



# 1 Comparison of greenhouse gas fluxes and microbial communities 2 from tropical forest and adjacent oil palm plantations on mineral soil

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13 **Abstract.** In Southeast Asia, oil palm plantations have largely replaced tropical forests. The impact of  
14 this shift in land-use on greenhouse gas (GHG) fluxes and soil microbial communities remains highly  
15 uncertain, mainly due to a relatively small pool of available data. The aim of this study is to quantify  
16 differences of nitrous oxide (N<sub>2</sub>O) and methane (CH<sub>4</sub>) fluxes as well as soil carbon dioxide (CO<sub>2</sub>)  
17 respiration rates from logged forests, oil palm plantations of different ages and an adjacent small riparian  
18 area. The focus of this study is on N<sub>2</sub>O fluxes, as these emissions are expected to increase significantly  
19 due to the introduction of nitrogen (N) fertiliser application. This study was conducted in the SAFE



20 (Stability of Altered Forest Ecosystems) landscape in Malaysian Borneo (Sabah) with measurements  
21 every two months over a two-year period. GHG fluxes were measured by static chambers; at the same  
22 time soil samples were collected for analysis of the key soil physicochemical parameters and for analysis  
23 of microbial biodiversity using next generation sequencing in dry and wet season. N<sub>2</sub>O fluxes were highly  
24 variable across the different sites, with the highest mean flux from OP ( $46.2 \pm 166 \mu\text{g m}^{-2} \text{h}^{-1} \text{N}_2\text{O-N}$ ) and  
25 riparian ( $31.8 \pm 220 \mu\text{g m}^{-2} \text{h}^{-1} \text{N}_2\text{O-N}$ ) sites, compared to lower fluxes from logged forest ( $13.9 \pm 171 \mu\text{g}$   
26  $\text{m}^{-2} \text{h}^{-1} \text{N}_2\text{O-N}$ ). Methane fluxes were generally small;  $-2.6 \pm 17.2 \mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$  for OP and  $1.3 \pm 12.6$   
27  $\mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$  for riparian with the range of measured CH<sub>4</sub> fluxes largest in logged forests ( $2.2 \pm 48.3$   
28  $\mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$ ). Soil respiration rates were larger from riparian areas ( $157.7 \pm 106 \text{mg m}^{-2} \text{h}^{-1} \text{CO}_2\text{-C}$ )  
29 and logged forests ( $137.4 \pm 95 \text{mg m}^{-2} \text{h}^{-1} \text{CO}_2\text{-C}$ ) than OP plantations ( $93.3 \pm 70 \text{mg m}^{-2} \text{h}^{-1} \text{CO}_2\text{-C}$ ) due to  
30 larger amounts of decomposing leaf litter. Microbial communities were distinctly different between the  
31 different land-use types and sites, bacterial communities linked to soil pH and fungal and eukaryotic  
32 communities to land-use. Despite measuring a number of environmental parameters, mixed models could  
33 only explain up to 17% of the variance of measured fluxes for N<sub>2</sub>O, 3% of CH<sub>4</sub> and 25% of soil respiration.  
34 Scaling up measured N<sub>2</sub>O fluxes to Sabah using land areas for forest and OP resulted in emissions  
35 increasing from 7.6 Mt (95% confidence interval, -3.0-22.3 Mt) per year in 1973 to 11.4 Mt (0.2-28.6 Mt)  
36 per year in 2015 due to the increasing area of forest converted to OP plantations over the last ~40 years.

37



## 38 **1 Introduction**

39 Deforestation in Southeast Asia is so intense that up to three quarters of its forests might be lost by the  
40 end of the 21st century (Sodhi et al., 2004) and most of the degradation happens because of conversion  
41 of forest to croplands and plantations (Wilcove et al., 2013). In Malaysia and Indonesia, more than 16  
42 million hectares of land, mainly from tropical forests but also to a lesser extent, other non-profitable  
43 agricultural land such as rubber plantations and peat, were cleared for oil palm (OP) (Yan, 2017). Many  
44 of the remaining forests are degraded forests, as they have been partially logged, to remove specific tree  
45 species and logging activity has caused an increase in forest openings (Houghton, 2012). In 20% of the  
46 world's tropical forests, selective logging occurs, and it is estimated that this accounts for at least half of  
47 the anthropogenic greenhouse gas emissions (GHG) from forest degradation (Pearson et al., 2017).  
48 Consequently, forest degradation has been recognised as a source of GHG emissions, but little is known  
49 of the emissions from the resulting secondary forests, especially in Malaysian Borneo, Sabah. Due to  
50 deforestation, fragments of forest remain isolated from each other, which can have consequences for  
51 biodiversity and ecosystem function (Ewers et al., 2011).

52

53 OP plantations are one of the main causes of deforestation and forest degradation in Southeast Asia (Lee-  
54 Cruz et al., 2013; Wilcove et al., 2013) with some disputes about the extent to which industrial plantations  
55 are responsible for the loss of old-growth and selectively logged forests in Borneo (Gaveau et al., 2016).  
56 OP generates the highest yield per hectare of land of any vegetable oil crops. It is used in food products,  
57 detergents, soaps, cosmetics, animal feed and bioenergy, and was hence praised as a wonder crop (Sayer



58 et al., 2012). However, OP agriculture is now known to be responsible for soil degradation, loss of soil  
59 carbon (C) and reduced soil fertility due to the conversion and management methods (Guillaume et al.,  
60 2015; Lee-Cruz et al., 2013). To create an OP plantation, complete deforestation followed by terracing of  
61 the land is often the chosen method, and not only in hilly terrain. Terracing can result in poor drainage,  
62 reduced soil fertility and increased soil erosion. Conversion of tropical forests may also lead to changes  
63 in the short- and long-term nutrient status of the converted land-use systems. It is important to understand  
64 impacts of these land-use changes in order to identify more environmentally friendly and sustainable  
65 management practices (Jackson et al., 2019).

66

67 OP plantations are assessed for their GHG emissions, but rarely have emissions from forests and  
68 plantations from the same region been reported together, despite the call to study fluxes in forest and  
69 converted land simultaneously (van Lent et al., 2015). Much of the focus has been on GHG emissions  
70 from peatland rather than mineral soil, either tropical forest on peatland or peatland drained for  
71 plantations. More attention has been given to carbon fluxes or storage (Germer and Sauerborn, 2008;  
72 Hassler et al., 2015) than emissions from the non-CO<sub>2</sub> GHG methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O).  
73 Meijide *et al.* (2020) identified the need to study all three GHGs to assess total emissions from OP  
74 plantations. Even though CH<sub>4</sub> and N<sub>2</sub>O are not emitted at the quantity of CO<sub>2</sub>, their global warming  
75 potentials (GWP) per molecule are 28 – 34 (without and with climate-carbon feedback) and 265 – 298  
76 times higher than CO<sub>2</sub> on a 100 year time horizon, respectively, which highlights their importance (Myhre  
77 et al., 2013). Due to a number of environmental issues arising from conversion of peatlands to OP



78 plantations, the focus will increasingly shift to mineral soil for conversion to plantations, especially in  
79 Malaysia (Shanmugam et al., 2018). There are too few measurements reported of N<sub>2</sub>O emissions from  
80 mineral soils in the tropics to draw firm conclusions about the increase of N<sub>2</sub>O emissions after land-use  
81 change from secondary forest to OP (Shanmugam et al., 2018).

82

83 Limited measurement and modelling studies have been carried out on N<sub>2</sub>O emissions from OP plantations  
84 (Pardon et al., 2016a; Pardon et al., 2016b; Pardon et al., 2017), and not in the context of comparing them  
85 with other land-uses on the same or similar soil type. Similarly, reported CH<sub>4</sub> emissions from mineral  
86 soils in the Tropics (other than from paddy soils) are lacking. Most studies relating land-use change to  
87 trace gas emissions have been conducted in South America and not South East Asia (Hassler et al., 2015;  
88 Veldkamp et al., 2013). An additional caveat of published studies is that most have only been conducted  
89 over short periods of time (Hassler et al., 2015). The lack of reliable long-term and multi-year datasets on  
90 GHG balances has been recognised (Corre et al., 2014; Courtois et al., 2019). Studies are often associated  
91 with high uncertainties (Henders et al., 2015). Nitrogen availability, soil moisture and texture are the main  
92 drivers of N<sub>2</sub>O fluxes in tropical forests and other soil ecosystems (Davidson et al., 2000). As well as  
93 agricultural soils, tropical forest soils have been identified as a major source of N<sub>2</sub>O (Werner et al., 2007),  
94 and soil type influences N<sub>2</sub>O fluxes in the Tropics (Dutaur and Verchot, 2007; Sakata et al., 2015). A  
95 recent meta-analysis concluded that tropical forests emit on average 2 kg N<sub>2</sub>O-N ha<sup>-1</sup> y<sup>-1</sup>, and emission  
96 rates will significantly increase after land-use change (van Lent et al., 2015). Tropical forest soils are  
97 estimated to contribute 28% to the global CH<sub>4</sub> uptake, hence large changes to this sink could alter the



98 accumulation of CH<sub>4</sub> in the atmosphere substantially (Dutaur and Verchot, 2007). However, uncertainties  
99 are large due to data scarcity. Only one study from Peninsula Malaysia reported that selectively logged  
100 forest may be converted into a weaker sink of CH<sub>4</sub> and greater source of N<sub>2</sub>O than undisturbed tropical  
101 rain forest, at least for a short period, because of the increased soil nitrogen availability and soil  
102 compaction due to disturbance by heavy machinery (Yashiro et al., 2008).

103

104 Forest conversion to OP has shown differences in soil microbial community composition and functional  
105 gene diversity (Tripathi et al., 2016). The diversity and abundance of plant communities fundamentally  
106 affect soil microbial community and their function (Eisenhauer, 2016; Tripathi et al., 2016). As yet, it  
107 remains uncertain how conversion from forest to OP impacts microbial communities, and their influence  
108 on N<sub>2</sub>O and CH<sub>4</sub> fluxes (Kaupper et al., 2019). Even though the importance of bacterial communities is  
109 recognised, little is known of changes in microbial communities due to land-use change (Tin et al., 2018).  
110 Transformation of tropical forest to, for example OP plantations, reduces bacterial abundance initially,  
111 alters the community composition but once established may not necessarily result in less bacterial richness  
112 in the OP soil (Lee-Cruz et al., 2013; Tripathi et al., 2016). Agricultural soils (including OP soils) are  
113 often thought to promote diversity through management, such as fertilisation and crop inputs and thereby  
114 reduce competition amongst soil microorganisms (Lee-Cruz et al., 2013). Information on microbial  
115 communities will help to understand the impact of anthropogenic land-use change and its impact on  
116 biogeochemical processes (Tin et al., 2018). The lack of our current understanding restricts our ability to  
117 predict and model responses to environmental change (Lee-Cruz et al., 2013). This is particularly



118 important as 80-90% of soil processes are mediated by microorganisms (Nannipieri et al., 2003). In our  
119 study, we aim to understand whether differences in microbial communities could also help understand  
120 measured differences in greenhouse gas (GHG) emissions. One part of this present study has investigated  
121 potential controlling factors and microbial pathways leading to GHG emissions from soil in controlled  
122 laboratory incubations, which complement the findings presented here from actual field measurements as  
123 the soil was taken from a subset of the sites (Drewer et al., 2020).

124 The objectives of this study were:

- 125 1) to compare GHG emission rates from different land-uses
- 126 2) to investigate whether management practices and land-use will have a larger effect on GHG fluxes  
127 than other measured abiotic and biotic parameters
- 128 3) to broadly upscale our measurements to Sabah scale

129

130 In light of countries committing to reduce and mitigate GHG emissions, e.g. 2015 Paris Agreement  
131 (UNFCCC, 2015), it is important to constrain each country's current emission rates, by providing data  
132 from measurements rather than relying on model estimates. In this study, we present much needed data  
133 of N<sub>2</sub>O and CH<sub>4</sub> emission rates from logged tropical forests and OP plantations on mineral soil as well as  
134 their biochemical characteristics and temporal and spatial variability. We present two years of  
135 measurements from logged forests and OP plantations in Malaysian Borneo, Sabah from the same  
136 geographical area and on mineral soil.



## 137 **2 Methods**

### 138 **2.1 Site description**

139 The present study was carried out within the Stability of Altered Forest Ecosystems (SAFE) project in  
140 Malaysian Borneo (4°49'N, 116°54'E) in 2015 and 2016. The SAFE project was set up in Sabah in 2011  
141 in a secondary forest, designated by the Sabah government for conversion to OP plantations. SAFE is a  
142 long-term landscape-scale experiment designed to study the effects of anthropogenic activities related to  
143 deforestation and OP agriculture on the ecosystem as a whole (Ewers et al., 2011). The main aim of the  
144 SAFE project is to study how habitat fragmentation affects the forest ecosystem, mainly its biodiversity.  
145 The design comprises forest fragments of 1 ha, 10 ha and 100 ha. Larger areas of forests, designated as  
146 continuous logged forests, and not part of the conversion plan, were selected as controls. All forest sites  
147 had been selectively logged for dipterocarps, first in the 1970s then again between 2000 and 2008, such  
148 that the logged forest and forest fragments have a similar land-use history (Ewers et al., 2011). We had  
149 the opportunity to investigate GHG fluxes within this experimental site. As our sampling took place when  
150 conversion was still ongoing (i.e. designated 'fragments' were not fragmented yet), we classify sampling  
151 locations in 'fragments' and 'logged forest' controls both as 'logged forest'. We selected a young OP  
152 plantation, around 2 years old at the time we started measurements (OP2) and a medium aged OP  
153 plantation, around 7 years old at the start of the project (OP7). The riparian area (RR) is adjacent and  
154 down slope from OP7. In addition, we selected a slightly older plantation, around 12 years of age at the  
155 start of the project (OP12). All OP plantations in this study were terraced. Logged forest sites are the 10  
156 ha plots of the logged forest (and future fragments) LF, B and E of the SAFE design.



157 The climate in the study area is wet tropical with a wet season typically from October to February and a  
158 dry season typically from March to September with average monthly temperatures of 32.5°C (irrespective  
159 of season) and average monthly rainfall of 164.1 mm (climate-data.org, 2019). At SAFE, the mean  
160 monthly rainfall over the two years of study period (2015 and 2016) was 190 mm, ranging from 45 mm  
161 during the driest month (Mar 2015) to 470 mm during the wettest month (Sep 2016; R. Walsh, Figure 1).  
162 Annual rainfall was 1927 mm in 2015 and 2644 mm in 2016 with 2015 being drier than usual. The soils  
163 at SAFE are classed as orthic Acrisols or Ultisols (Riutta et al., 2018).

164

## 165 **2.2. Field measurements**

166 In order to measure fluxes of N<sub>2</sub>O and CH<sub>4</sub> from the chosen logged forests and OP plantations, a total of  
167 56 static chambers were installed in the SAFE area. Four chambers were placed in each of the two 10 ha  
168 plots in LF, B, and E, resulting in 8 chambers per site. In the OP plantations, 12 chambers were installed  
169 in the ~7-year old OP plantation, 8 in a ~2-year old, and 8 in a ~12-year old OP plantation. These were  
170 the plantation ages when we started sampling in 2015, hence, the sites are labelled OP2, OP7 and OP12.  
171 For exact GPS locations see the published dataset (Drewer et al., 2019). Fluxes were measured from all  
172 56 chambers every two months over a two-year period, from January 2015 to November 2016; resulting  
173 in 12 measurement occasions for each of the chambers and a total of 672 individual flux measurements.

174

175 We received basic fertiliser information from the estate managers at the beginning of our study. Our  
176 measurement sites OP2 and OP7 were managed by the same estate. Fertiliser was applied as slow release



177 (over 4 – 6 months) bags (500 g) of the brand ‘PlantSafe®’ (N as Ammonium Sulphate). For palms 0 – 5  
178 years of age PlantSafe® 12-8-16-1.5+trace elements (Diammonium Phosphat ((NH<sub>4</sub>)<sub>2</sub>PO<sub>4</sub>), Murite of  
179 Potash (KCl), Ammonium Sulphate ((NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub>), Magnesium Sulphate (MgSO<sub>4</sub>) + Borax Penthydrate)  
180 was used, and for palms >5 years PlantSafe® 8-8-27-15 was applied as 2 kg bag per plant, three times  
181 per year. Planting density was approximately 9 x 9 m spacing between palms and in addition to the mineral  
182 fertiliser, empty fruit bunches (EFB) were spread, however, there appeared to be no obvious pattern of  
183 application and most EFB were piled up along the main roads, rather than distributed evenly throughout  
184 the plantations. The site OP12 was managed by a different estate. Distance between the palms and  
185 planting density here was 8 x 8 m. Application of fertiliser also occurred as PlantSafe® bags with two  
186 applications a year with 3-4 kg per palm each time, totalling about 8 kg N ha<sup>-1</sup> y<sup>-1</sup>. EFB were not returned  
187 to this plantation and Glyphosate was applied three times per year around each palm stem to control  
188 weeds. We assume Glyphosate was also applied to the OP2 and OP7 plantations in the other estate.  
189 Generally, fertiliser management was according to recommendations by the Malaysian Palm Oil Board  
190 (MPOB). As our sampling frequency was every two months, we were not able to capture individual  
191 fertilisation events and that was not the scope of this study.

192

### 193 **2.2.1 Soil nitrous oxide (N<sub>2</sub>O) and methane (CH<sub>4</sub>) fluxes**

194 The static chamber method was used for N<sub>2</sub>O and CH<sub>4</sub> flux measurements as described in previous studies  
195 (Drewer et al., 2017a; Drewer et al., 2017b). Round static chambers (diameter = 40 cm) consisting of  
196 opaque polypropylene bases of 10 cm height were inserted into the ground to a depth of approximately 5



197 cm for the entire study period. Lids of 25 cm height were fastened onto the bases using four strong clips,  
198 only during the 45-minute measurement periods. A strip of commercially available draft excluder glued  
199 onto the flange of the lid provided a gas tight seal between chamber and lid. The lids were fitted with a  
200 pressure compensation plug to maintain ambient pressure in the chambers during and after sample  
201 removal. Gas samples were taken at regular intervals (0, 15, 30, 45 min) from each chamber. A three-way  
202 tap was used for gas sample removal using a 100 ml syringe. 20 ml glass vials were filled with a double  
203 needle system to flush the vials with five times their volume and remained at ambient pressure rather than  
204 being over-pressurised. The sample vials were sent to CEH Edinburgh for analysis usually between 4-7  
205 weeks after sampling. A specifically conducted storage test confirmed no significant loss of concentration  
206 during that time period. Samples and three sets of four certified standard concentrations (N<sub>2</sub>O, CH<sub>4</sub> in N<sub>2</sub>  
207 with 20% O<sub>2</sub>) were analysed using a gas chromatograph (Agilent GC7890B with headspace autosampler  
208 7697A; Agilent, Santa Clara, California) with micro electron capture detector ( $\mu$ ECD) for N<sub>2</sub>O analysis  
209 and flame ionization detector (FID) for CH<sub>4</sub> analysis. These detectors were setup in parallel allowing the  
210 analysis of the two GHGs at the same time. Limit of detection was 5 ppb for N<sub>2</sub>O and 40 ppb for CH<sub>4</sub>.  
211 Peak integration was carried out with OpenLab© Software Suite (Agilent, Santa Clara, California).

212

213 The flux  $F$  ( $\mu\text{g m}^{-2} \text{s}^{-1}$ ) for each sequence of gas samples from the different chambers was calculated  
214 according to Equation 1:

$$215 \quad F = \frac{dC}{dt} \times \frac{\partial V}{A} \quad (\text{Equation 1})$$



216 Where  $dC/dt$  is the concentration ( $C$ ,  $\mu\text{mol mol}^{-1}$ ) change over time ( $t$ , in s), which was calculated by  
217 linear regression,  $\rho V/A$  is the number of molecules in the enclosure volume to ground surface ratio, where  
218  $\rho$  is the density of air ( $\text{mol m}^{-3}$ ),  $V$  ( $\text{m}^3$ ) is the air volume in the chamber and  $A$  ( $\text{m}^2$ ) is the surface area in  
219 the chamber (Levy et al., 2012).

220

221 Applying the analytical limit of detection to the flux calculation, the resulting detection limits and  
222 therefore uncertainties associated with the flux measurements are  $1.6 \mu\text{g N m}^{-2} \text{h}^{-1}$  for  $\text{N}_2\text{O}$  and  $5 \mu\text{g C}$   
223  $\text{m}^{-2} \text{h}^{-1}$  for  $\text{CH}_4$  in the units used in the results section.

224

### 225 **2.2.2 Soil respiration ( $\text{CO}_2$ ) fluxes**

226 In addition, soil  $\text{CO}_2$  respiration rates were measured close to each chamber location using a dynamic  
227 chamber (volume:  $0.001171 \text{ m}^3$ ) covering  $0.0078 \text{ m}^2$  of soil for 120 s with an EGM-4 infrared gas analyser  
228 (IRGA: InfraRed Gas Analyser; PP Systems; Hitchin, Hertfordshire, England). To do so, cut drainpipes  
229 of 7 cm height matching the diameter of the IRGA chamber were inserted into the ground to a depth of  
230 about 5 cm for the duration of the study to allow for a good seal with the soil surface. All vegetation and  
231 litter was removed from the surface to guarantee soil-only respiration measurements. Taking into account  
232 the time of measurement and the soil temperature, fluxes were calculated based on the linear increase of  
233  $\text{CO}_2$  concentrations. Soil respiration was measured every time the static chambers were measured,  
234 resulting in 12 measurement occasions for each of the 56 locations and 672 individual measurements.

235



### 236 **2.2.3 Auxiliary physical and chemical soil measurements**

237 Other environmental parameters were measured during time of chamber enclosure as possible explanatory  
238 variables for correlation with recorded GHG fluxes. Soil and air temperatures were measured using a  
239 handheld Omega HH370 temperature probe (Omega Engineering UK Ltd., Manchester, UK) at each  
240 chamber location at a soil depth of 10 cm and by holding the temperature sensor 30 cm above the soil  
241 surface at chamber height. Volumetric soil moisture content (VMC) was measured at a depth of 7 cm  
242 using with a portable probe (Hydrosense 2; Campbell Scientific, Loughborough, UK). For determining  
243 KCl-extractable soil nitrogen (N) in the field, soil samples were collected to a depth of 10 cm around each  
244 of the chamber locations on each of the chamber measurement days, using a gouge auger. Extractions  
245 were carried out in the field laboratory on the same day. Soil samples were mixed well, stones were  
246 removed, and subsamples of ca. 6 g soil (fresh weight) was transferred into 50 ml falcon tubes containing  
247 25-ml 1 M KCl solution. The samples were shaken for 1 min every 15 min for one hour, then filtered  
248 through Whatman 42© filter paper (GE Healthcare, Chicago, USA) and kept in the fridge after addition  
249 of a drop of 75% H<sub>2</sub>SO<sub>4</sub> as a preservative. Analysis for ammonium (NH<sub>4</sub><sup>+</sup>) and nitrate (NO<sub>3</sub><sup>-</sup>)  
250 concentrations was carried out at Forest Research Centre in Sandakan (Sabah, Malaysia) using a  
251 colorimetric method (Astoria 2 Analyzer (Astoria-Pacific Inc., USA).

252

253 The following parameters were measured less frequently. Soil pH was measured on three occasions from  
254 the top 0-10 cm, close to each chamber at the start of the measurement period and two months later, and  
255 inside the chambers after the last flux measurements at the end of the experiment. For pH measurements



256 10 g of fresh soil was mixed with deionised H<sub>2</sub>O (ratio 1:2), and after 1 hour analysed on a MP 220 pH  
257 meter (Mettler Toledo GmbH, Schwerzenbach, Switzerland). Soil samples for bulk density were collected  
258 from inside each chamber after the final flux measurement. Galvanised iron rings (98.17 cm<sup>3</sup>) with a sharp  
259 edge were inserted in the upper soil layer with a hammer to 5 cm depth without compaction. Samples  
260 were oven-dried at 105°C until constant weight (usually 48 hours) and bulk density (g cm<sup>-3</sup>) was  
261 calculated based on the dry weight occupying the volume of the ring. Total C and N in soil and litter was  
262 measured once on the last sampling occasion. Soil samples were taken from the top 0-10 cm inside the  
263 chambers. The samples were air dried in the field laboratory and a subsample of each were dried at 105°C  
264 to constant weight in the laboratory to convert the results to oven-dry weight, ground and analysed at the  
265 Forest Research Centre in Sandakan on an elemental analyser (Vario Max CN Elemental Analyzer  
266 (Elementar Analysensysteme, Germany). Litter was collected from the surface area of each chamber, air  
267 dried at 30 °C and analysed for total C and N as described above.

268

#### 269 **2.2.4 Soil microbial community composition**

270 Soil samples for microbial analysis were taken on two occasions from all 56 flux chamber locations. Soil  
271 samples were taken in March 2016 and November 2016 (the last sampling occasion). On the first sampling  
272 date, soil was taken close to each chamber in order not to disturb the soil inside the chamber. In November  
273 2016, soil was taken from inside each chamber, as this was the experimental end date. Approximately 5  
274 g of soil was taken from the top 3 cm and stored in ziplok bags at ambient air temperature until posting  
275 to CEH Wallingford for analysis. The soil samples had to be sent as ‘fresh’ samples as there were no



276 freezers operating continuously at the field station, therefore it was not possible to keep the soil frozen  
277 during storage and transport. The samples were frozen at  $-80^{\circ}\text{C}$  once they reached CEH Wallingford until  
278 analyses.

279

280 For sequencing analyses of bacterial, and fungal and soil eukaryotic communities, DNA was extracted  
281 from 0.2 g of soil using the PowerSoil-htp 96 Well DNA Isolation kit (Qiagen Ltd, Manchester, UK)  
282 according to manufacturer's protocols. The dual indexing protocol of Kozich et al. (2013) was used for  
283 Illumina MiSeq sequencing (Kozich et al., 2013) with each primer consisting of the appropriate Illumina  
284 adapter, 8-nt index sequence, a 10-nt pad sequence, a 2-nt linker and the amplicon specific primer. The  
285 V3–V4 hypervariable regions of the bacterial 16S rRNA gene were amplified using primers 341F  
286 (Muyzer et al., 1993) and 806R (Yu et al., 2005), CCTACGGGAGGCAGCAG and  
287 GCTATTGGAGCTGGAATTAC respectively; the ITS2 region for fungi using primer ITS7f  
288 (GTGARTCATCGAATCTTTG) and ITS4r (TCCTCCGCTTATTGATATGC) (Ihrmark et al., 2012) for  
289 eukaryotes the 18S rRNA amplicon primers from (Baldwin; A.J et al., 2005) were used  
290 (AACCTGGTTGATCCTGCCAGT and GCTATTGGAGCTGGAATTAC). After an initial denaturation  
291 at  $95^{\circ}\text{C}$  for 2 minutes PCR conditions were: denaturation at  $95^{\circ}\text{C}$  for 15 seconds; annealing at  
292 temperatures  $55^{\circ}\text{C}$ ,  $52^{\circ}\text{C}$ ,  $57^{\circ}\text{C}$  for 16S, ITS and 18S reactions respectively; annealing times were 30  
293 seconds with extension at  $72^{\circ}\text{C}$  for 30 seconds; cycle numbers were 30; final extension of 10 minutes at  
294  $72^{\circ}\text{C}$  was included. Amplicon concentrations were normalized using SequalPrep Normalization Plate Kit  
295 (Thermo Fisher Scientific Ltd, Altrincham, UK) prior to sequencing each amplicon library separately on



296 the Illumina MiSeq using V3 chemistry using V3 600 cycle reagents at concentrations of 8 pM with a 5%  
297 PhiX Illumina control library (Illumina Ltd, Cambridge, UK).

298

299 Illumina demultiplexed sequences were processed in R software package, version 3.6.1 (R Core Team,  
300 2017) using DADA2 (Callahan et al., 2016) to quality filter, merge, denoise and construct sequence tables  
301 as follows: Amplicons reads were trimmed to 270 and 220 bases, forward and reverse respectively for  
302 ITS, and forward reads were trimmed to 250 and 280 bases for 16S and 18S respectively. Filtering settings  
303 were maximum number of Ns (maxN) = 0, maximum number of expected errors (maxEE) = (1,1).  
304 Sequences were dereplicated and the DADA2 core sequence variant inference algorithms applied.  
305 Forward and reverse reads were merged using mergePairs function as appropriate. Sequence tables were  
306 constructed from the resultant actual sequence variants and chimeric sequences were removed using  
307 removeBimeraDenovo default settings.

308

### 309 **2.3 Data analysis**

310 Environmental data, especially soil N<sub>2</sub>O fluxes, are typically highly variable in space and time, which  
311 makes their analysis challenging. Much of the variation cannot be explained by co-variates, as the driving  
312 microbial processes are not directly observed. They are also usually strongly left skewed (containing a  
313 high number of very small fluxes), and are expected to approximate a lognormal distribution. Against this  
314 background, trying to detect effects of land-use (or experimental treatments) is difficult. The calculation



315 of a confidence interval on the mean of a log-normal distribution is problematic when variability is high  
316 and sample size is small (e.g. Finney 1941), as is generally the case with flux measurements.

317

318 Here we applied a Bayesian methodology to address this problem, using a model similar to that described  
319 by Levy et al. (2017). This accounts for the lognormal distribution of observations, while including  
320 hierarchical effects of land-use, and effects of sites within land-use types as well as the repeated measures.  
321 In the current statistical terminology, this is a generalised linear mixed-effect model (GLMM) with a  
322 lognormal response and identity link function. The model consists of a fixed effect of land-use (Forest,  
323 Oil Palm, or Riparian), with a random effect representing the variation among sites within a land-use type.  
324 The parameters were estimated by the Markov chain Monte Carlo (MCMC) method, using Gibbs  
325 sampling as implemented in Just Another Gibbs Sampler (JAGS) (Plummer 1994), and described in more  
326 detail by Levy et al. (2017).

327

328 All other statistical analyses were conducted using the R software package, version 3.4.3 (R Core Team,  
329 2017) using the lme4 package for linear mixed-effects models (Bates et al., 2015) and ordinary multiple  
330 regression. Model selection was examined by sequentially dropping terms and assessing AIC and similar  
331 criteria using the MuMIn package (Bartoń, 2013). For N<sub>2</sub>O and CH<sub>4</sub>, where negative values occurred, the  
332 minimum was added to all data points (-30 and -115  $\mu\text{g m}^{-2} \text{h}^{-1}$ , respectively) so that a lognormal  
333 distribution could be fitted.

334



335 For microbial community composition samples within each sampling point were assessed in R for  
336 sequencing depth. Samples with fewer than 4000 reads were deemed as containing insufficient data and  
337 discarded. Package Vegan was used to rarefy each sampling occasion's samples to the minimum read  
338 number. Vegan functions specnumber, diversity and metaMDS were used to generate the statistics for  
339 richness, Shannon's diversity and Nonmetric Multidimensional Scaling, respectively. Analysis of  
340 similarities (ANOSIM) was used to test statistically whether there was a significant difference between  
341 two or more groups of parameters in relation to the microbial communities.

342

#### 343 **2.4 Upscaling of N<sub>2</sub>O fluxes to Sabah scale**

344 In an attempt to broadly upscale our findings, we calculated the annual soil N<sub>2</sub>O emission for the Sabah  
345 state based on the data from this study (Table 2), together with land cover areas estimates (Gaveau et al.,  
346 2016) of forests, pulpwood and OP plantations for 1973 and six 5 yearly intervals from 1990-2015. We  
347 included the pulpwood plantation area in the total forest area, as to our knowledge there are no data of  
348 N<sub>2</sub>O emissions from this sector. We used mean emissions and the 95% confidence interval calculated by  
349 the GLMM and posterior probability to account for variability and associated uncertainties.

### 350 **3 Results**

#### 351 **3.1 Soil parameters**

352 Results are presented by site (B, E, LF, OP2, OP7, OP12, RR) or land-use (logged forest (B, E, LF), oil  
353 palm (OP2, OP7, OP12), riparian (RR)). Soil pH was acidic from logged forest site B (pH 3.65±0.44)



354 compared to forest E and LF, which were closer to neutral (pH  $6.38\pm 0.67$  and  $6.14\pm 0.5$ ), and the OP  
355 plantations were more acidic (pH  $4.5-4.7\pm 0.2$ ) compared to the riparian area (pH  $5.8\pm 0.55$ ) (Table 1).  
356 Bulk density was lower at the forest sites ( $\sim 0.81 \text{ g cm}^{-3}$ ) compared to the OP plantations ( $\sim 1.26 \text{ g cm}^{-3}$ )  
357 mainly due to a higher amount of organic matter and litter in the forest sites (B, E, LF) and a combination  
358 of compaction due to land management and lower organic matter content in the OP plantations and  
359 riparian area (OP2, OP7, OP12, RR) (Table 1). Total carbon (C) and nitrogen (N) in soil were higher in  
360 the logged forest sites ( $\sim 3-7\%$  C and  $\sim 0.25-0.4\%$  N, albeit with a very high variability) than the OP  
361 plantations ( $<1\%$  C and  $<0.1\%$  N) (Table 1) due to larger amount of litter present. The riparian reserve  
362 had higher content of C and N in the soil ( $1.2\%$  C,  $0.15\%$  N) than the OP plantations but not as high as  
363 the logged forests. Variability even within one site was large for the forest sites which is also reflected in  
364 the C/N ratios (Table 1). Litter was present in all of the forest and riparian reserve chambers and only in  
365 a few of the OP chambers. The average litter weight in the forest chambers was between 50 and 150 g  
366 dry weight with a very high variability, about 15 g in the riparian area, and hardly any litter in the OP  
367 chambers, with no litter in OP12, only in one of the OP7 chambers and an average amount of 50 g of litter  
368 in the young OP2, again with a very high variability (Table 1). The total C and N content in litter was  
369 similar in logged forest and OP ( $\sim 35-40\%$  C and  $\sim 1.5-1.8\%$  N); the main difference was the  
370 presence/absence of litter and the amount present. For all these measured parameters the variability within  
371 each site was high apart from pH in OP which was most likely regulated by plantation management  
372 operations. None of the soil physicochemical parameters were significantly different for the different  
373 land-uses or sites apart from pH from site B.



374

375 Soil moisture had high variability both spatially and temporal, with a large range for all land-uses (Figure  
376 2a) and no discernable temporal trend. The riparian reserve tended to have slightly higher soil moisture  
377 than the adjacent OP plantation due to proximity to a little stream and ground cover vegetation. The  
378 highest soil temperatures were measured in the young OP which had no canopy closure or shaded areas  
379 (Figure 2b). Soil temperature was slightly higher in the riparian reserve than the adjacent OP7, likely due  
380 to softwood trees with much less canopy cover compared to the 7 year old OP plantation. In summary,  
381 there was no discernible temporal trend of soil moisture or temperature over the two year measurement  
382 period and no apparent difference between wet and dry seasons.

383

384 Soil extractable mineral N (both  $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) was highly variable across the OP plantations with mean  
385 values of  $8 \pm 23$  and  $6.3 \pm 18$  mg N  $\text{g}^{-1}$ , respectively,  $4.5 \pm 5$  and  $2.3 \pm 4$  mg N  $\text{g}^{-1}$  in riparian and  $3.9 \pm 5$  and  
386  $5.3 \pm 5$  mg N  $\text{g}^{-1}$  in the forests (Figure 3, Table 2). We measured the lowest average  $\text{NH}_4^+$  and  $\text{NO}_3^-$   
387 concentrations in the 12 year old plantation (OP12), and the highest in the youngest OP plantation (OP2)  
388 with maxima of  $>150$  mg  $\text{g}^{-1}$ , however, with a very high spatial variability (Figure 3, Table 2). Due to the  
389 low frequency of soil and flux sampling (every 2 months), and the lack of knowledge of the fertilisation  
390 dates, it is not possible to correlate soil mineral N concentrations with individual fertiliser events.  $\text{NH}_4^+$   
391 and  $\text{NO}_3^-$  concentrations of the logged forest sites, older OP plantation and riparian reserve were very  
392 similar.

393



## 394 **3.2 Greenhouse gases**

### 395 **3.2.1 Nitrous oxide (N<sub>2</sub>O)**

396 There were no temporal trends of nitrous oxide (N<sub>2</sub>O-N) fluxes and no distinct differences between wet  
397 (usually Oct to Feb) and dry (Mar to Sep) seasons (Figure 4a). Variability in N<sub>2</sub>O-N fluxes for all sites  
398 was high and the largest range was measured in the OP plantations (Figure 4a, Table 2). We find that the  
399 largest fluxes observed were from the young (OP2) and old (OP12) oil palm plantations and exceed 1500  
400  $\mu\text{g m}^{-2} \text{h}^{-1}$  N<sub>2</sub>O-N for individual chambers. In the logged forest, largest fluxes were  $\sim 400 \mu\text{g m}^{-2} \text{h}^{-1}$  for  
401 individual chambers at site B. On a given day, very large as well as very small fluxes were measured in  
402 the OP plantations. For each land-use standard deviation was a lot larger than the mean (Table 2); logged  
403 forest  $13.9 \pm 171 \mu\text{g m}^{-2} \text{h}^{-1}$  N<sub>2</sub>O-N, OP  $46.2 \pm 166 \mu\text{g m}^{-2} \text{h}^{-1}$  N<sub>2</sub>O-N and riparian  $31.8 \pm 220 \mu\text{g m}^{-2} \text{h}^{-1}$  N<sub>2</sub>O-  
404 N. By fitting the GLMM to the data, we estimated the posterior probability density of the effect of land-  
405 use on N<sub>2</sub>O flux: mean fluxes to be 13.9 (95 % CI: -6.3 to 41.5)  $\mu\text{g m}^{-2} \text{h}^{-1}$  for logged forests, 46.2 (18.4  
406 to 97.5)  $\mu\text{g m}^{-2} \text{h}^{-1}$  for OP and 31.8 (-6.3 to 130.0)  $\mu\text{g m}^{-2} \text{h}^{-1}$  for the riparian area (Figure 4b, Table 2).  
407 The output using the Bayesian approach can be interpreted as follows: The area of the OP curve does not  
408 overlap with the area of the forest curve, which means that the probability is higher that the flux from OP  
409 plantation is higher than the flux from logged forest, with the riparian zone being intermediate. To  
410 investigate effects of additional variables, we used the automated model selection algorithm in the MuMIn  
411 R package, which uses all possible combinations of fixed effect terms and ranks them by AIC (Bartoń,  
412 2013). Possible terms included land-use, pH, soil moisture, NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup>, bulk density, soil and air  
413 temperature, and the microbial NMDS axes. This procedure found the inclusion of NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>, soil



414 moisture and soil temperature, in addition to land-use, to give the optimal model. However, whilst land-  
415 use (including the site-level effects) explained 13% of the variance (expressed as conditional  $R^2$ , (Bartoń,  
416 2013)), the additional four terms increased this by only 4%. The microbial NMDS axes did not improve  
417 the model fit, as measured by AIC.

418

### 419 **3.2.2 Methane (CH<sub>4</sub>)**

420 For methane, both negative fluxes (= CH<sub>4</sub> oxidation) and positive fluxes (CH<sub>4</sub> emission) were measured  
421 at all sites throughout the measurement period (Figure 5). Highest emission and uptake rates were  
422 measured in the logged forest sites, with emissions reaching almost 300  $\mu\text{g m}^{-2} \text{h}^{-1}$  CH<sub>4</sub>-C at site E, and  
423 uptake rates of up to 85  $\mu\text{g m}^{-2} \text{h}^{-1}$  CH<sub>4</sub>-C at sites LF and B. In the OP plantations highest emissions were  
424 measured at OP7 (~100  $\mu\text{g m}^{-2} \text{h}^{-1}$  CH<sub>4</sub>-C), and uptake rates were <50  $\mu\text{g m}^{-2} \text{h}^{-1}$  CH<sub>4</sub>-C. Overall, CH<sub>4</sub>  
425 flux ranges were larger in the logged forests than OP plantations. Grouping fluxes by land-use, mean  
426 fluxes were about  $2.2 \pm 48.3 \mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$  for logged forest,  $-2.6 \pm 17.2 \mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$  for OP and  
427  $1.3 \pm 12.6 \mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$  for riparian reserve (Table 2). The magnitudes of CH<sub>4</sub>-C fluxes in the riparian  
428 reserve were more similar to the logged forests sites than the OP plantations. Standard deviation again  
429 was large but not as large as for N<sub>2</sub>O.

430

431 As for N<sub>2</sub>O, possible drivers of CH<sub>4</sub> fluxes were investigated using linear mixed effect models and the  
432 same model selection methods. However, no correlations with co-variates could be established, even with  
433 land-use. For example, a model including terms for land-use, pH, soil moisture, NO<sub>3</sub>, NH<sub>4</sub>, bulk density,



434 soil and air temperature could explain only 3% of the variance. Land-use was clearly not a strong  
435 determinant of CH<sub>4</sub> flux, and the posterior distributions are not shown.

436

### 437 **3.2.3 Soil respiration (CO<sub>2</sub>)**

438 Soil respiration CO<sub>2</sub>-C fluxes also had a high spatial variability (Figure 6). There was a trend to slightly  
439 higher respiration rates at logged forest sites than OP plantations. Grouping fluxes by land-use, gave mean  
440 fluxes of 137.4±95 mg m<sup>-2</sup> h<sup>-1</sup> for logged forests, 93.3±70 mg m<sup>-2</sup> h<sup>-1</sup> for OP plantations and 157.7±106  
441 mg m<sup>-2</sup> h<sup>-1</sup> for the riparian site (Table 2). Soil respiration in the measured riparian reserves was therefore  
442 in the range of the soil respiration of logged forest, which was higher than from OP sites. Data was log  
443 transformed before statistical analysis. A linear mixed-effects model including all terms could explain  
444 25% of the variance, and land-use alone explained 7% of the variance.

445

### 446 **3.3 Soil biodiversity**

447 Soil samples for biodiversity measurements were collected in the low rainfall month, March 2016 (~50  
448 mm), and the high rainfall month, November 2016 (~250 mm, Figure 1), in order to quantify broad  
449 differences in communities due to land-use and provide additional biodiversity variables for modelling  
450 fluxes. Three different amplicon sequencing assays were performed on extracted DNA targeting bacteria  
451 (16S rRNA gene), fungi (ITS region), and broad groups of soil eukaryotic taxa (18S rRNA gene, including  
452 principally fungi, protists and algae). The ordinations and multivariate permutation effects of land-use  
453 were generally consistent across the two sampling points irrespective of seasonal climatic differences



454 (Figure 7). Fitting environmental vectors to the ordination axis scores revealed that the bacterial  
455 communities were highly related to soil pH ( $r^2 = 0.85$  and  $0.84$ ,  $p < 0.001$ , for the two sample dates  
456 respectively), with acid soils (pH 3.6) at site B, compared to near neutral pH of 6.1 and 6.4 at sites LF  
457 and E, Table 1). Weaker relationships with the land-use factors ( $r^2 = 0.23$  and  $0.11$ ,  $p < 0.05$ ) were  
458 observed. Logged forests E and LF had very similar bacterial communities, which were distinct from the  
459 three OP sites and also the riparian site. In contrast, fungal and eukaryotic communities were not as  
460 strongly related to soil pH (fungal  $r^2 = 0.67$  and  $0.72$ , and eukaryotic  $r^2 = 0.73$  and  $0.79$  for the two sample  
461 dates respectively,  $p < 0.001$ ), and were more strongly related to above ground land-use than bacterial  
462 communities (fungal  $r^2 = 0.52$  and  $0.57$ , and eukaryotic  $r^2 = 0.50$  and  $0.42$ ,  $p < 0.001$ ). As can be seen in  
463 the fungal ordinations particularly, the forested sites formed a distinct cluster separate from the OP sites,  
464 despite the large differences in soil acidity.

465

### 466 **3.4 Upscaling of N<sub>2</sub>O fluxes to Sabah scale**

467 In an attempt to broadly upscale our findings, we calculated the annual soil N<sub>2</sub>O emission for the Sabah  
468 state based on the data from this study (Table 2), together with land cover areas estimates (Gaveau et al.,  
469 2016). Nitrous oxide emissions calculated for the Sabah region showed a strong dependence on the  
470 conversion of forest to OP plantations from 1973 to present day. By 2015, the total estimated N<sub>2</sub>O  
471 emissions from OP plantations were roughly 40% of total emissions, with 60% of the emissions from  
472 forested areas, despite the OP area being less than 40% of the forest area. The Sabah scale median N<sub>2</sub>O  
473 emission estimate had increased from 7.6 Mt (95% confidence interval, -3.0-22.3 Mt) per year in 1973 to



474 11.4 Mt (0.2-28.6 Mt) per year in 2015. As the measured CH<sub>4</sub> fluxes were fluctuating around zero, the  
475 changes in land-use also resulted in small changes of CH<sub>4</sub> flux rates over the 42-year period. Our median  
476 results suggest that Sabah is a sink for CH<sub>4</sub> (4 Mt y<sup>-1</sup>) throughout the time period presented.

#### 477 **4 Discussion**

478 This study focussed on comparing GHG fluxes from different land-use types in the Tropics. Our data,  
479 although not high frequency measurements, provide a comprehensive insight in the potential impact of  
480 converting logged forests to OP plantations on GHG fluxes. The focus of this study is on N<sub>2</sub>O, with  
481 auxiliary measurements of CH<sub>4</sub> and soil respiration. To date only four studies published data of N<sub>2</sub>O  
482 emissions from OP plantations on mineral soil in Southeast Asia using the chamber method that included  
483 measurements from a time period of longer than 6 months (Skiba et al., 2020). Only one of these studies  
484 included measurements in Malaysia (Sakata et al., 2015). Globally tropical forests are the largest natural  
485 source of N<sub>2</sub>O (Werner et al., 2007). Therefore, the question is whether the N input to OP plantations with  
486 lower organic matter (TC/TN content) compared to tropical forests (lots of organic matter input, warm,  
487 humid), lead to larger N<sub>2</sub>O emissions than forest. Although it has been recognised that N<sub>2</sub>O emissions are  
488 induced by N-fertiliser application in OP, when considering annual or long-term emissions from mineral  
489 soil, these fertilisation patterns might not have a pronounced or clear effect (Kaupper et al., 2019). For  
490 example, N-fertiliser induced N<sub>2</sub>O fluxes comprised only 6-21% of the annual soil N<sub>2</sub>O fluxes in OP  
491 plantations in Sumatra, Indonesia (Hassler et al., 2017), the rest was due to other natural processes  
492 occurring in the soil. Therefore, our study can be considered representative, particularly as measurements



493 were carried out over two years. All three land-use types (logged forest, oil palm and riparian) showed  
494 positive N<sub>2</sub>O fluxes albeit with a high variability.

495

496 On some occasions, our measured fluxes exceeded the range reported by Shizuka et al. (2005) of N<sub>2</sub>O  
497 emissions from OP plantations on mineral soil in Indonesia, ranging from ~1-29 μg m<sup>-2</sup> h<sup>-1</sup>, by an order  
498 of magnitude (maximum measured 350 μg m<sup>-2</sup> h<sup>-1</sup>). The highest values reported by Shizuka et al. (2005)  
499 were from young plantations, while the lowest were reported from older plantations. They suggested the  
500 low N uptake of young plantations after fertiliser application and the fixation of N by the legume cover  
501 crop could be the reason for the high emissions. On the other hand, the low emissions from older  
502 plantations could result from higher N uptake by the OP and the absence of legume cover. In their study,  
503 N<sub>2</sub>O emissions were mainly determined by soil moisture (Ishizuka et al., 2005); which was not the case  
504 here. Mean N<sub>2</sub>O fluxes from a sandy soil in Malaysia were reported to range from 0.80 to 3.81 and 1.63  
505 to 5.34 μg N m<sup>-2</sup> h<sup>-1</sup> in the wet and dry seasons, respectively (Sakata et al., 2015). This was lower than  
506 from a sandy loam soil in Indonesia (27.4 to 89.7 and 6.27 to 19.1 μg N m<sup>-2</sup> h<sup>-1</sup> in the wet and dry seasons,  
507 respectively) (Sakata et al., 2015). Despite the limited number of measurements in OP plantations on  
508 mineral soils and the high variability of results, emissions seem to generally be higher in the early years  
509 of the OP plantations (Pardon et al., 2016a). This is not necessarily reflected in our data, as the OP2  
510 (young) and OP12 sites (older) showed higher fluxes than the OP7 (medium age) site; though with a  
511 lifespan of up to 30 years, all plantations measured in this study can still be regarded as immature. As in  
512 our study, Aini et al. (2015) also found no differences in N<sub>2</sub>O fluxes in the wet and dry months with fluxes



513 ranging from 0.08 to 53  $\mu\text{g N m}^{-2} \text{h}^{-1}$ . The range of our measured fluxes exceeded those of these previously  
514 published studies. However, it is difficult to generalise, as variability appeared to be high in all studies.

515

516 Our measured  $\text{N}_2\text{O}$  fluxes from the riparian area were similar to those measured in the OP plantation, as  
517 soil properties were more similar to OP than logged forest. There is currently a knowledge gap on GHG  
518 emissions from riparian buffers (Luke et al., 2019) and more studies are needed to evaluate the  
519 effectiveness in terms of nutrient retention and potential GHG mitigation of such buffers. A previously  
520 published study from Peninsula Malaysia reported mean  $\text{N}_2\text{O}$  emission rates from logged tropical forest  
521 sites ranging from 17.7 to 92.0  $\mu\text{g m}^{-2} \text{h}^{-1} \text{N}_2\text{O-N}$  which was significantly larger than from their measured  
522 unlogged sites (Yashiro et al., 2008). Even though the range of our measured fluxes from logged forest  
523 sites was wider, it is broadly in the same order of magnitude ( $13.9 \pm 171 \mu\text{g m}^{-2} \text{h}^{-1} \text{N}_2\text{O-N}$ ).

524

525 As often the case with GHG studies, the variation in the measured GHG fluxes could not be explained  
526 with certainty by any of the measured soil parameters. Our sampling frequency was not high enough to  
527 investigate, for example, emission rates after fertiliser application in the OP plantations and besides, this  
528 was not the aim of our study. The wide ranges we measured for soil mineral N concentrations and  $\text{N}_2\text{O}$   
529 fluxes were likely due to the spatial and temporal variability of the fertiliser application, as the slow  
530 release fertiliser bags were randomly placed around the trees, and with time, the fertiliser release rate  
531 slowed down. Apart from no strong correlations with single environmental factors, multiple regression  
532 and mixed models were only able to explain around 17% of the variance including multiple measured



533 parameters. However, applying the Bayesian method, the posterior probability density of the effect of  
534 land-use on N<sub>2</sub>O flux confirmed that fluxes from the OP plantations were evidently higher than those  
535 from the forests (the area of the OP curve does not overlap with the forest curve), with the riparian zone  
536 being intermediate (mean fluxes 13.9 (95 % CI: -6.3 to 41.5)  $\mu\text{g m}^{-2} \text{h}^{-1}$  for logged forests, 46.2 (18.4 392  
537 to 97.5)  $\mu\text{g m}^{-2} \text{h}^{-1}$  for OP and 31.8 (-6.3 to 130.0)  $\mu\text{g m}^{-2} \text{h}^{-1}$  for the riparian area).

538

539 Agricultural soils such as OP soils can be methane sinks, with uptake rates usually being lower than in  
540 forest soils (Hassler et al., 2015) which could also be seen in our data with logged forest showing higher  
541 uptake rates but at the same time also showing the highest emission rates. However, we did not see the  
542 seasonal cycle reported in Hassler et al., (2015) from Indonesia and generally differences between all  
543 three land-uses (logged forest, oil palm and riparian) were small. The lack of seasonal variability seen in  
544 our study might be due to the fact that dry and wet seasons are not as pronounced in Sabah as in other  
545 tropical regions (Kerdraon et al., 2020) and that temperature is fairly constant throughout the year.

546

547 Higher soil respiration (sum of heterotrophic and autotrophic respiration) is often considered as a sign of  
548 good soil health, it reflects the capacity of soil to support soil life including microorganisms and crops.  
549 Heterotrophic soil respiration defines the level of microbial activity, soil organic matter content and its  
550 decomposition whilst autotrophic respiration is the metabolism of organic matter by plants. In a recently  
551 published study investigating litter decomposition, soil respiration fluxes in Sabah (also in the SAFE area)  
552 were higher from forest than OP (Kerdraon et al., 2020). This was also the general trend in our study



553 despite the high variability of all measured fluxes. Litter input in our plots was larger in the logged forest  
554 plots and riparian reserve than the OP. In litter decomposition experiments, in both Borneo and Panama,  
555 litter input was more important than litter type, which stresses the importance of the amount of  
556 aboveground litter for soil processes in general, especially in disturbed habitats or forest converted to  
557 plantations (Kerdraon et al., 2020).

558

559 Analyses of soil microbial communities with different assays targeting different microbial components,  
560 revealed strong influences of soil properties such as pH, but also highlighted that fungal and eukaryotic  
561 communities were more affected by management and land-use than bacteria. Soil pH is known to have  
562 an impact on soil microbial community in the Tropics (Kaupper et al., 2019; Tripathi et al., 2012) which  
563 may explain the very different bacterial communities in logged forest B with the lowest measured pH of  
564 all our sites. Typically, C and N availability or generally soil fertility is known to decrease after  
565 deforestation (Allen et al., 2015; Hassler et al., 2017; Hassler et al., 2015; Kaupper et al., 2019), this is  
566 also reflected in our data (Table 1), especially the very low total N values in all OP plantations. Nutrient  
567 input through litter is higher in the forest than OP plantations and consistently replenished (Guillaume et  
568 al., 2015). Therefore, for microorganisms, OP plantations represent a nutrient deprived environment  
569 (Kaupper et al., 2019). Low total C input can also limit the methanotrophic population size and hence  
570 limit CH<sub>4</sub> uptake (Krause et al., 2012). Lower N in OP soil has also shown to limit CH<sub>4</sub> uptake when  
571 compared with forest soil (Hassler et al., 2015). Exactly how shifts in C and N after converting forest to  
572 OP may affect processes involved in N<sub>2</sub>O and CH<sub>4</sub> fluxes remains highly uncertain (Kaupper et al., 2019).



573 On mineral soil, changes in bulk density after conversion from forest to plantation are often marginal  
574 (Aini et al., 2015; Chiti et al., 2014), however in our study we did see a distinct difference between logged  
575 forest and OP soil (Table 1), which was likely due to the higher organic matter content in the logged forest  
576 soil.

577

578 We found distinct differences of microbial communities in the different land-uses. In a recently published  
579 study of a natural rainforest and an OP plantation in Sabah, bacterial community diversity (richness and  
580 evenness) was comparable or even slightly higher in the OP site (Tin et al., 2018). Also, Kaupper et al.  
581 (2019) have suggested that microbial biodiversity loss occurs soon after clearance and that bacterial  
582 diversity might either be resilient to the change or changes cannot be detected after a sufficient recovery  
583 period (>8 years) after deforestation (Kaupper et al., 2019). Agricultural OP soil has previously been  
584 found to be more functionally diverse compared to forest soil (Mendes et al., 2015; Tripathi et al., 2016)  
585 while microbial functioning in forest soil appears to be dependent on microbial abundance rather than  
586 diversity (Mendes et al., 2015). Reason for this could be that in agricultural soils (i.e. OP plantations)  
587 there is a need for functional diversity in order to maintain a sufficient level of idleness for continued  
588 functioning under stress events such as deforestation and soil management. Despite these few recent  
589 studies on microbial communities, the link to processes leading to GHG fluxes has not been made  
590 (Kaupper et al., 2019), hence predictions on the impact of land-use change are difficult to make. Despite  
591 our data showing land-use and soil property effect on components of the microbial community, inclusion  
592 of derived community metrics in models to predict fluxes did not improve fits; it is possible that a more



593 specific focus on relevant functional gene abundances will yield greater predictive ability. In a laboratory  
594 incubation study that used soil from some of these field study sites, it was found that both logged forest  
595 and OP soil had the same potential for substantial N<sub>2</sub>O fluxes under laboratory conditions (Drewer et al.,  
596 2020). However, under these controlled conditions, riparian reserve soil had negligible N<sub>2</sub>O fluxes, which  
597 is in contrast to the fluxes measured in the field. The same study also concluded that despite the high  
598 variability found amongst replicates, the main contribution to N<sub>2</sub>O emissions came from proteobacterial  
599 *nirS* and *AniA-nirK* containing denitrifiers and archaeal ammonia oxidizers (Drewer et al., 2020). The  
600 conversion of forest to monoculture plantations is a big threat to ecosystem functioning (Tripathi et al.,  
601 2016), yet we are still missing data on microbial communities to make accurate predictions.

602

603 Plantation management, for example returning palm fronds and empty fruit bunches to the plantation soil,  
604 will likely change nutrient cycling (Pardon et al., 2017) and therefore microbial composition. Presence  
605 of, for example, leaf litter as a source of organic matter is essential to maintain soil processes (Kerdraon  
606 et al., 2020). It is vital to understand underlying longer-term processes that ultimately might regulate  
607 GHG fluxes to be able to develop GHG mitigation strategies. More environmentally friendly plantation  
608 management would likely help with maintaining ecosystem functioning and reduce GHG emissions.

609

610 In an attempt to broadly upscale our findings, we calculated the annual soil N<sub>2</sub>O emission for the Sabah  
611 state based on the data from this study (Table 2), together with land cover areas estimates (Gaveau et al.,  
612 2016). The Sabah scale median N<sub>2</sub>O emission estimate had increased from 7.6 Mt per year in 1973 to



613 11.4 Mt per year in 2015. However, this change is small considering the associated uncertainties,  
614 demonstrated by the interquartile range, -3.0-22.3 Mt per year in 1973 and 0.2-28.6 Mt per year in 2015.  
615 The changes in land-use resulted in small changes of CH<sub>4</sub> flux rates over the 42-year period. Our median  
616 results suggest that Sabah is a sink for CH<sub>4</sub> (4 Mt y<sup>-1</sup>) throughout the time period presented. There was a  
617 slight decrease to the interquartile range of our estimate as more land was converted to OP plantation,  
618 suggesting that the strength of the sink decreased. However, this is much lower than the uncertainty  
619 associated with this analysis, hence; it is difficult to draw strong conclusions.

## 620 **5 Conclusions**

621 N<sub>2</sub>O emission rates in Sabah on mineral soil were higher from OP than logged forest over a two-year  
622 study with N<sub>2</sub>O emission rates from riparian intermediate. Mean CH<sub>4</sub> fluxes were low with very high  
623 variability, showed no clear trend and the highest range of fluxes was measured in logged forests. Fungal  
624 and eukaryotic communities were related to management whilst bacterial communities were strongly  
625 affected by soil pH, which might have masked any management impacts. Mixed models and multiple  
626 regression analysis could only explain 17% of the variation in the measured N<sub>2</sub>O fluxes, 3% of the CH<sub>4</sub>  
627 fluxes and 25% of soil respiration, despite the large number of measured abiotic and biotic parameters.  
628 This is not uncommon for GHG fluxes, but demonstrates that many more studies, ideally at high temporal  
629 and spatial resolution, are required to inform on the impact of land-use and climate change on GHG  
630 fluxes. Scaling up measured N<sub>2</sub>O fluxes to Sabah using land areas for forest and OP (Gaveau et al., 2016)  
631 imply that the emissions have increased over the last 42 years, with the proportion of emissions from OP



632 plantations increasing in comparison to the emissions from forests. Using the range of measured fluxes  
633 with mean and interquartile ranges highlights the large uncertainties still associated with these emission  
634 estimates, despite having almost 700 individual data points over two years. For CH<sub>4</sub>, the picture is even  
635 more uncertain. More studies on GHG fluxes from tropical forests and OP plantations on mineral soils  
636 (including experiments deriving N<sub>2</sub>O emission factors) are needed to reduce the uncertainty of their  
637 emission rates. Furthermore, the impact of current management systems and future potentially more  
638 environmentally friendly plantation management needs to be investigated in order to predict how to  
639 maintain ecosystem function and biodiversity which could have a positive impact on reducing GHG  
640 emissions.



641 **Data availability**

642 Drewer, Julia, Leduning, Melissa, Sentian, Justin, & Skiba, Ute. (2019). Soil greenhouse gas fluxes and  
643 associated parameters from forest and oil palm in the SAFE landscape [Data set]. Zenodo.

644 <http://doi.org/10.5281/zenodo.3258117>

645

646 **Author contributions**

647 JD&US designed the project, ML carried out field measurements with help of JD&US and JS as local  
648 collaborator. RG&TG carried out microbial analysis. PL carried out statistical analysis. NC assisted with  
649 data analysis. ECP&GH carried out upscaling, NM supervised soil parameter analysis. JD wrote the  
650 manuscript with contributions from all co-authors.

651

652 **Competing interests**

653 No conflict of interest to declare

654

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860 **Tables and Figures**

861 **Table 1.** Soil physicochemical parameters: pH (mean of three sampling occasions and replicate chambers  
 862 at each site); bulk density (mean of replicate chambers at each site from one sampling occasion); total C  
 863 and total N in soil from the top 1-10 cm and leaf litter in the chambers (from replicate chambers on one  
 864 sampling occasion), from the different sites (LF (n=8), B (n=8), E (n=8) = logged forest, OP2 (n=8), OP7  
 865 (n=12), OP12 (n=8) = oil palm, RR (n=4) = riparian reserve).

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site	pH		bulk density [g cm <sup>-3</sup> ]		soil total N [%]		soil total C [%]		C/N (soil)		Total litter dry mass [g]		litter total N [%]		litter total C [%]	
	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
<b>LF</b>	6.14	0.50	0.80	0.16	0.24	0.14	3.21	2.04	14.4	4.97	53	18.18	1.76	0.39	36.44	6.82
<b>B</b>	3.65	0.44	0.80	0.11	0.30	0.07	4.65	1.23	15.5	1.47	114	51.97	1.51	0.31	33.78	7.33
<b>E</b>	6.38	0.67	0.84	0.21	0.38	0.26	6.40	6.72	13.8	5.44	92	41.38	1.82	0.15	40.01	3.88
<b>OP2</b>	4.54	0.21	1.22	0.12	0.05	0.02	0.70	0.21	14.0	1.81	53	70.54	1.78	0.28	40.62	5.88
<b>OP7</b>	4.71	0.22	1.28	0.18	0.07	0.05	0.97	0.47	15.2	4.18	19*	N/A	1.54	N/A	31.99	N/A
<b>OP12</b>	4.60	0.14	1.27	0.07	0.08	0.03	0.72	0.15	9.3	2.34	N/A	N/A	N/A	N/A	N/A	N/A
<b>RR</b>	5.77	0.55	1.25	0.10	0.14	0.06	1.18	0.32	9.6	3.61	17	3.00	1.78	0.28	40.62	5.88

867

868 \*only one of the OP7 chambers had litter present

869



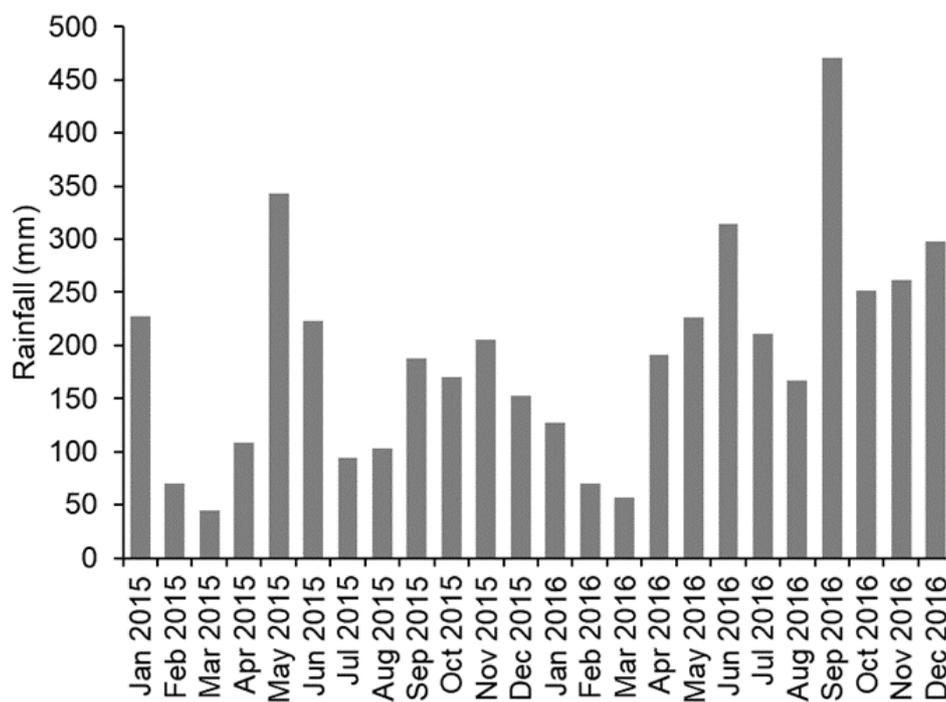
870 **Table 2.** Greenhouse gas fluxes ( $N_2O-N$ ,  $CH_4-C$ , soil respiration  $CO_2-C$ ) and soil mineral nitrogen ( $NH_4-$   
 871  $N$  and  $NO_3-N$ ) averaged over the entire measurement period (January 2015 – November 2016) by land-  
 872 use.  $N$  = number of individual data points,  $sd$  = standard deviation; forest = logged forest, OP = oil palm,  
 873 RR = riparian reserve.

874

<i>Variable</i>	<i>Land-use</i>	<i>N</i>	<i>Mean</i>	<i>SD</i>	<i>Median</i>
$N_2O-N$ ( $\mu g m^{-2} h^{-1}$ )	<b>forest</b>	286	13.87	171.49	13.90
	<b>OP</b>	335	46.20	166.35	45.84
	<b>RR</b>	48	31.83	220.40	30.86
$CH_4-C$ ( $\mu g m^{-2} h^{-1}$ )	<b>forest</b>	216	2.20	48.34	-5.63
	<b>OP</b>	251	-2.57	17.18	-3.00
	<b>RR</b>	36	1.27	12.60	-0.38
$CO_2-C$ ( $mg m^{-2} h^{-1}$ )	<b>forest</b>	288	137.39	94.63	115.35
	<b>OP</b>	336	93.30	69.65	75.55
	<b>RR</b>	48	157.70	105.80	142.60
$NH_4-N$ $mg g^{-1}$	<b>forest</b>	288	3.92	5.41	2.85
	<b>OP</b>	336	7.99	22.72	2.50
	<b>RR</b>	48	4.50	5.40	2.50
$NO_3-N$ $mg g^{-1}$	<b>forest</b>	288	5.30	5.28	3.40
	<b>OP</b>	336	6.32	18.16	1.40
	<b>RR</b>	48	2.25	4.19	1.35

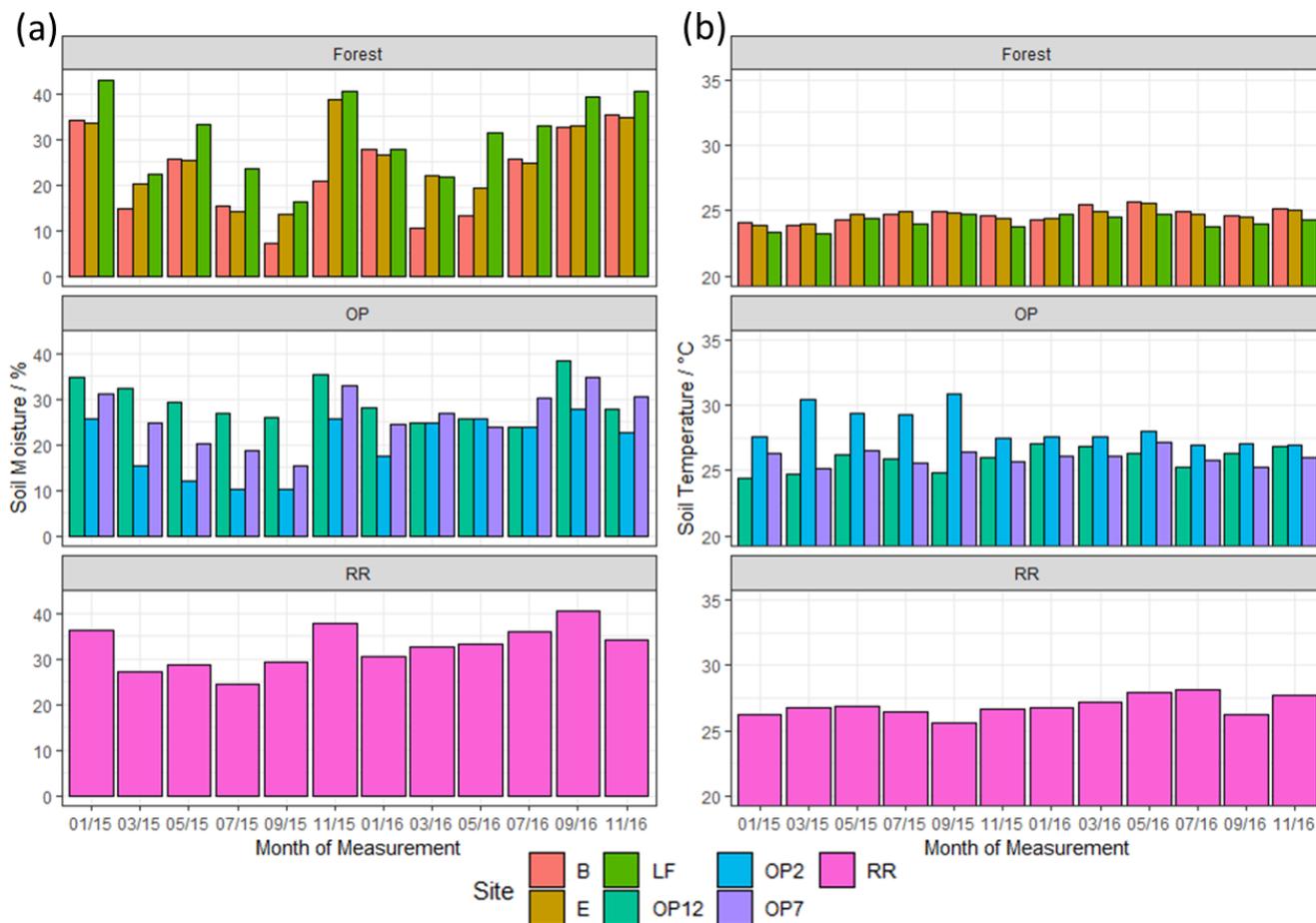
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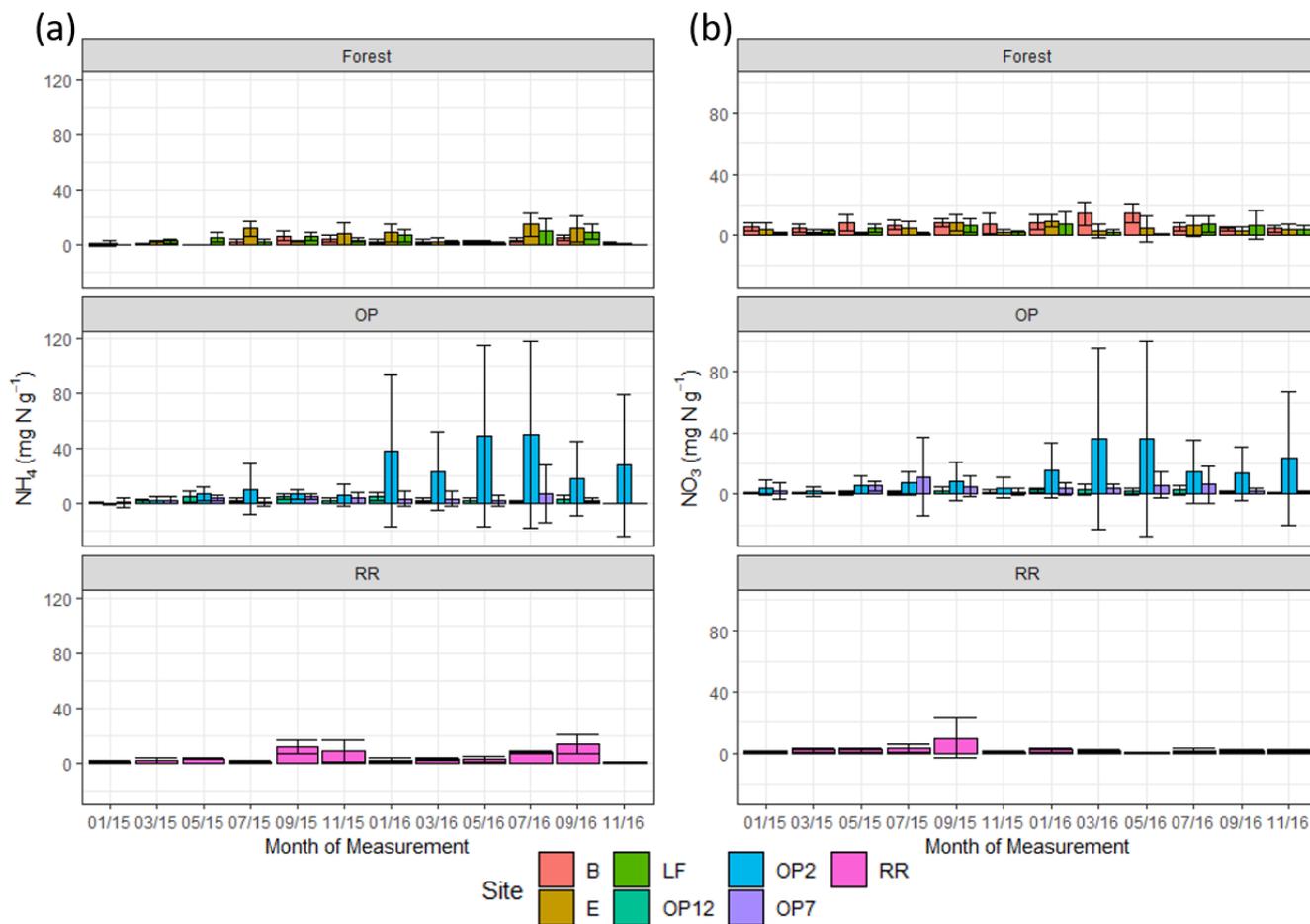
877

878 **Figure 1.** Monthly rainfall (mm) in the SAFE area in 2015 and 2016 (R. Walsh).



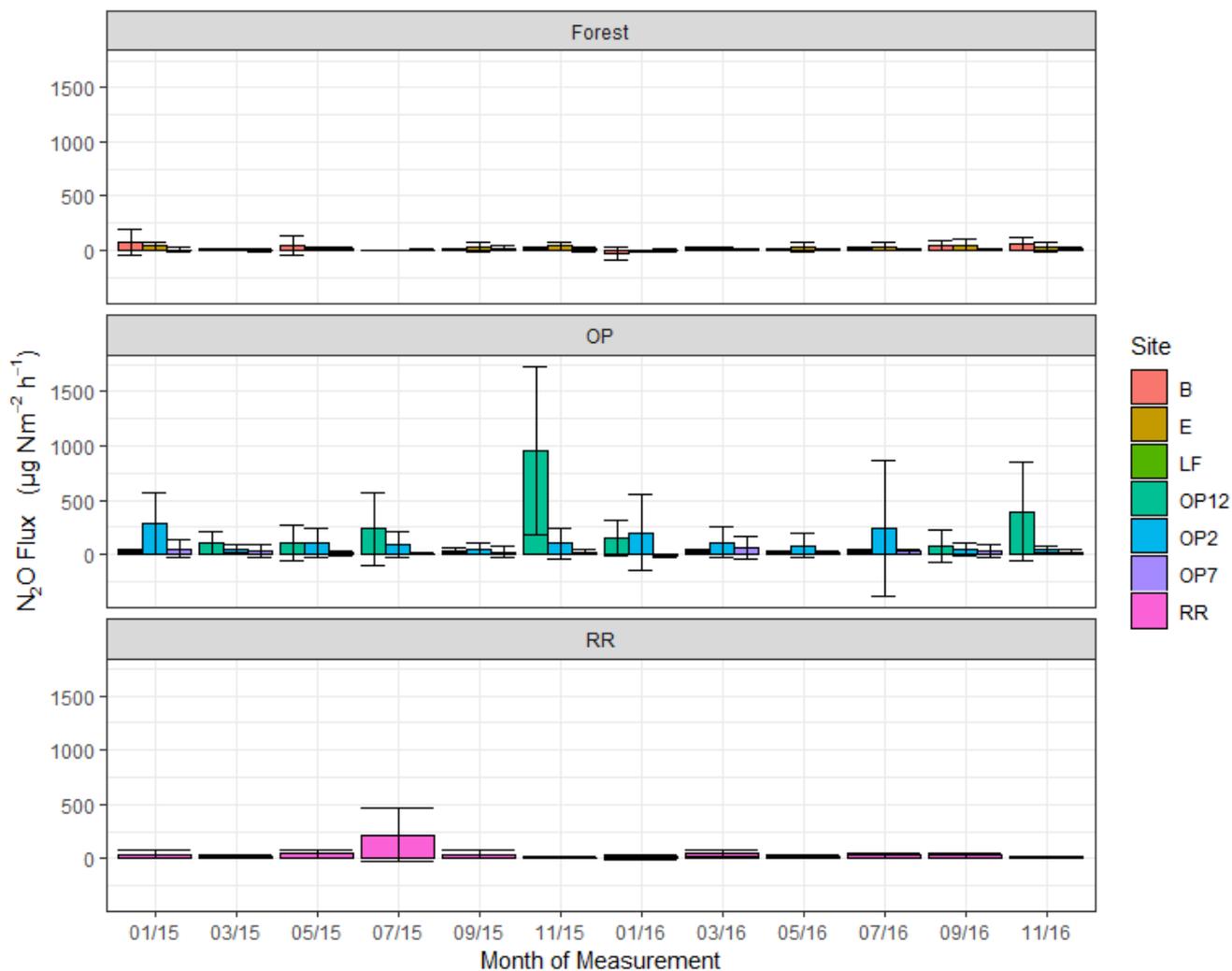
879

880 **Figure 2.** Barplots of mean volumetric soil moisture (a) and mean soil temperature (b) from January 2015  
 881 - November 2016, every two months: (upper panel: B, E, LF = logged forests, middle panel: OP12, OP2,  
 882 OP7 = oil palm plantations, bottom panel: RR = riparian reserve).



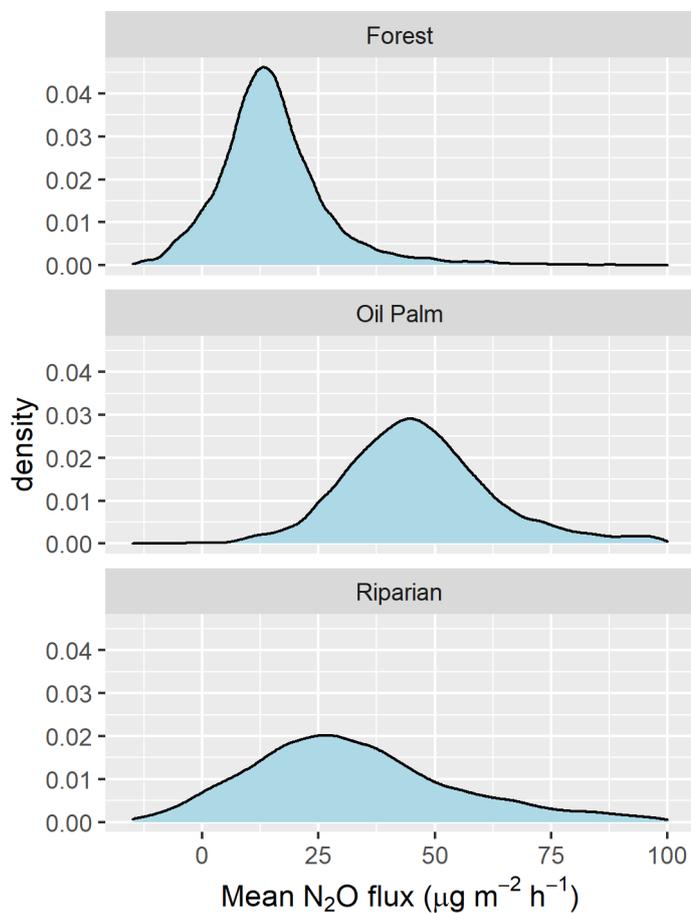
883

884 **Figure 3.** Mean mineral N as KCl extractable  $\text{NH}_4^+$  (a) and  $\text{NO}_3^-$  (b) from January 2015 - November  
885 2016, every two months (upper panel: B, E, LF = logged forests, middle panel: OP12, OP2, OP7 = oil  
886 palm plantations, bottom panel: RR = riparian reserve). Error bars represent standard deviation of the  
887 samples around the mean.



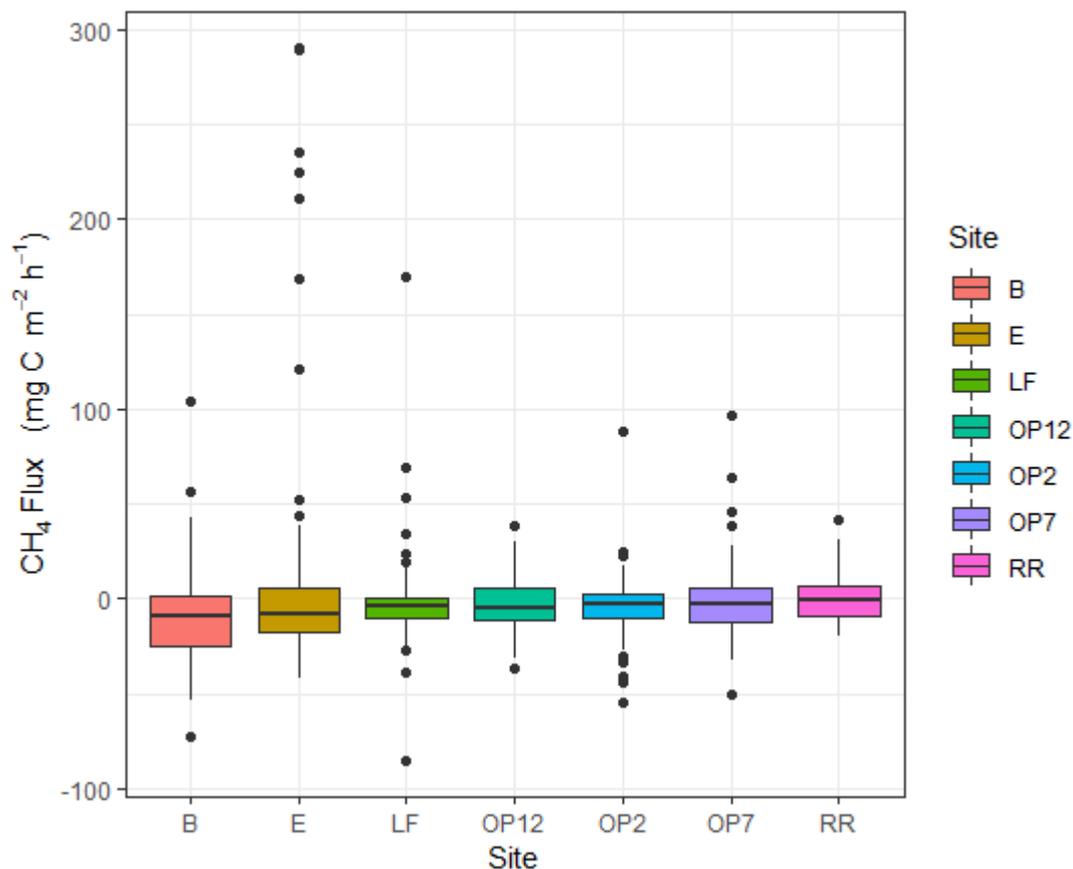
888

889 **Figure 4. a)** Nitrous oxide ( $N_2O$ -N) fluxes in  $\mu g m^{-2} h^{-1}$  from January 2015 - November 2016, every two  
890 months (upper panel: B, E, LF = logged forests, middle panel: OP12, OP2, OP7 = oil palm plantations,  
891 bottom panel: RR = riparian reserve). Bars are mean for each site and error bars are standard deviation of  
892 number of chambers per site.



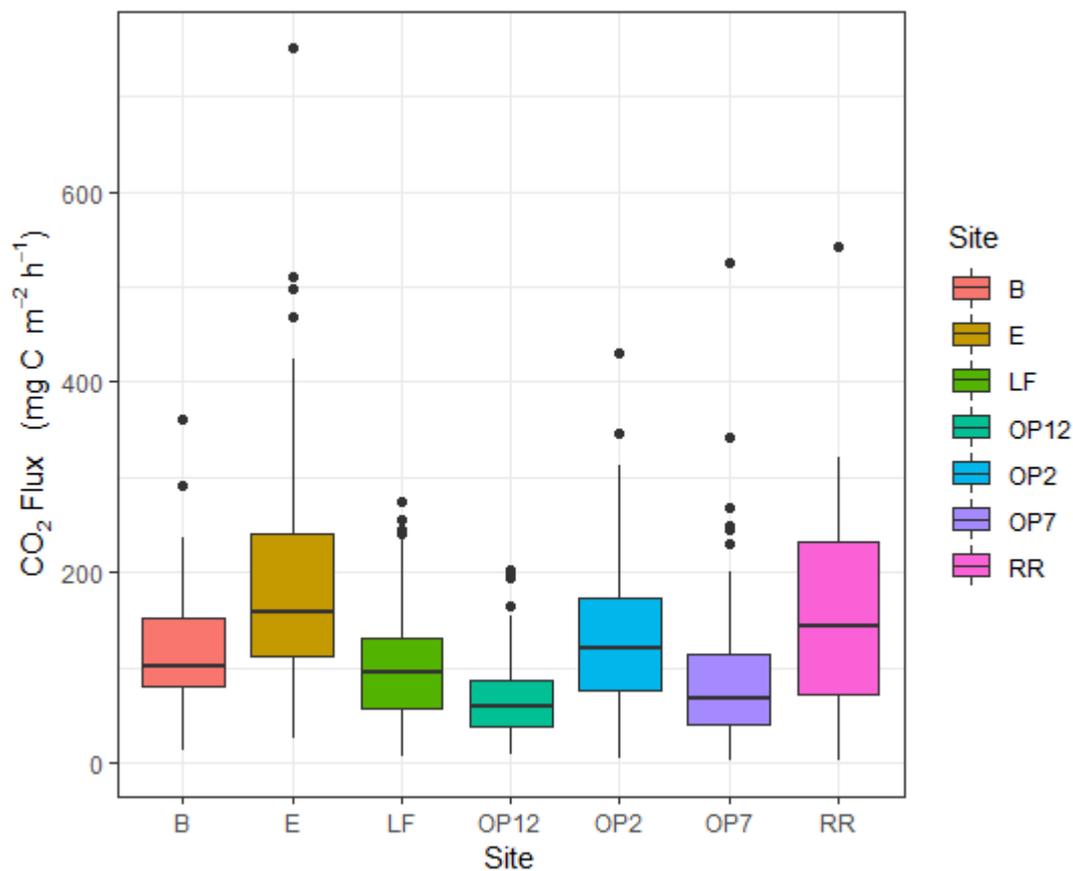
893

894 **Figure 4. b)** Posterior probability density of the mean nitrous oxide flux from each land-use, estimated  
895 by the Bayesian GLMM described in the text.



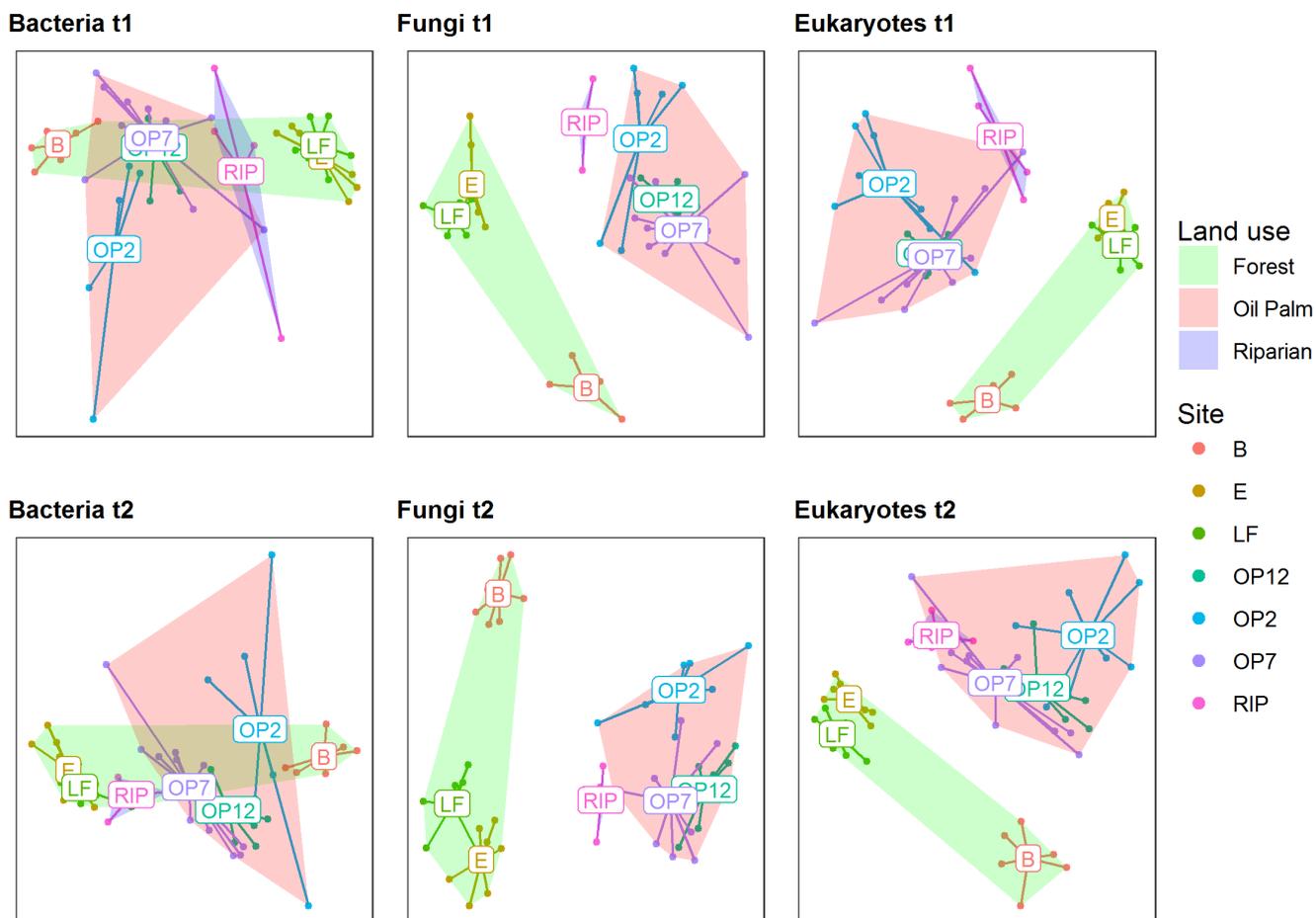
896

897 **Figure 5.** Methane ( $\text{CH}_4\text{-C}$ ) fluxes in  $\mu\text{g m}^{-2} \text{h}^{-1}$  from the different sites from January 2015 - November  
898 2016, every two months (B, E, LF = logged forests, OP12, OP2, OP7 = oil palm plantations, RR = riparian  
899 reserve). The ends of the box are the upper and lower quartiles, so the box spans the interquartile range.  
900 The median is marked by a horizontal line inside the box. The whiskers are the two lines outside the box  
901 that extend to the highest and lowest observations with outliers marked with an asterisk (\*).



902

903 **Figure 6.** Soil respiration ( $\text{CO}_2\text{-C}$ ) fluxes in  $\text{mg m}^{-2} \text{h}^{-1}$  from January 2015 - November 2016, every two  
904 months (B, E, LF = logged forests, OP12, OP2, OP7 = oil palm plantations, RR = riparian reserve). The  
905 ends of the box are the upper and lower quartiles, so the box spans the interquartile range. The median is  
906 marked by a horizontal line inside the box. The whiskers are the two lines outside the box that extend to  
907 the highest and lowest observations with outliers marked with an asterisk (\*).



908

909 **Figure 7.** 2D Non metric multidimensional scaling ordination plots of bacteria, fungal and eukaryotic  
910 communities from two sample dates March 2016 (upper panel, t1) and November 2016 (lower panel,  
911 t2). Coloured points designate replicates from each site (B, E, LF = logged forests, OP12, OP2, OP7 =  
912 oil palm plantations, RIP = riparian reserve), as indicated in the legend with additional site centroids  
913 denoted on the plots. In addition, hulls indicate broad land-use categories as indicated in the legend.

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915