2016). Oil palm soils had higher C:N and lower SOM
433 quality, and lower N availability than forest soils, despite application of N fertilizers.

434 A higher ratio of aromatic to aliphatic carbon compounds in oil palm than forest soils
435 indicates that oil palm soils are more highly decomposed, reflecting the influence of drainage.

436 When the water table drops, soil organic matter is no longer protected by physical mechanisms
437 (von Lützow *et al.*, 2006; Schmidt *et al.*, 2011), and it can be mineralized or chemically
438 transformed. Fires may also have played a role in oil palm plots and K-FOR-1. Fire creates
439 recalcitrant “black carbon” at the soil surface (Gonzalez-Perez *et al.*, 2004, Singh *et al.*, 2012). In
440 addition, peat fires result in mass loss from surface layers (Rein *et al.*, 2008) which exposes
441 subsurface peat layers with a relatively higher proportion of recalcitrant organic matter (Wright
442 *et al.*, 2011). The shift to higher aromatic:aliphatic ratio may also reflect decreased quantity and
443 quality of litter inputs in oil palm. Palm fronds decompose more slowly than deciduous tree
444 leaves due to their higher lignin content and different nutrient balance (Arnason *et al.*, 1984; de
445 Neiff *et al.*, 2006). Lower input rates from root mortality and litterfall (Hergoualc’h & Verchot
446 2014) may also increase peat aromatic:aliphatic ratio post conversion.

447 Higher C:N ratio in oil palm soils compared to forest soils in Kalimantan is in agreement
448 with some observations of an increase in peat C:N ratio resulting from agricultural uses on peat
449 (Jauhiainen *et al.*, 2014). However, change in C:N ratio following conversion shows no
450 consistent trend in the literature. Leaching associated with peat drainage and agricultural use can
451 drive decreases in the soil N pool (Humphrey & Pluth 1996) and increases in the C:N ratio over
452 time, while mineral fertilization may result in the opposite effect (e.g. Krüger *et al.*, 2015). Soil
453 N is readily volatilized during peat fires, and ash remaining on site contains P, K, and other base
454 cations that may promote N mineralization and microbial immobilization (Certini 2005, Santín &
455 Doerr 2016). Ash also raises the pH which could increase microbial activity for peat soils with a
456 pH ~4, accelerating N losses (Certini 2005). Pyromineralization and increased hydrophobicity of
457 soil organic matter resulting from fire can lead to additional nutrient losses due to erosion,
458 leaching, exchange with the atmosphere, or uptake by plants (Certini 2005, Santín and Doerr

459 2016). Significant N export may also occur during harvest of palm oil bunches. While deposition
460 of ash from regional fires could be a source of nutrient inputs (Ponette-Gonzalez *et al.*, 2016),
461 on-site fires are the more likely driver of nutrient availability in our plots. Our oil palm sites
462 underwent single or multiple fires following conversion, resulting in apparent N loss compared
463 to the forest site.

464 While available N was 30% lower in Kalimantan oil palm **than forest**, due to high
465 variability in Kalimantan forest sites, the difference was not significant. Kimura *et al.* (2012)
466 also observed a trend towards lower available N associated with conversion of peat swamp forest
467 to oil palm in Sarawak, though Melling *et al.* (2007) observed the opposite. Significantly higher
468 levels of NO_3^- contribute to higher available N in Kalimantan oil palm and likely reflects
469 application of nitrogen fertilizer the week prior to soil sample collection. Lower levels of
470 available N in oil palm than in forest soils despite fertilizer application suggests a relatively high
471 rate of N loss from the soil system, most likely through leaching, gaseous N emissions, and
472 export of N in harvest.

473 *Chemical drivers of microbial decomposition in peat soils*

474 CO_2 production was related to substrate quality, as measured by aromatic:aliphatic and C:N
475 ratios, not substrate quantity (organic matter and total C). **We explored the importance of C**
476 **quality as a driver of microbial respiration over C quantity, as well as the importance and**
477 **potential drivers of N limitation.** Higher aromatic:aliphatic ratio is consistent with exposure of
478 soil organic matter to decomposition in peat soils (Haberhauer *et al.*, 1998; Ernakovich 2014).
479 Aliphatic C is preferentially mineralized, increasing the proportion of aromatic compounds as a
480 component of SOM. The decomposition of aromatic compounds yields less net energy to
481 microbes than aliphatic compounds, thus SOM becomes increasingly recalcitrant to

482 decomposition as aromatic:aliphatic ratio increases. As expected, microbial respiration in
483 unamended soils decreased with increasing aromatic:aliphatic ratio.

484 CO₂ production also declined significantly with increasing C:N ratio (Figure 6d) and
485 increased with available N (Figure 6f), suggesting that nitrogen availability was limiting to CO₂
486 production. Higher CO₂ production by N-treated soils confirmed the observations from
487 unamended soils. Nitrogen can directly limit SOM decomposition primarily when labile carbon
488 substrates are available to support microbial growth and activity (e.g. MacLean & Wein, 1978;
489 Haynes 1986; Berg & Matzner 1997; Schimel & Weintraub, 2003; Moorhead & Sinsabaugh,
490 2006, Hopkins *et al.*, 2006). A lower aromatic:aliphatic ratio in Kalimantan forest as compared
491 to Kalimantan and Sumatran oil palm indicates that indeed higher quality C substrate was
492 available in Kalimantan forest soils (Figure 6).

493 Like N, P can directly limit decomposition when labile carbon substrates are available
494 (Cleveland *et al.*, 2002). The weak negative relationship between CO₂ production and available P
495 in untreated soils suggests that substrate quality and available N were more strongly limiting to
496 CO₂ production than available P. High P treatments increased CO₂ production by Kalimantan
497 forest soils, with relatively higher substrate quality and lower initial P, and did not increase CO₂
498 production by Kalimantan or Sumatran oil palm soils with relatively lower substrate quality.

499 We observed a trend towards higher CO₂ production, especially in the forest peat, in the
500 low N and P treatments that were comparable to actual fertilization rates in the field, but the
501 effect was too small to be significant. Similarly, increased rates of heterotrophic respiration in
502 response to nitrogen fertilizer in the field, at application rates typical in Indonesia, are small and
503 transient (Comeau *et al.*, 2016). Microbial respiration in our soils likely remained limited by N,
504 since our low N treatment was not sufficient to bring C:N to the level generally required to meet

505 microbial requirements. Assuming a microbial C:N ratio of 8:1 (Cleveland & Liptzin 2007;
506 Chapin et al., 2011) and growth efficiency of 33% (Kroer 1993), a C:N ratio of 24:1 represents
507 the threshold between C limitation and N limitation for microbial growth. Soil C:N ratio was
508 above this threshold at both oil palm sites, and was marginal at the forest site (23.2 ± 1.1).

509 Our high N treatment was sufficient to alleviate N constraints on microbes, but limitation
510 then may have shifted to SOM quality: Sumatran oil palm did not respond but Kalimantan oil
511 palm and forest did. Our study suggests the magnitude of increase will be influenced by both
512 application rate and peat substrate quality and nutrient availability. Conversion of forest to oil
513 palm plantations may drive progressive N limitation and limitation by SOM quality. Fertilization
514 at typical field rates may not increase CO₂ production from peat decomposition *in situ*.
515 Ultimately, fire effects and time since drainage, through impacts on peat substrate quality and
516 nutrient availability, may have a more profound influence than fertilization on CO₂ emissions
517 from peat soils.

518 Glucose addition raised CO₂ production, however, in this study, the response was only
519 significant in the presence of added N and P. Addition of glucose with N and P temporarily
520 removed both N and SOM quality constraints. This was true even for the Sumatran oil palm soils
521 with low SOM quality which did not respond to high N and P treatments in the absence of
522 glucose. Amendment with glucose temporarily alleviated labile C constraints in Sumatran oil
523 palm soils, allowing N and P to directly limit microbial respiration; the effect quickly
524 disappeared if glucose were not also accompanied by added nutrients (Figure 5, 7). CO₂ evolved
525 from glucose could not be distinguished from peat-evolved CO₂ in our NPG experiment, and the
526 difference between glucose treated soils and controls was not greater than the amount of C added

527 in glucose treatments (4,000 $\mu\text{g C}$). Therefore, we cannot assess any enhancement effect on
528 mineralization of recalcitrant C or “priming”.

529 *Comparing CO₂ production across geographies and land use*

530 Substrate quality played a strong role in determining rates of CO₂ production by peats
531 from different islands and under different land uses. Sumatran oil palm soils had more C
532 available for microbial decomposition than Kalimantan oil palm soils (Table 3), however, CO₂
533 production was similar on per g d.m. basis and significantly lower on per g C basis (Figure 4).
534 Lower CO₂ production reflected the lower quality of the substrate: higher ratios of
535 aromatic:aliphatic (I) and C:N (Table 3, Figures 3 and 6). Likewise, Kalimantan forest and oil
536 palm soils had similar quantity of C available for microbial decomposition. Nevertheless, CO₂
537 production was significantly higher, on per g d.m. and per g C basis, in Kalimantan forest soils
538 with higher quality SOM and lower C:N ratio.

539 CO₂ production by Kalimantan forest soils was two orders of magnitude lower than that
540 of Panamanian peat swamp forest soils (Hoyos-Santillan *et al.*, 2016), most likely due to lower
541 SOM quality in Kalimantan peats. CO₂ production by oil palm soils in both Kalimantan and
542 Sumatra was ca. 50% lower than *ex situ* CO₂ production from a deforested, drained, and
543 abandoned peat (with no oil palm) in Central Kalimantan (Jauhiainen *et al.*, 2016). Rates for our
544 forest soil were five times lower than *ex situ* rates for an undrained forest adjacent to the
545 abandoned peat in Jauhiainen *et al.* (2016). However, comparing results is difficult because the
546 incubation methods were quite different (a slurry versus field moist soil).

547 *Land use change and future CO₂ emissions from tropical peatlands*

548 In addition to management practices that enhance peat decomposition over the short term, e.g.
549 drainage, land use change may influence peat CO₂ emissions over the long term through effects

550 on peat soil properties. Our *ex situ* results are consistent with observed or inferred decreases in
551 CO₂ fluxes from drained peat soils under agricultural use over time (Wösten *et al.*, 1997; Hooijer
552 *et al.*, 2012). As suggested by comparing forest to oil palm in Kalimantan, recently drained
553 peatlands, high in labile carbon compounds, may emit CO₂ at higher rates in years immediately
554 following conversion compared to later years. In addition, changes in vegetation will alter inputs
555 of organic matter over time, with quality (Pardon *et al.*, 2017) and quantity (Hergoualc'h &
556 Verchot 2014) varying as the agro-ecosystem ages and the microbial community changes
557 (Tripathi *et al.*, 2016).

558 In Kalimantan, peat quality varied dramatically between undrained forest and oil palm
559 plantations cleared 10 to 26 years prior and managed for oil palm production for another four to
560 eight years. Both aromatic:aliphatic and C:N ratios were roughly 15% lower in forest than in oil
561 palm. Our incubation results indicate a substantial (50%) potential decline in substrate driven
562 rates of peat decomposition a decade or more after initial conversion to oil palm. Comparisons
563 between oil palm soils from Kalimantan and Sumatra, and within sites at both locations indicate
564 that variation in substrate quality across space will also influence CO₂ emissions from peatlands
565 under the same land use. Assessments of carbon emissions from land use change should consider
566 the dynamic nature of the soil substrate available for decomposition. Rates are likely to be higher
567 in the early period following conversion and in places where substrate quality is higher. Time
568 since disturbance has been assessed in temperate forests with remote sensing approaches that
569 have potential application in the tropics (e.g. Pan *et al.*, 2011b). If substrate quality is related to
570 canopy foliar nutrients, it could also be sensed remotely (Asner *et al.*, 2008; Balzotti *et al.*,
571 2016). The elements for an improved method of estimating region-wide CO₂ production may be

572 within reach. Given the importance of peat emissions for Indonesia and the global carbon cycle,
573 a more refined approach to scaling up emissions from land use change is needed.

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Table 1. Soil chemical properties measured on Southeast Asian peats.

Property	This study		Previous studies		Reference
	Mean	Range	Mean	Range	
pH	3.9	3.7 – 4.1	3.8	3.2 – 4.8	d), e), h), i)
OM (g 100 g ⁻¹)	77	47 – 93	96.0	45.0 – 99.8	c), d), h), i)
C (g 100 g ⁻¹)	45	28 – 55	53.7	30.9 – 66.2	a), b), d), e), f), h), i)
N (g 100 g ⁻¹)	1.7	1.3 – 2.3	1.7	1.3 – 2.3	b), d), e), i)
C:N	26.3	20.3 – 30.0	36.4	24.6 – 47	b), d), e)
NH ₄ ⁺ + NO ₃ ⁻ (mg kg ⁻¹)	79.7	29.4 – 184.2	169.1	20.6 – 472.5	b), e), k)

a) Shimada et al. 2001, b) Takakai et al. 2006, c) Reiley and Page 2008, d) Ismawi et al. 2012, e) Kimura et al. 2012, f) Warren et al. 2012, h) Gandois et al. 2013, i) Melling et al. 2013, j) Inubushi et al. 2003, k) Melling et al. 2005

Table 3. Chemical properties of peat samples collected from the top 0-5 cm (n=18 for BD, n = 9 for other) and top 0-10 cm (pH only, n = 3) in the Kalimantan forest site (KAL FOR) and oil palm site (KAL OP) and the Sumatra oil palm site (SUM OP). Mean values are presented with standard errors.

Property	Depth (cm)	KAL FOR		KAL OP		SUM OP	
		Mean	SE	Mean	SE	Mean	SE
BD (g cm ⁻³)	0-5	0.16	± 0.06	0.24	± 0.06	0.19	± 0.02
pH	0-10	3.97	± 0.07	3.70	± 0.20	3.97	± 0.18
OM (g 100 g ⁻¹)	0-5	72.5	± 6.3	66.1	± 3.1 ^A	91.8	± 0.6 ^B
C (g 100 g ⁻¹)	0-5	40.8	± 3.2	41.2	± 2.8 ^A	53.8	± 0.8 ^B
N (g 100 g ⁻¹)	0-5	1.8	± 0.2	1.5	± 0.1 ^A	1.9	± 0.1 ^B
C:N	0-5	23.2	± 1.1 ^a	27.4	± 0.7 ^b	28.6	± 1.0
NH ₄ ⁺ (mg kg ⁻¹)	0-5	100.3	± 21.5 ^a	38.7	± 9.4 ^b	37.7	± 5.7
NO ₃ ⁻ (mg kg ⁻¹)	0-5	14.6	± 5.8 ^a	45.3	± 8.8 ^{b, A}	2.6	± 0.8 ^B
NH ₄ ⁺ + NO ₃ ⁻ (mg kg ⁻¹)	0-5	114.9	± 23.8	84.0	± 6.6 ^A	40.3	± 5.5 ^B
Bray II P (mg kg ⁻¹)	0-5	3.9	± 2.0 ^a	12.9	± 3.2 ^b	32.2	± 8.6

Significant differences in mean values between KAL FOR and KAL OP are indicated by superscripts a, b. Significant differences in mean values between KAL OP and SUM OP are indicated by superscripts A, B. Abbreviations are BD: bulk density, OM: organic matter.

Table 2. Characteristics of the sampling plots at the three study sites.

Code	Island	Location	Landuse	Plantation Age	Clearance Date	Fires	Distance to River	Peat Depth
K-FOR-1	Kalimantan	S 02° 49.4' E 111° 48.8'	Forest	-	pre 1982	Multiple	0.5 km	27 cm
K-FOR-2	Kalimantan	S 02° 49.3' E 111° 50.4'	Forest	-	-	-	1 km	155 cm
K-FOR-3	Kalimantan	S 02° 50.9' E 111° 48.1'	Forest	-	-	-	2 km	290 cm
K-OP-2011	Kalimantan	S 02° 47.3' E 111° 48.6'	Smallholder oil palm	4 Year	1989	Multiple	3.5 km	20 cm
K-OP-2009	Kalimantan	S 02° 47.3' E 111° 48.1'	Smallholder oil palm	6 Year	2005	Multiple	3.5 km	47 cm
K-OP-2007	Kalimantan	S 02° 47.2' E 111° 48.1'	Smallholder oil palm	8 Year	2005	Multiple	3.5 km	47 cm
S-OP-2010	Sumatra	S 01° 38.4' E 103° 54.3'	Industrial oil palm	5 Year	2004	Multiple	20 km	850 cm
S-OP-2007	Sumatra	S 01° 38.2' E 103° 52.3'	Industrial oil palm	8 Year	2004	Multiple	20 km	665 cm
S-OP-2005	Sumatra	S 01° 38.5' E 103° 50.0'	Industrial oil palm	10 Year	2004	Single	20 km	575 cm

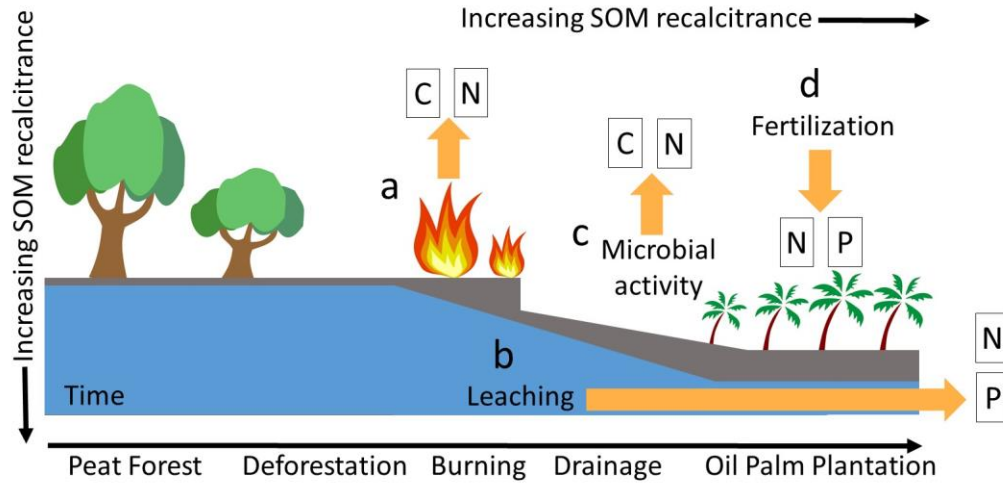


Figure 1. Conceptual model of changes in peat soil organic matter quality (SOM) and nutrient availability associated with conversion of tropical peat swamp forest to oil palm plantation. Burning results in removal of surface peat layers (a) and enhances drainage-facilitated leaching of N and P (b). Microbial activity is enhanced by increased oxygen availability in drained peat layers (c). This drives decomposition of labile C compounds resulting in increasing SOM recalcitrance over time, and gaseous N losses. **Decreased quantity and quality of litter inputs in may also enhance the accumulation of recalcitrant C in soil organic matter.** N and P inputs are received from fertilization in oil palm plantations (d) leading to additional C and N losses to the atmosphere and drainage waters. **Refer to text for citations.**

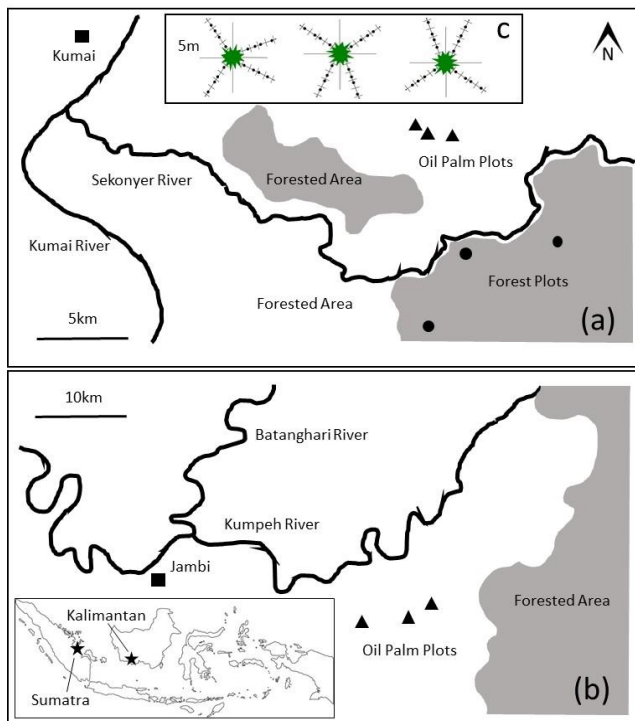


Figure 2. Research sites and soil sampling design. Peat soils were collected at sites on the islands of Kalimantan and Sumatra (inset, lower left) from three plots in undrained forest and three plots in nearby smallholder oil palm plantations in Kalimantan (a) and from three plots in an industrial oil palm plantation in Sumatra (b). At each plot, soil samples were collected from three locations determined using a systematic random approach. At each location soils were collected along 5 m transects arrayed in a stratified random design, centered on an individual palm or tree (c). Each circle in (c) represents one soil sample collected from the top 0-5 cm with a bulk density ring. Maps are hand digitized images from GoogleEarth. Source: DigitalGlobe 2016

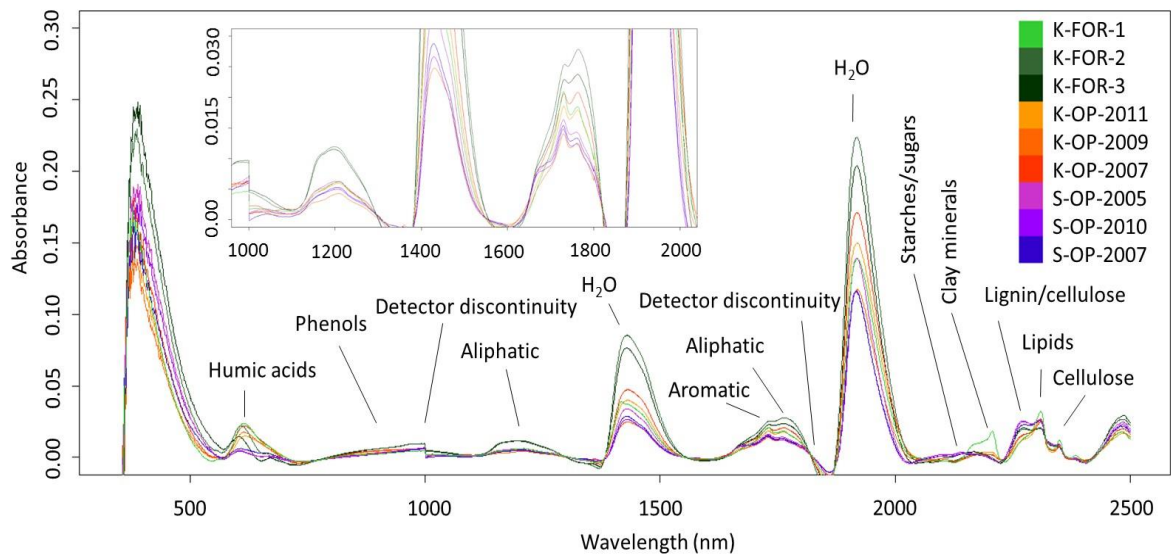


Figure 3. Vis-NIR baseline corrected absorbance spectra of soil from plots in Kalimantan undrained forest (K-FOR-1, K-FOR-2, K-FOR-3), Kalimantan smallholder oil palm plantations (K-OP-2011, K-OP-2009, K-OP-2007) and Sumatran industrial oil palm plantations (S-OP-2010, S-OP-2007, S-OP-2005) on peat. Noticeable peaks around 1400 nm and 1900 nm are associated with H-O-H and O-H absorption bands (Shenk *et al.*, 1992), and indicate that some water remained in soils after air drying. A strong absorption around 2200 nm by soils from K-FOR-1 was likely due to high mineral content. The waveband 1000-2000 nm is magnified in the inset. Each spectra represents the average of measurements collected on soil samples from three within plot locations (n=3).

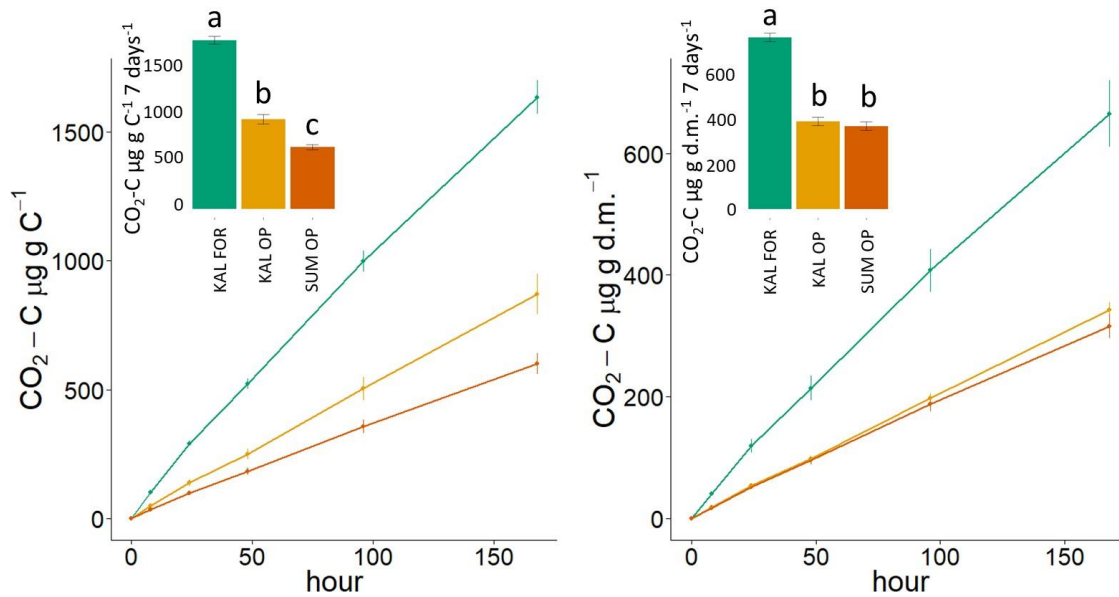


Figure 4. Mean cumulative CO₂ production by peat soils from Kalimantan forest (KAL FOR, green) and oil palm (KAL OP, orange) sites and Sumatran oil palm (SUM OP, blue) sites during incubation without amendment. Production is expressed on per g C basis in (a) and per g d.m. basis in (b). Significant differences in mean total cumulative CO₂ production over the 7 day incubation values are indicated by different letters in inset (a) and inset (b). Error bars represent standard error of the mean (n = 27).

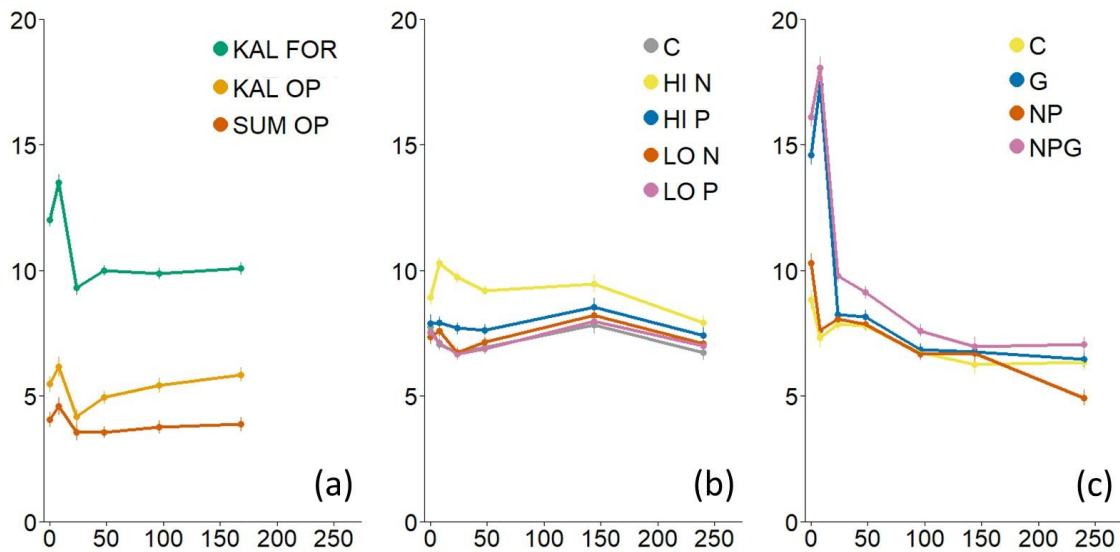


Figure 5. Mean CO₂ production rate by peat soils (a) from Kalimantan forest (KAL FOR) and oil palm (KAL OP) sites and Sumatran oil palm (SUM OP) sites during incubation without amendment; (b) with three levels of nitrogen (N) and phosphorus (P) amendment (no amendment: C; high level: hi; low level: lo); and (c) with glucose in the presence (NPG) or absence (G) of N and P amendment, with N and P amendment without glucose (NP) and in controls (C). Error bars represent standard error of the mean. In (a) n = 27, (b) n = 18, and (c) n = 18.

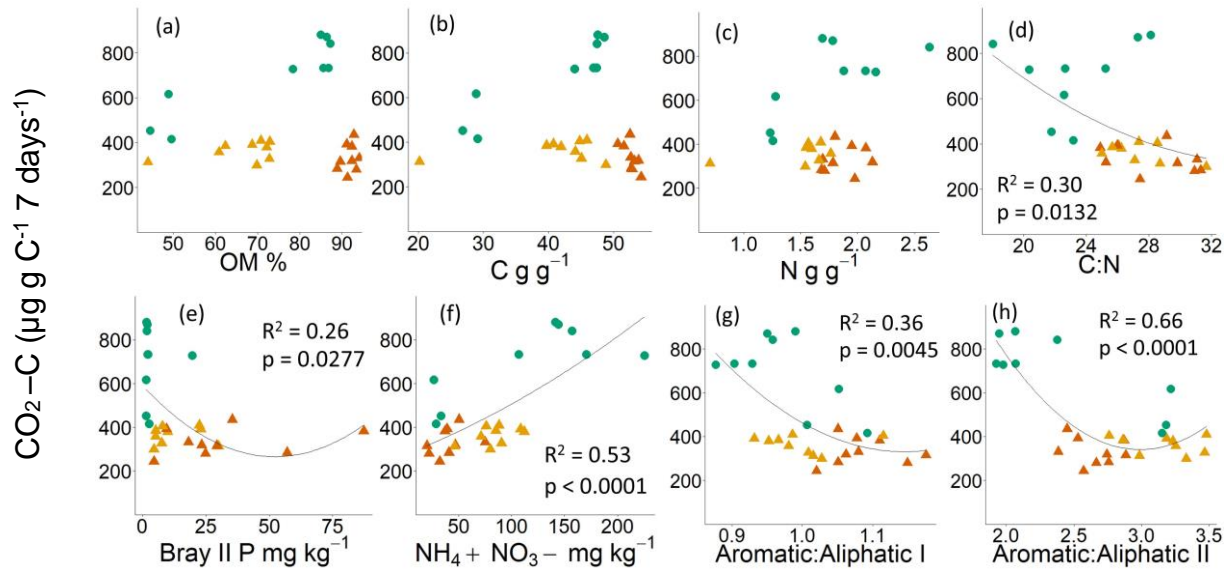


Figure 6. Mean cumulative CO_2 production over seven days by soils incubated without amendment as a function of soil properties ($n = 27$). Each data point represents the average of three replicates of soil from each of the tree three within plot locations. Green circle: peat forest in Kalimantan, gold triangle: oil palm in Kalimantan, orange triangle: oil palm in Sumatra.

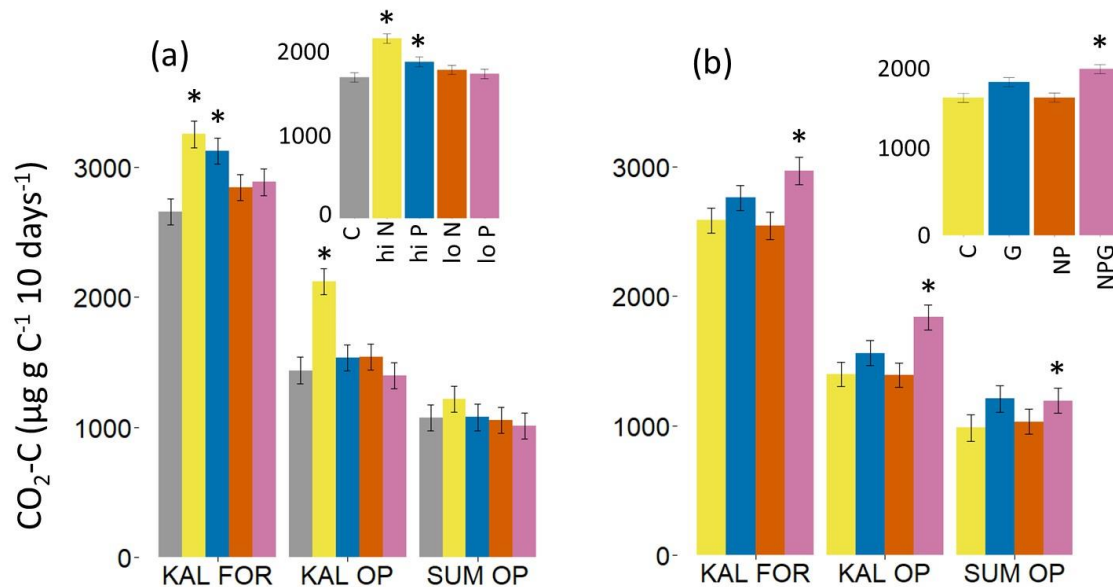


Figure 7. Mean cumulative CO_2 production by peat soils from Kalimantan forest (KAL FOR) and oil palm (KAL OP) and Sumatran oil palm (SUM OP) sites in (a) each treatment group incubated with nitrogen (N) and phosphorous (P) amendment and in (b) each treatment group incubated with glucose (G) amendment in the presence or absence of N and P amendment. Significant difference compared to control is indicated with *. Error bars represent standard error of the mean ($n=6$).