Comparison of greenhouse gas fluxes ~~and microbial communities~~ from tropical forests and ~~adjacent~~ oil palm plantations on mineral soil

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Abstract. In Southeast Asia, oil palm (OP) plantations have largely replaced tropical forests. The impact of this shift in land-use on greenhouse gas (GHG) fluxes ~~and soil microbial communities~~ remains highly uncertain, mainly due to a relatively small pool of available data. The aim of this study is to quantify differences of nitrous oxide (N_2O) and methane (CH_4) fluxes as well as soil carbon dioxide (CO_2) respiration rates from logged forests, oil palm plantations of different ages and an adjacent small riparian area. Nitrous oxide fluxes are t~~T~~he focus of this study ~~is on N_2O fluxes~~, as these emissions are expected to increase significantly due to the ~~introduction of~~ nitrogen (N) fertiliser application in the plantations.

This study was conducted in the SAFE (Stability of Altered Forest Ecosystems) landscape in Malaysian Borneo (Sabah) with measurements every two months over a two-year period. GHG fluxes were measured by static chambers~~; at the same time soil samples were collected for analysis of the~~ together with key soil physicochemical parameters and ~~for analysis of~~ microbial biodiversity ~~using next generation sequencing in dry and wet season~~. At all sites, N_2O fluxes were spatially and temporally highly variable~~. across the different sites, with the highest mean flux~~On average largest fluxes (incl. 95% CI) were measured from ~~oil palm (~~OP plantations~~)~~ (~~46.2±166~~45.1 (24.0 – 78.5) µg m^{-2} h^{-1} N_2O-N), ~~and~~ slightly smaller from the riparian area (~~31.8±220~~29.4 (2.8 – 84.7) µg m^{-2} h^{-1} N_2O-N) ~~sites, compared to lower~~and smallest ~~fluxes~~ from logged forests (~~13.9±171~~16.0 (4.0 – 36.3) µg m^{-2} h^{-1} N_2O-N). Methane fluxes were generally small (~~here~~ mean ±sd); -2.6±17.2 µg CH_4-C m^{-2} h^{-1} for OP and 1.3±12.6 µg CH_4-C m^{-2} h^{-1} for riparian with the range of measured CH_4 fluxes largest in logged forests (2.2±48.3 µg CH_4-C m^{-2} h^{-1}). Soil respiration rates were larger from riparian areas (157.7±106 mg m^{-2} h^{-1} CO_2-C) and logged forests (137.4±95 mg m^{-2} h^{-1} CO_2-C) than OP plantations (93.3±70 mg m^{-2} h^{-1} CO_2-C) ~~due to larger~~~~as a result~~because of larger amounts of decomposing leaf litter. Microbial communities were distinctly different between the different land-use types and sites~~.~~~~,~~ ~~B~~bacterial communities were linked to soil pH and fungal and eukaryotic communities to land-use. Despite measuring a large number of environmental parameters, mixed models could only explain up to 17% of the variance of measured fluxes for N_2O, 3% of CH_4 and 25% of soil respiration. Scaling up measured N_2O fluxes to Sabah using land areas for forest and OP resulted in emissions 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) per year in 2015 due to the increasing area of forest converted to OP plantations over the last ~40 years.

1 Introduction

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

OP plantations are one of the main causes of deforestation and forest degradation in Southeast Asia (Lee-Cruz et al., 2013; Wilcove et al., 2013) with some disputes about the extent to which industrial plantations are responsible for the loss of old-growth and selectively logged forests in Borneo (Gaveau et al., 2016). OP generates the highest yield per hectare of land of any vegetable oil crops. It is used in food products, detergents, soaps, cosmetics, animal feed and bioenergy, and was hence praised as a wonder crop (Sayer et al., 2012). However, OP agriculture is now known to be responsible for soil degradation, loss of soil carbon (C) and reduced soil fertility due to the conversion and management methods (Guillaume et al., 2015; Lee-Cruz et al., 2013). To create an OP plantation, complete deforestation followed by terracing of the land is often the chosen method, and not only in hilly terrain. Terracing can result in poor drainage, reduced soil fertility and increased soil erosion. Conversion of tropical forests ~~may~~ also leads to changes in the short- and long-term nutrient status of the converted land-use systems. It is important to understand impacts of these land-use changes in order to identify more environmentally friendly and sustainable management practices (Jackson et al., 2019).

OP plantations are assessed for their GHG emissions, but rarely have emissions from forests and plantations from the same region been reported together, despite the science community calling for- flux measurements from ~~call to study fluxes in~~ forest and converted land simultaneously (van Lent et al., 2015). Much of the focus has been on GHG emissions from tropical forests on peatland and peatland drained for plantations~~peatland~~ rather than from tropical mineral soils, because of the serious carbon losses when draining the peatlands for crop production~~either tropical forest on peatland or peatland~~

drained for plantations. In addition, More attention has been given to carbon fluxes or and storage (Germer and Sauerborn, 2008; Hassler et al., 2015) than emissions from the non-CO_2 GHG methane (CH_4) and nitrous oxide (N_2O). Meijide et al. (2020) identified the need to study all three GHGs together in order to assess total emissions from OP plantations. Even though CH_4 and N_2O are not emitted at the quantity of CO_2, their global warming potentials (GWP) per molecule are 28 —and 34 (without and with climate-carbon feedback) and 265 —and 298 times higher than CO_2 on a 100 year time horizon, respectively, which highlights their importance in the climate change debate (Myhre et al., 2013). Due to a number ofthe serious environmental issues arising from conversion of peatlands to OP plantations, the focus will increasingly shift to mineral soil for conversion to plantations, especially in Malaysia (Shanmugam et al., 2018). However, tThere are too few measurements reported of N_2O emissions from mineral soils in the tropics to draw firm conclusions about the increase of N_2O emissions after land-use change from secondary forest to OP (Shanmugam et al., 2018).

Limited measurement and modelling studies have been carried out on N_2O emissions from OP plantations (Pardon et al., 2016a; Pardon et al., 2016b; Pardon et al., 2017), and not in the context of comparing them with other land-uses on the same or similar soil type. Similarly, reported CH_4 emissions from mineral soils in the Tropics (other than from paddy soils) are lacking. Most studies relating land-use change to trace gas emissions have been conducted in South America and not South East Asia (Hassler et al., 2015; Veldkamp et al., 2013). An additional caveat of published studies is that most have only been conducted over short periods of time (Hassler et al., 2015). The lack of reliable long-term and multi-year datasets on

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GHG balances has been recognised (Corre et al., 2014; Courtois et al., 2019). Studies are often associated with high uncertainties (Henders et al., 2015). Nitrogen availability, soil moisture and texture are the main drivers of N_2O fluxes in tropical forests and other soil ecosystems (Davidson et al., 2000). As well as agricultural soils, tropical forest soils have been identified as a major source of N_2O (Werner et al., 2007), and soil type influences N_2O fluxes in the Tropics (Dutaur and Verchot, 2007; Sakata et al., 2015). A recent meta-analysis concluded that globally tropical forests emit on average 2 kg N_2O-N ha^{-1} y^{-1}, and emission rates will significantly increase after land-use change (van Lent et al., 2015). Tropical forest soils are estimated to contribute 28% to the global CH_4 uptake, hence large changes to this sink could alter the accumulation of CH_4 in the atmosphere substantially (Dutaur and Verchot, 2007). However, uncertainties are large due to data scarcity. Only one study from Peninsula Malaysia reported that selectively logged forests may be ~~converted into a~~ weaker sinks of CH_4 and ~~greater~~ larger sources of N_2O than undisturbed tropical rain forest, at least for a short period, because of the increased soil nitrogen availability and soil compaction due to disturbance by heavy machinery (Yashiro et al., 2008).

Forest conversion to OP has not only shown differences in the chemical and physical soil properties, but also in the soil microbial community composition and functional gene diversity (Tripathi et al., 2016). The diversity and abundance of plant communities fundamentally affect the soil microbial community and their function (Eisenhauer, 2016; Tripathi et al., 2016). As yet, it remains uncertain how conversion from forest to OP impacts microbial communities, and their influence on N_2O and CH_4 fluxes (Kaupper et al., 2019;~~). Even though the importance of bacterial communities is recognised, little is known of~~

~~changes in microbial communities due to land-use change (~~Tin et al., 2018). Transformation of tropical forest to, for example OP plantations, reduces bacterial abundance initially and~~,~~ alters the community composition but once established may not necessarily result in ~~less~~ reduced bacterial richness in the OP soil (Lee-Cruz et al., 2013; Tripathi et al., 2016).

Although the focus of this paper lies on the comparison of soil GHG flux rates (especially for N_2O) and their soil chemical and physical properties, we have taken the opportunity ~~Agricultural soils (including OP soils) are often thought to promote diversity through management, such as fertilisation and crop inputs and thereby reduce competition amongst soil microorganisms (Lee-Cruz et al., 2013). Information on microbial communities will help to understand the impact of anthropogenic land-use change and its impact on biogeochemical processes (Tin et al., 2018). The lack of our current understanding restricts our ability to predict and model responses to environmental change (Lee-Cruz et al., 2013). This is particularly important as 80-90% of soil processes are mediated by microorganisms (Nannipieri et al., 2003). In our study, we aim~~ to understand ~~whether~~ the differences in microbial ~~communities~~ community composition between forests and OP *in situ*.~~could also help understand measured differences in greenhouse gas (GHG) emissions.~~ ~~One part of this present~~A previous study has investigated ~~potential controlling factors~~ environmental drivers and microbial pathways leading to GHG emissions ~~from soil in~~under controlled laboratory incubations using soils~~,~~ ~~which complement the findings presented here from actual field measurements as the soil was taken from a subset of the sites~~from a subset of the field locations discussed here (Drewer et al., 2020). ~~We did not carry out the same measurements in the present study.~~ The aim here was to broadly characterise the microbial communities at the different sites in the

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different land-uses and use the information alongside other measured abiotic factors in mixed models in an attempt to explain the measured fluxes.

The objectives of this study were:

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

With following specific hypotheses:

(1) N_2O fluxes will be larger from OP plantations due to N fertiliser addition compared to tropical forest

(2) Land-use determines microbial diversity, and thereby influences N_2O flux rates

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In light of countries committing to reduce and mitigate GHG emissions, e.g. 2015 Paris Agreement (UNFCCC, 2015), it is important to constrain each country's current emission rates, by providing data from measurements rather than relying on model estimates. In this study, we present much needed data of N_2O and CH_4 ~~emission rates~~fluxes from logged tropical forests and OP plantations on mineral soil as well as their biochemical characteristics and temporal and spatial variability. ~~We present two years of~~

~~measurements from logged forests and OP plantations in Malaysian Borneo, Sabah from the same geographical area and on mineral soil.~~

2 Methods

2.1 Site description

The present study was carried out within the Stability of Altered Forest Ecosystems (SAFE) project in Malaysian Borneo (4°49'N, 116°54'E) in 2015 and 2016. The SAFE project was set up in Sabah in 2011 in a secondary forest, designated by the Sabah government for conversion to OP plantations. SAFE is a long-term landscape-scale experiment designed to study the effects of anthropogenic activities related to deforestation and OP agriculture on the ecosystem as a whole (Ewers et al., 2011). The main aim of the SAFE project is to study how habitat fragmentation affects the forest ecosystem, mainly its biodiversity. The design comprises forest fragments of 1 ha, 10 ha and 100 ha. Larger areas of forests, designated as continuous logged forests, and not part of the conversion plan, were selected as controls. All forest sites had been selectively logged for dipterocarps, first in the 1970s then again between 2000 and 2008, such that the logged forest and forest fragments have a similar land-use history (Ewers et al., 2011). We had the opportunity to investigate GHG fluxes within this experimental site. To ~~keep in line~~ be consistent with previous and future SAFE publications, we ~~are using~~ use the site labelling as per the SAFE convention, detailed below. As our sampling took place when forest conversion to OP was still ongoing (i.e. designated 'fragments' were not fragmented yet), we classify sampling locations in 'fragments' and 'logged forest' ~~controls~~ both as 'logged forest'. We selected a young OP plantation, around 2 years old at

the time we started measurements (OP2) and a medium aged OP plantation, around 7 years old at the start of the project (OP7). The riparian reserve area (RR), draining into a small shallow stream, is adjacent and down slope from OP7. In addition, we selected a slightly older plantation, around 12 years of age at the start of the project (OP12). All OP plantations in this study were terraced. Logged forest sites are the 10 ha plots of the logged forest (and future fragments) LF, B and E of the SAFE design.

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

2.2. Field measurements

In order to measure fluxes of N_2O and CH_4 from the chosen logged forests and OP plantations, a total of 56 static chambers were installed in the SAFE area landscape (total area 8,000 ha). Four Eight chambers were placed in each of the two 10 ha plots in logged forests LF, B, and E, resulting in 8 chambers per site. In the OP plantations, 12 chambers were installed in the ~7 year old OP plantation, 8 chambers were placed in a ~2-year old (OP2), and 8 in a ~12-year old OP plantation (OP12); 12 chambers were installed

in the ~7-year old OP plantation (OP7), and 4 in an adjacent riparian reserve area (RR). These were the plantation ages when ~~we started~~soil sampling and flux measurements started in 2015, hence, the sites are labelled OP2, OP7 and OP12. For exact GPS locations see the published dataset (Drewer et al., 2019). Fluxes were measured from all 56 chambers every two months over a two-year period, from January 2015 to November 2016; resulting in 12 measurement occasions for each of the chambers and a total of 672 individual flux measurements.

We only received basic fertiliser information from the estate managers at the beginning of our study. ~~Our measurement sites~~The OP2 and OP7 plantations were managed by the same estate. Fertiliser was applied as slow-~~-~~release (over 4 – 6 months) bags (500 g) of the brand 'PlantSafe®' (N as Ammonium Sulphate). For palms 0 – 5 years of age PlantSafe® 12-8-16-1.5+trace elements (Diammonium Phosphat ($(NH_4)_2PO_4$), Murite of Potash (KCl), Ammonium Sulphate ($(NH_4)_2SO_4$), Magnesium Sulphate ($MgSO_4$) + Borax Penthydrate) was used, and for palms >5 years PlantSafe® 8-8-27-15 was applied as 2 kg bag per plant, three times per year. Planting density was approximately 9 x 9 m spacing between palms and in addition to the mineral fertiliser, empty fruit bunches (EFB) were spread, however, there appeared to be no obvious pattern of application and most EFB were piled up along the main roads, rather than distributed evenly throughout the plantations. The ~~site~~ OP12 plantation was managed by a different estate. Distance between the palms and planting density here was 8 x 8 m. Application of fertiliser also occurred as PlantSafe® bags with two applications ~~a~~ per year ~~with~~ and rates of 3-4 kg per palm each time, totalling about 8 kg N ha^{-1} y^{-1}. EFB were not returned to this plantation and Glyphosate was applied three times

per year around each palm stem to control weeds. We assume Glyphosate was also applied to the OP2 and OP7 plantations in the other estate as well. Generally, fertiliser management was according to recommendations by the Malaysian Palm Oil Board (MPOB). Because of the slow release nature of the fertiliser, we did not expect large peaks following fertilisation, and we sampled ~~As our sampling frequency was~~ every two months over two years to capture the long-term differences.~~, we were not able to capture individual fertilisation events and that was not the scope of this study.~~

2.2.1 Soil nitrous oxide (N_2O) and methane (CH_4) fluxes

The static chamber method was used for N_2O and CH_4 flux measurements as described in previous studies (Drewer et al., 2017a;Drewer et al., 2017b). Round static collars (diameter = 40 cm, height 10 cm) fitted with a 5 cm wide flange at the top end, were inserted into the ground to a depth of approximately 5 cm for the entire two year study period. For flux measurements chambers (diameter = 40 cm, height 25 cm) fitted with a flange at the bottom of the chamber were fastened onto the bases using four strong clips, only during the 45-minute measurement periods. The collars, chamber and flanges consist~~ed~~ of opaque polypropylene. ~~Round static chambers (diameter = 40 cm) consisting of opaque polypropylene bases of 10 cm height were inserted into the ground to a depth of approximately 5 cm for the entire study period. Lids of 25 cm height were fastened onto the bases using four strong clips, only during the 45-minute measurement periods.~~ A strip of commercially available draft excluder glued onto the flange of the lid provided a gas tight seal between chamber and lid. The lids were fitted with a pressure compensation plug to maintain ambient pressure in the chambers during and after sample removal. Gas samples were taken

at regular intervals (0, 15, 30, 45 min) from each chamber. A three-way tap was used for gas sample removal using a 100 ml syringe. 20 ml glass vials were filled with a double needle system to flush the vials with five times their volume and remained at ambient pressure rather than being over-pressurised. The sample vials were sent to UKCEH Edinburgh for analysis usually between 4-7 weeks after sampling. A specifically conducted storage test confirmed no significant loss of concentration during that time period. Samples and three sets of four certified standard concentrations (N_2O, CH_4 in N_2 with 20% O_2) were analysed using a gas chromatograph (Agilent GC7890B with headspace autosampler 7697A; Agilent, Santa Clara, California) with micro electron capture detector (μECD) for N_2O analysis and flame ionization detector (FID) for CH_4 analysis. These detectors were setup in parallel allowing the analysis of the two GHGs at the same time. Limit of detection was 5 ppb for N_2O and 40 ppb for CH_4. Peak integration was carried out with OpenLab© Software Suite (Agilent, Santa Clara, California).

The flux F (μg m^{-2} s^{-1}) for each sequence of gas samples from the different chambers was calculated according to Equation 1:

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

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

Fluxes were quality checked and checked for linearity and no saturation occurred during the time sampled (2 min for CO_2 and 45 min for N_2O and CH_4), so linear was the best fit for all fluxes presented here. Applying the analytical limit of detection to the flux calculation, the resulting detection limits and therefore uncertainties associated with the flux measurements are 1.6 µg N m^{-2} h^{-1} for N_2O and 5 µg C m^{-2} h^{-1} for CH_4 in the units used in the results section.

2.2.2 Soil respiration (CO_2) fluxes

In addition, soil CO_2 respiration rates were measured close to each chamber location using a dynamic chamber (volume: 0.001171 m^3) covering 0.0078 m^2 of soil for 120 s with an EGM-4 infrared gas analyser (IRGA: InfraRed Gas Analyser; PP Systems; Hitchin, Hertfordshire, England). To do so, cut drainpipes of 7 cm height matching the diameter of the IRGA chamber were inserted into the ground to a depth of about 5 cm for the duration of the study to allow for a good seal with the soil surface. All vegetation and litter was removed from the surface at the beginning of the measurement period to guarantee soil-only respiration measurements. Taking into account the time of measurement and the soil temperature, fluxes were calculated based on the linear increase of CO_2 concentrations. Soil respiration was measured every time ~~the static chambers~~N_2O and CH_4 fluxes were measured, resulting in 12 measurement occasions for each of the 56 locations and 672 individual measurements.

2.2.3 Auxiliary physical and chemical soil measurements

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Other environmental parameters were measured during time of chamber enclosure as possible explanatory variables for correlation with recorded GHG fluxes. Soil and air temperatures were measured using a handheld Omega HH370 temperature probe (Omega Engineering UK Ltd., Manchester, UK) at each chamber location at a soil depth of 10 cm and by holding the temperature sensor 30 cm above the soil surface at chamber height. Volumetric soil moisture content (VMC) was measured at a depth of 7 cm using with a portable probe (Hydrosense 2; Campbell Scientific, Loughborough, UK). For determining KCl-extractable soil nitrogen (N) in the field, soil samples were collected to a depth of 10 cm around each of the chamber locations on each of the chamber measurement days, using a gouge auger. Extractions were carried out in the field laboratory on the same day. Soil samples were mixed well, stones were removed, and subsamples of ca. 6 g soil (fresh weight) was transferred into 50 ml falcon tubes containing 25-ml 1 M KCl solution. The samples were shaken for 1 min every 15 min for one hour, then filtered through Whatman 42© filter paper (GE Healthcare, Chicago, USA) and kept in the fridge after addition of a drop of 75% H_2SO_4 as a preservative. Analysis for ammonium (NH_4^+) and nitrate (NO_3^-) concentrations was carried out at Forest Research Centre in Sandakan (Sabah, Malaysia) using a colorimetric method (Astoria 2 Analyzer (Astoria-Pacific Inc., USA).

The following parameters were measured less frequently. Soil pH was measured on three occasions from the top 0-10 cm, close to each chamber at the start of the measurement period and two months later, and inside the chambers after the last flux measurements at the end of the experiment. For pH measurements 10 g of fresh soil was mixed with deionised H_2O (ratio 1:2), and after 1 hour analysed on a MP 220 pH

meter (Mettler Toledo GmbH, Schwerzenbach, Switzerland). Soil samples for bulk density were collected from inside each chamber after the final flux measurement at the end of this study. Galvanised iron rings (98.17 cm^3) with a sharp edge were inserted in the upper soil layer with a hammer to 5 cm depth without compaction. Samples were oven-dried at 105°C until constant weight (usually 48 hours) and bulk density (g cm^{-3}) was calculated based on the dry weight occupying the volume of the ring. Total C and N in soil and litter was measured once on the last sampling occasion. Soil samples were taken from the top 0-10 cm inside the chambers. The samples were air dried in the field laboratory and a subsample of each were dried at 105°C to constant weight in the laboratory to convert the results to oven-dry weight, ground and analysed at the Forest Research Centre in Sandakan on an elemental analyser (Vario Max CN Elemental Analyzer (Elementar Analysensysteme, Germany). Litter was collected from the surface area of each chamber, air dried at 30 °C and analysed for total C and N as described above.

2.2.4 Soil microbial community composition

Soil samples for microbial analysis were taken on two occasions from all 56 flux chamber locations~~. Soil samples were taken~~ in March 2016 and November 2016 (the last sampling occasion). On the first sampling date, soil was taken close to each chamber in order not to disturb the soil inside the chamber. In November 2016, soil was taken from inside each chamber, as this was the experimental end date. Approximately 5 g of soil was taken from the top 3 cm and stored in ziplok bags at ambient air temperature until posting to UKCEH Wallingford for analysis. The soil samples had to be sent as 'fresh' samples as there were no freezers operating continuously at the field station, therefore it was not possible to keep the soil frozen

during storage and transport. The samples were frozen at -80°C once they reached UKCEH Wallingford until analyses.

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

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

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

2.3 Data analysis

Environmental data, especially soil N_2O fluxes, are typically highly variable in space and time, which makes their statistical analysis challenging. Much of the variation cannot be explained by co-variates, as the driving microbial processes are not directly observed. They are also usually strongly left skewed (containing a high number of very small fluxes), and are expected to approximate a lognormal distribution. Against this background, trying to detect effects of land-use (or experimental treatments) is difficult. The calculation of a confidence interval on the mean of a log-normal distribution is problematic

when variability is high and sample size is small (e.g. Finney 1941), as is generally the case with flux measurements.

Here we applied a Bayesian methodology to address this problem, using a model similar to that described by Levy et al. (2017). This accounts for the lognormal distribution of observations, while including hierarchical effects of land-use, and effects of sites within land-use types as well as the repeated measures. In the current statistical terminology, this is a generalised linear mixed-effect model (GLMM) with a lognormal response and identity link function. The model consists of a fixed effect of land-use (Forest, Oil Palm, or Riparian), with a random effect representing the variation among sites within a land-use type. The parameters were estimated by the Markov chain Monte Carlo (MCMC) method, using Gibbs sampling as implemented in Just Another Gibbs Sampler (JAGS) (Plummer 1994), and described in more detail by Levy et al. (2017). The model can cope with the slight imbalance in the design, and propagates the uncertainty associated with the relatively small sample sizes appropriately.~~works well for small samples sizes irrespective of numbers of samples per site/land-use.~~

All other statistical analyses were conducted using the R software package, version 3.4.3 (R Core Team, 2017) using the lme4 package for linear mixed-effects models (Bates et al., 2015) and ordinary multiple regression. Model selection was examined by sequentially dropping terms and assessing AIC and similar criteria using the MuMIn package (Bartoń, 2013). For N_2O and CH_4, where negative values occurred, the

minimum was added to all data points (-30 and -115 µg m^{-2} h^{-1}, respectively) so that a lognormal distribution could be fitted.

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

2.4 Upscaling of N_2O fluxes to Sabah scale

In an attempt to broadly upscale our findings, we calculated the annual soil N_2O emission for the Sabah state based on the data from this study (Table 2), together with land cover areas estimates (Gaveau et al., 2016) of forests, pulpwood and OP plantations for 1973 and six 5 yearly intervals from 1990-2015. We included the pulpwood plantation area in the total forest area, as to our knowledge there are no data of N_2O emissions from this sector. We used mean emissions and the 95% confidence interval calculated by the GLMM and posterior probability to account for variability and associated uncertainties.

3 Results

3.1 Soil parameters

Results are presented by site (B, E, LF, OP2, OP7, OP12, RR) or land-use (logged forest (B, E, LF), oil palm (OP2, OP7, OP12), riparian (RR)). Soil pH was acidic from logged forest site B (pH 3.65±0.44) compared to forest E and LF, which were closer to neutral (pH 6.38±0.67 and 6.14±0.5), and the OP plantations were more acidic (pH 4.5-4.7±0.2) compared to the riparian area (pH 5.8±0.55) (Table 1). Bulk density was lower at the forest sites (~0.81 g cm^{-3}) compared to the OP plantations (~1.26 g cm^{-3}) mainly due to a higher amount or organic matter and litter in the forest sites (B, E, LF) and a combination of compaction due to land management and lower organic matter content in the OP plantations and riparian area (OP2, OP7, OP12, RR) (Table 1). Total carbon (C) and nitrogen (N) in soil were higher in the logged forest sites (~3-7% C and ~0.25-0.4% N, albeit with a very high variability) than the OP plantations (<1% C and <0.1% N) (Table 1) due to larger amount of litter present. The riparian reserve 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 the logged forests. Variability even within one site was large for the forest sites which is also reflected in the C/N ratios (Table 1). Litter was present in all of the forest and riparian reserve chambers and only in a few of the OP chambers. The average litter weight in the forest chambers was between 50 and 150 g dry weight with a very high variability, about 15 g in the riparian area, and hardly any litter in the OP chambers, with no litter in OP12, only in one of the OP7 chambers and an average amount of 50 g of litter in the young OP2 , again with a very high variability (Table 1). The total C and N content in litter was similar in logged forest and OP (~35-40% C and ~1.5-1.8% N); the main difference was the

presence/absence of litter and the amount present. For all these measured parameters the variability within each site was high apart from pH in OP which was most likely regulated by plantation management operations. Because of the large temporal and spatial variabilities ~~N~~none of the soil physicochemcial parameters were significantly different for the different land-uses or sites apart from pH from site B.

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

Soil extractable mineral N (both NH_4^+ and NO_3^-) was highly variable across the OP plantations with mean values of 8±23 and 6.3±18 mg N g^{-1}, respectively, 4.5±5 and 2.3±4 mg N g^{-1} in riparian and 3.9±5 and 5.3±5 mg N g^{-1} in the forests (Figure 3, Table 2). We measured the lowest average NH_4^+ and NO_3^- concentrations in the 12 year old plantation (OP12), and the highest in the youngest OP plantation (OP2) with maxima of >150 mg g^{-1}, however, with a very high spatial variability (Figure 3, Table 2). It is not possible to correlate soil mineral N concentrations with individual fertiliser events d~~D~~ue to the low

frequency of soil and flux sampling (every 2 months), ~~and~~ the lack of knowldege of the fertilisation dates~~,~~ and release rates from the fertiliser bags~~it is not possible to correlate soil mineral N concentrations with individual fertiliser events~~. NH_4^+ and NO_3^- concentrations of the logged forest sites, older OP plantation and riparian reserve were very similar.

3.2 Greenhouse gases

3.2.1 Nitrous oxide (N_2O)

There were no temporal trends of nitrous oxide (N_2O-N) fluxes and no distinct differences between wet (usually Oct to Feb) and dry (Mar to Sep) seasons (Figure 4a). Variability in N_2O-N fluxes for all sites was high and the largest range was measured in the OP plantations (Figure 4a, Table 2, Supplementary Figure S1). On a given day, very large as well as very small fluxes were measured in the OP plantations. ~~We find that the l~~Largest fluxes were observed ~~were~~ from the young (OP2) and old (OP12) oil palm plantations and exceeded 1500 µg m^{-2} h^{-1} N_2O-N for individual chambers. In the logged forest, largest fluxes were ~400 µg m^{-2} h^{-1} for individual chambers at site B. ~~On a given day, very large as well as very small fluxes were measured in the OP plantations.~~ For each land-use standard deviation was a lot larger than the mean (Table 2); logged forest 13.9±171 µg m^{-2} h^{-1} N_2O-N, OP 46.2±166 µg m^{-2} h^{-1} N_2O-N and riparian area 31.8±220 µg m^{-2} h^{-1} N_2O-N. By fitting the GLMM to the data, we estimated the posterior probability density of the effect of land-use on N_2O flux: mean fluxes to be 13.9 (95 % CI: -6.3 to 41.5) µg m^{-2} h^{-1} for logged forests, 46.2 (18.4 to 97.5) µg m^{-2} h^{-1} for OP and 31.8 (-6.3 to 130.0) µg m^{-2} h^{-1} for the riparian area (Figure 4b, Table 2). The output using the Bayesian approach can be interpreted as

follows: The area of the OP curve does not overlap with the area of the forest curve, which means that the probability is higher that the flux from OP plantation is higher than the flux from logged forest, with the riparian ~~zone~~ area being intermediate. To investigate effects of additional variables, we used the automated model selection algorithm in the MuMIn R package, which uses all possible combinations of fixed effect terms and ranks them by AIC (Bartoń, 2013). Possible terms included land-use, pH, soil moisture, NH_4^+, NO_3^-, bulk density, soil and air temperature, and the microbial NMDS axes. This procedure found the inclusion of NH_4^+ and NO_3^-, soil moisture and soil temperature, in addition to land-use, to ~~give~~ provide the optimal model. However, whilst land-use (including the site-level effects) explained 13% of the variance (expressed as conditional R^2, (Bartoń, 2013)), the additional four terms increased this by only 4%. The microbial NMDS axes did not improve the model fit, as measured by AIC.

3.2.2 Methane (CH_4)

For methane, both negative fluxes (= net CH_4 oxidation) and positive fluxes (net CH_4 emission) were measured at all sites throughout the measurement period (Figure 5, Supplementary Figure S2). Highest emission and uptake rates were measured in the logged forest sites, with emissions reaching almost 300 µg m^{-2} h^{-1} CH_4-C at site E, and uptake rates of up to 85 µg m^{-2} h^{-1} CH_4-C at sites LF and B. In the OP plantations highest emissions were measured at OP7 (~100 µg m^{-2} h^{-1} CH_4-C), and uptake rates were <50 µg m^{-2} h^{-1} CH_4-C. Overall, CH_4 flux ranges were larger in the logged forests than OP plantations. Grouping fluxes by land-use, mean fluxes were about 2.2±48.3 µg CH_4-C m^{-2} h^{-1} for logged forest, -2.6±17.2 µg CH_4-C m^{-2} h^{-1} for OP and 1.3±12.6 µg CH_4-C m^{-2} h^{-1} for riparian reserve (Table 2). The

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magnitudes of CH_4-C fluxes in the riparian reserve were more similar to the logged forests sites than the OP plantations. Standard deviations again were~~as~~ large but not as large as for N_2O.

As for N_2O, possible drivers of CH_4 fluxes were investigated using linear mixed effect models and the same model selection methods. However, no correlations with co-variates could be established, even with land-use. For example, a model including terms for land-use, pH, soil moisture, NO_3, NH_4, bulk density, soil and air temperature could explain only 3% of the variance. Land-use was clearly not a strong determinant of CH_4 flux, and the posterior distributions are not shown.

3.2.3 Soil respiration (CO_2)

Soil respiration CO_2-C ~~fluxes~~ rates also ~~had a high~~were spatially highly variable~~ility~~ (Figure 6, Supplementary Figure S3). There was a trend ~~to~~ of slightly higher respiration rates at logged forest sites than OP plantations. Grouping fluxes by land-use, gave mean ~~fluxes~~ respiration rates of 137.4±95 mg m^{-2} h^{-1} for logged forests, 93.3±70 mg m^{-2} h^{-1} for OP plantations and 157.7±106 mg m^{-2} h^{-1} for the riparian ~~site~~ area (Table 2). Soil respiration rates in the measured riparian reserves ~~was~~ were therefore within the range of the soil respiration rate of logged forest, which was higher than from the OP sites. Data was log transformed before statistical analysis. A linear mixed-effects model including all terms could explain 25% of the variance, and land-use alone explained 7% of the variance.

3.3 Soil biodiversity

Soil samples for analysis of microbial biodiversity ~~measurements~~ were collected in the low rainfall month, March 2016 (~50 mm), and the high rainfall month, November 2016 (~250 mm, Figure 1), in order to quantify broad differences in communities due to land-use and provide additional biodiversity variables for modelling fluxes using the GLMM in addition to using abiotic soil parameters such as pH and bulk density. Three different amplicon sequencing assays were performed on extracted DNA targeting bacteria (16S rRNA gene), fungi (ITS region), and broad groups of soil eukaryotic taxa (18S rRNA gene, including principally fungi, protists and algae). The ordinations and multivariate permutation effects of land-use were generally consistent across the two sampling points irrespective of seasonal climatic differences (Figure 7). Fitting environmental vectors to the ordination axis scores (see ~~s~~Supplementary Table 1) revealed that the bacterial communities were highly related to soil pH (r^2 = 0.85 and 0.84, $p<0.001$, for the two sample dates respectively), with acid soils (pH 3.6) at site B, compared to near neutral pH of 6.1 and 6.4 at sites LF and E, Table 1). Weaker relationships with the land-use factors (r^2= 0.23 and 0.11, $p<0.05$) were observed, though l~~. L~~ogged forests E and LF had very similar bacterial communities, which were distinct from the three OP sites and also the riparian site. In contrast, fungal and eukaryotic communities were not as 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 dates respectively, $p<0.001$), and were more strongly related to above ground land-use than bacterial 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 the fungal ordinations particularly, the forested sites formed a distinct cluster separate from the OP sites, despite the large differences in soil acidity.

3.4 Upscaling of N_2O fluxes to Sabah scale

In an attempt to broadly upscale our findings, we calculated the annual soil N_2O emission for the Sabah state based on the data from this study (Table 2), together with land cover areas estimates (Gaveau et al., 2016). Nitrous oxide emissions calculated for the Sabah region showed a strong dependence on the conversion of forest to OP plantations from 1973 to present day. By 2015, the total estimated N_2O emissions from OP plantations were roughly 40% of total emissions, with 60% of the emissions from forested areas, despite the OP area being less than 40% of the forest area. The Sabah scale median N_2O emission estimate had increased 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) per year in 2015. As the measured CH_4 fluxes were fluctuating around zero, the changes in land-use also resulted in small changes of CH_4 flux rates over the 42-year period. Our median results suggest that Sabah is a sink for CH_4 (4 Mt y^{-1}) throughout the time period presented.

4 Discussion

This study focussed on comparing GHG fluxes from different land-use types in the Tropics. Our data, although not high frequency measurements, provide a comprehensive insight in the potential impact of converting logged forests to OP plantations on GHG fluxes. The ~~focus~~ emphasis of this study is on N_2O, with auxiliary measurements of CH_4 and soil respiration. To date only four studies published data of N_2O emissions from OP plantations on mineral soil in Southeast Asia using the chamber method that included measurements from a time period of longer than 6 months (Skiba et al., 2020). Only one of these studies included measurements in Malaysia (Sakata et al., 2015). Globally tropical forests are the largest natural

source of N_2O (Werner et al., 2007). Therefore, the question ~~is~~ whether the N input to OP plantations with lower organic matter (TC/TN) content~~)~~ compared to tropical forests ~~(lots of organic matter input, warm, humid),~~will lead to larger N_2O emissions than from forests. Although it has been recognised that N_2O emissions are induced by N-fertiliser application in OP, when considering annual or long-term emissions from mineral soil, these fertilisation patterns ~~might~~ may not have a pronounced or clear effect (Kaupper et al., 2019). For example, N-fertiliser induced N_2O fluxes comprised only 6-21% of the annual soil N_2O fluxes in OP plantations in Sumatra, Indonesia (Hassler et al., 2017), the rest was due to other natural processes occurring in the soil. Therefore, our study can be considered representative, particularly as measurements were carried out over two years. All three land-use types (logged forest, oil palm and riparian) showed positive N_2O fluxes albeit with a high variability.

On some occasions, our measured fluxes exceeded the range reported by Is~~S~~hizuka et al. (2005) of N_2O emissions from OP plantations on mineral soil in Indonesia, ranging from ~1-29 µg m^{-2} h^{-1}, by an order of magnitude (maximum measured 350 µg m^{-2} h^{-1}). The highest values reported by Is~~S~~hizuka et al. (2005) were from young plantations, while ~~the~~ lowest fluxes were reported from older plantations. They suggested the low N uptake of young plantations after fertiliser application and the fixation of N by the legume cover crop could be the reason for the high emissions. On the other hand, ~~the~~ low emissions from older plantations could result from higher N uptake by the OP and the absence of legume cover. In their study, N_2O emissions were mainly determined by soil moisture (Ishizuka et al., 2005); which was not the case here. Mean N_2O fluxes from a sandy soil in Malaysia were reported to range from 0.80 to 3.81 and

549 1.63 to 5.34 µg N m^{-2} h^{-1} in the wet and dry seasons, respectively (Sakata et al., 2015). This was lower
550 than from a sandy loam soil in Indonesia (27.4 to 89.7 and 6.27 to 19.1 µg N m^{-2} h^{-1} in the wet and dry
551 seasons, respectively) (Sakata et al., 2015) indicating the importance of soil texture, provided that
552 management is the same.
553
554 .-Despite the limited number of measurements in OP plantations on mineral soils and the high variability
555 of results, emissions seem to be generally ~~be~~ higher in ~~the early years of the~~ younger OP plantations
556 (Pardon et al., 2016a). This conclusion is not ~~necessarily~~ reflected in our data, as ~~the~~ OP2 (young) and
557 OP12 ~~sites~~ (older) plantations showed ~~higher~~ larger fluxes than the OP7 (medium age) site; although with
558 a lifespan of up to 30 years, all plantations measured in this study can still be regarded as immature. As
559 in our study, Aini et al. (2015) also found no differences in N_2O fluxes in the wet and dry months with
560 fluxes ranging from 0.08 to 53 µg N m^{-2} h^{-1}. The range of our measured fluxes exceeded those of these
561 previously published studies. However, it is difficult to generalise, as variability appeared to be high in
562 all studies.
563
564 Our measured N_2O fluxes from the riparian area were similar to those measured in the OP plantation, as
565 soil properties such as bulk density were more similar to OP than logged forest. There is currently a
566 knowledge gap on GHG emissions from riparian ~~buffers~~ areas (Luke et al., 2019) and more studies are
567 needed to evaluate the effectiveness in terms of nutrient retention and potential GHG mitigation of such
568 buffers. A previously published study from Peninsula Malaysia reported mean N_2O emission rates from

logged tropical forest sites ranging from 17.7 to 92.0 µg m^{-2} h^{-1} N_2O-N which was significantly larger than from their measured unlogged sites (Yashiro et al., 2008). Even though the range of our measured fluxes from logged forest sites was wider, ~~it is~~they are broadly in the same order of magnitude (13.9±171 µg m^{-2} h^{-1} N_2O-N).

As often the case with GHG studies, the variation in the measured GHG fluxes could not be explained with certainty by any of the measured soil parameters. Our sampling frequency was not high enough to investigate, for example, emission rates after fertiliser application in the OP plantations and besides, this was not the aim of our study. The wide ranges ~~we~~ measured for soil mineral N concentrations and N_2O fluxes were likely due to the spatial and temporal variability of the fertiliser application, as the slow release fertiliser bags were randomly placed around the trees, and with time, the fertiliser release rate slowed down. Apart from no strong correlations with single environmental factors, multiple regression and mixed models were only able to explain around 17% of the variance including multiple measured parameters. However, applying the Bayesian method, the posterior probability density of the effect of land-use on N_2O flux confirmed that fluxes from the OP plantations were evidently higher than those from the forests (the area of the OP curve does not overlap with the forest curve), with the riparian ~~zone~~ area being intermediate (mean fluxes 13.9 (95 % CI: -6.3 to 41.5) µg m^{-2} h^{-1} for logged forests, 46.2 (18.4 392 to 97.5) µg m^{-2} h^{-1} for OP and 31.8 (-6.3 to 130.0) µg m^{-2} h^{-1} for the riparian area). We therefore confirm our first hypothesis that N_2O fluxes are higher from OP than tropical forests.

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

High~~er~~ soil respiration rates (sum of heterotrophic and autotrophic respiration) ~~is often~~are considered ~~as~~ to be a sign of good soil health, as it reflects the capacity of soil to support soil life including microorganisms and crops. Heterotrophic soil respiration defines the level of microbial activity, soil organic matter content and its decomposition whilst autotrophic respiration is the metabolism of organic matter by plants. In a recently published study investigating litter decomposition, soil respiration fluxes in Sabah (also in the SAFE area) were higher from forests than OP plantations (Kerdraon et al., 2020). This was also the general trend in our study despite the high variability of all measured fluxes. Litter input in our plots was larger in the logged forest plots and riparian reserve than the OP. ~~In l~~Litter decomposition experiments, conducted in ~~both~~ Borneo and Panama, and revealed that litter input was more important than litter type.~~, which~~ This observation stresses the importance of the amount of aboveground litter for

soil processes in general, especially in disturbed habitats or forest converted to plantations (Kerdraon et al., 2020).

To further characterise the different land-uses and sites within each land-use, ~~A.~~analyses of soil microbial communities with different assays targeting different microbial components, revealed strong influences of soil properties such as pH, but also highlighted that fungal and eukaryotic communities were more affected by management and land-use than bacteria. Soil pH is known to have an impact on soil microbial community in the Tropics (Kaupper et al., 2019;Tripathi et al., 2012) which may explain the very different bacterial communities in logged forest B with the lowest measured pH of all our sites.

Typically, C and N availability ~~or~~ and generally soil fertility is known to decrease after deforestation (Allen et al., 2015; Hassler et al., 2017; Hassler et al., 2015; Kaupper et al., 2019)~~.~~, T~~t~~his is also reflected in our data (Table 1), ~~especially the very low~~where total C and N values in all OP plantations were lower than from forest soils. Nutrient input through litter is higher in the forest than OP plantations and ~~consistently~~ continuously replenished (Guillaume et al., 2015). Therefore, for microorganisms, OP plantations represent a nutrient deprived environment (Kaupper et al., 2019). Low total C input can also limit the methanotrophic population size and hence limit CH_4 uptake (Krause et al., 2012). Lower soil N concentrations in OP soil have~~s~~ also shown to limit CH_4 uptake when compared with forest soil (Hassler et al., 2015). Exactly how shifts in C and N after converting forest to OP may affect microbial processes involved in N_2O and CH_4 fluxes remains highly uncertain (Kaupper et al., 2019). ~~On mineral soil, changes~~

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

Kaupper et al. (2019) have suggested that microbial biodiversity loss occurs soon after clearance and that bacterial diversity may either be resilient to the change or changes cannot be detected after a sufficient recovery period (>8 years) after deforestation. This conclusion is supported by -Tin et al. (2018), who reported that the diversity of the bacterial community in a natural forest in the Maliau Basin in Sabah was comparable or even slightly higher in an OP plantation. Contrary, our study implies distinct differences in bacterial, fungal and eukaryotic community structures between OP plantations and forests. To what extend these differences impact on microbial processes leading to GHG fluxes is hardly known (Kaupper et al., 2019).~~We found distinct differences of microbial communities in the different land uses. In a recently published study of a natural rainforest and an OP plantation in Sabah, bacterial community diversity (richness and evenness) was comparable or even slightly higher in the OP site (Tin et al., 2018). Also, Kaupper et al. (2019) have suggested that microbial biodiversity loss occurs soon after clearance and that bacterial diversity might either be resilient to the change or changes cannot be detected after a sufficient recovery period (>8 years) after deforestation (Kaupper et al., 2019). Agricultural OP soil has previously been found to be more functionally diverse compared to forest soil (Mendes et al., 2015; Tripathi et al., 2016) while microbial functioning in forest soil appears to be dependent on microbial abundance rather than diversity (Mendes et al., 2015). Reason for this could be that in agricultural soils

~~(i.e. OP plantations) there is a need for functional diversity in order to maintain a sufficient level of idleness for continued functioning under stress events such as deforestation and soil management.~~ ~~Despite these few recent studies on microbial communities, the link to processes leading to GHG fluxes has not been made (Kaupper et al., 2019),);~~ ~~hence predictions on the impact of land-use change are difficult to make.~~ Despite our data showing effects of land-~~-~~use and soil ~~property~~ properties ~~effect~~ on components of the microbial ~~community~~communities (fungal and eukaryote), ~~inclusion~~ including of ~~derived~~ microbial community metrics in the GLMM ~~in models to predict~~ did not help to explain variability in N_2O fluxes ~~did not improve fits.~~; ~~it~~ Hence, we partially prove our hypothesis that microbial diversity is determined by land-use but have to disprove the latter part of the second hypothesis (microbial diversity did not influence N_2O fluxes).

~~.~~

It is possible that a more specific focus on relevant functional gene abundances ~~will~~ would yield greater predictive ability. Our parallel laboratory investigation, using soils collected from the field study sites reported here, provides a small piece of– information on this matter. We concluded that the main contribution to N_2O emissions from the logged forests and OP plantations were driven by proteobacterial *nirS* and *AniA-nirK* genes from denitrifier and archaeal ammonia oxidizer communities (Drewer et al., 2020). Providing the combined information of soil biochemical reactions with microbial biodiversity may in future enable better predictions of GHG fluxes. ~~In a laboratory incubation study that used soil from some of these field study sites, it was found that both logged forest and OP soil had the same potential for~~

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~~substantial N_2O fluxes under laboratory conditions (Drewer et al., 2020). However, under these controlled conditions, riparian reserve soil had negligible N_2O fluxes, which is in contrast to the fluxes measured in the field. The same study also concluded that despite the high variability found amongst replicates, the main contribution to N_2O emissions came from proteobacterial *nirS* and *AniA nirK* containing denitrifiers and archaeal ammonia oxidizers (Drewer et al., 2020). The conversion of forest to monoculture plantations is a big threat to ecosystem functioning (Tripathi et al., 2016), yet we are still missing data on microbial communities to make accurate predictions.~~

~~Plantation management, for example returning palm fronds and empty fruit bunches to the plantation soil, will likely change nutrient cycling (Pardon et al., 2017) and therefore microbial composition. Presence of, for example, leaf litter as a source of organic matter is essential to maintain soil processes (Kerdraon et al., 2020).~~ It is vital to understand underlying longer-term processes that ultimately might regulate GHG fluxes to be able to develop GHG mitigation strategies. The conversion of forest to monoculture plantations is a big threat to ecosystem functioning (Tripathi et al., 2016), yet we are still missing data on microbial communities to make accurate predictions of their fate and function.~~More environmentally friendly plantation management would likely help with maintaining ecosystem functioning and reduce GHG emissions.~~

In an attempt to broadly upscale our findings, we calculated ~~the~~ annual soil N_2O emission for the Sabah state based on the data from this study (Table 2), together with land cover areas estimates (Gaveau et al.,

2016). The Sabah scale median N_2O emission estimate had increased from 7.6 Mt per year in 1973 to 11.4 Mt per year in 2015. However, this change is small considering the associated uncertainties, demonstrated by the ~~interquartile range~~95% CI, -3.0-22.3 Mt per year in 1973 and 0.2-28.6 Mt per year in 2015. The changes in land-use resulted in small changes of CH_4 flux rates over the 42-year period. M~~O~~ur median results suggest that Sabah is a sink for CH_4 (4 Mt y^{-1}) throughout the time period presented. There was a slight decrease to the ~~interquartile~~ range of our estimate suggesting that the sink strength will decrease as more land is converted from forest to OP plantations. These estimates, although highly uncertain, highlight the point that the GHG burden of Sabah is likely to increase as a result of land use change from forest to OP plantations and management. ~~as more land was converted to OP plantation, suggesting that the strength of the sink decreased. However, this is much lower than the uncertainty associated with this analysis, hence; it is difficult to draw strong conclusions.~~

5 Conclusions

This two-year field study of bi-monthly measurements demonstrated that N_2O emission rates from mineral soils in Sabah were largest~~:~~ from OP plantations, intermediate from a riparian area and smallest from logged forests. Very large spatial and temporal variability of fluxes and soil chemical and physical properties were encountered at all sites. ~~N_2O emission rates in Sabah on mineral soil were higher from OP than logged forest over a two-year study, with N_2O emission rates from the riparian zone intermediate.~~ Mean CH_4 fluxes were low with very high variability, showed no clear trend and the highest range of

fluxes was measured in logged forests. Fungal and eukaryotic communities were related to management whilst bacterial community structures ~~ies~~ were strongly affected by soil pH, which might have masked any management impacts. Mixed models and multiple regression analysis could only explain 17% of the variation in the measured N_2O fluxes, 3% of the CH_4 fluxes and 25% of soil respiration, despite the large number of measured abiotic and biotic parameters. This is not uncommon for GHG fluxes, but demonstrates that many more studies, ideally at high temporal and spatial resolution, are required to inform on the impact of land-use and climate change on GHG fluxes. Scaling up measured N_2O and CH_4 fluxes to Sabah using land areas for forest and OP ~~(Gaveau et al., 2016)~~ implies~~y~~ that since ~~the~~ 1973 N_2O emissions have increased ~~over the last 42 years~~and CH_4 uptake declined, in line with the proportion of ~~emissions from~~ OP plantations ~~increasing in comparison to the emissions from~~replacing forest~~s~~ areas. Using the range of measured fluxes with mean and ~~interquartile ranges~~95% CI highlights the large uncertainties still associated with these emission estimates, despite having almost 700 individual data points over two years. For CH_4, the picture is even more uncertain. More studies on ~~GHG~~ N_2O and CH_4 fluxes from tropical forests and OP plantations on mineral ~~soils (including experiments deriving N_2O emission factors)~~ are needed to reduce the uncertainty of their emission rates, and especially for experiments deriving N_2O emission factors. Furthermore, the impact of current management systems and future potentially more environmentally friendly plantation management needs to be investigated in order to predict how to maintain ecosystem function and biodiversity which could have a positive impact on reducing GHG emissions.

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Data availability

Drewer, Julia, Leduning, Melissa, Sentian, Justin, & Skiba, Ute. (2019). Soil greenhouse gas fluxes and associated parameters from forest and oil palm in the SAFE landscape [Data set]. Zenodo. http://doi.org/10.5281/zenodo.3258117

Author contributions

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

Competing interests

No conflict of interest to declare

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Tables and Figures

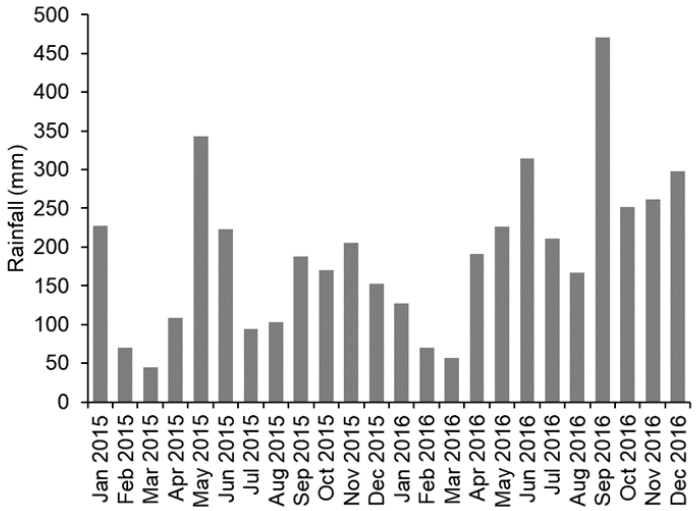
Table 1. Soil physicochemical parameters: pH (mean of three sampling occasions and replicate chambers at each site); bulk density (mean of replicate chambers at each site from one sampling occasion); total C and total N in soil from the top 1-10 cm and leaf litter in the chambers (from replicate chambers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

site	*pH*		*bulk density [g cm^{-3}]*		*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**
LF	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	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
E	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
OP2	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
OP7	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
OP12	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
RR	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

*only one of the OP7 chambers had litter present

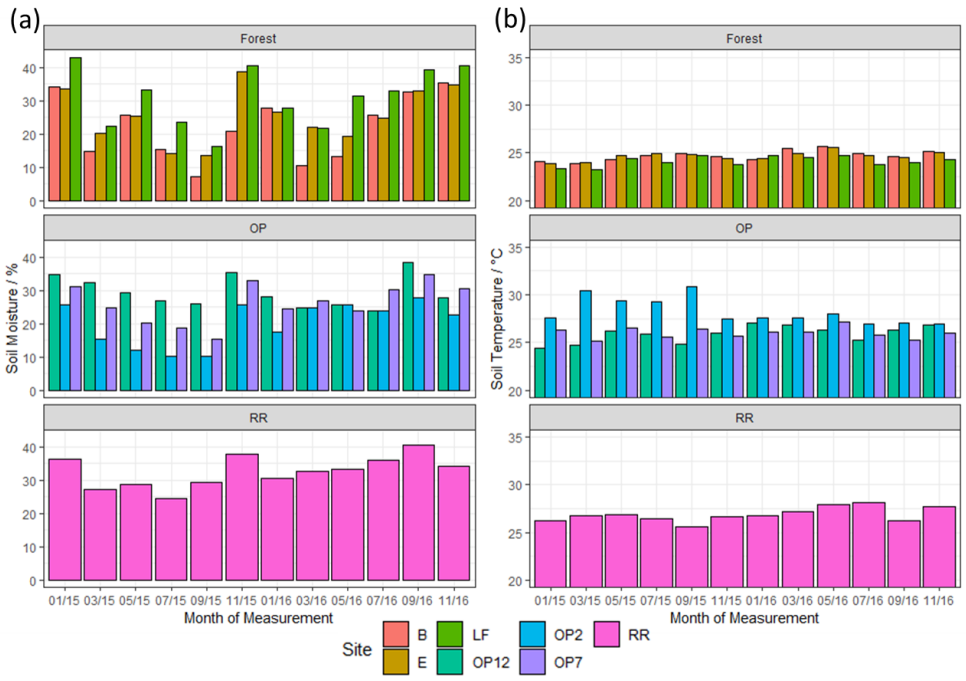
Table 2. Greenhouse gas fluxes (N_2O-N, CH_4-C, soil respiration CO_2-C) and soil mineral nitrogen (NH_4-N and NO_3-N) averaged over the entire measurement period (January 2015 – November 2016) by land-use. N = number of individual data points, sd = standard deviation; forest = logged forest, OP = oil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

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



965

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


(a)
(b)
Forest
OP
RR
Soil Moisture / %
Soil Temperature / °C
0
10
20
30
40
20
25
30
35
01/15 03/15 05/15 07/15 09/15 11/15 01/16 03/16 05/16 07/16 09/16 11/16
Month of Measurement
Site
B
E
LF
OP12
OP2
OP7
RR

967

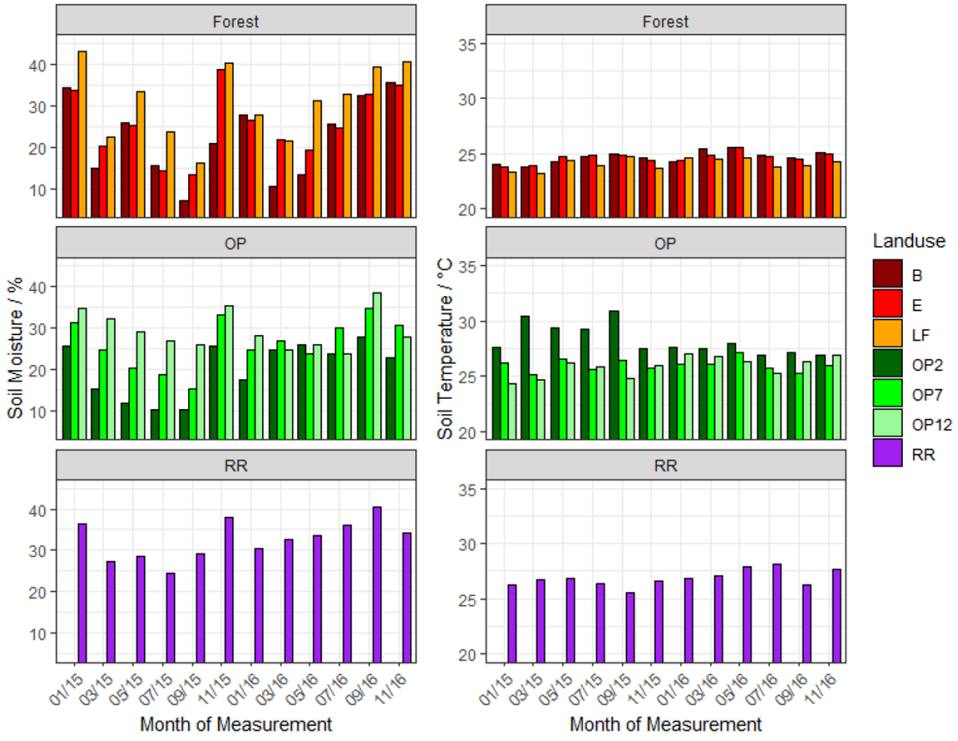
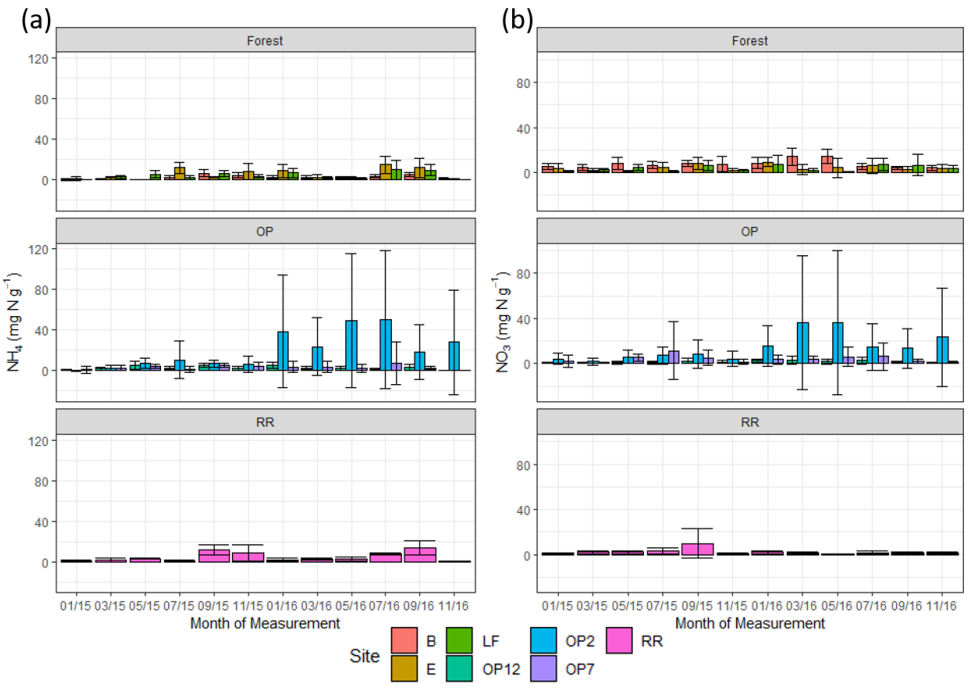


Figure 2. ~~Barplots of~~ Mmean volumetric soil moisture (a) and mean soil temperature (b) from January 2015 - November 2016, every two months: (upper panel: B, E, LF = logged forests, middle panel: OP~~1~~2, OP~~2~~7, OP12~~7~~ = oil palm plantations, bottom panel: RR = riparian reserve).


(a)
(b)
Forest
OP
RR
NH_4 (mg N g^{-1})
NO_3 (mg N g^{-1})
01/15 03/15 05/15 07/15 09/15 11/15 01/16 03/16 05/16 07/16 09/16 11/16
Month of Measurement
Site
B
E
LF
OP12
OP2
OP7
RR

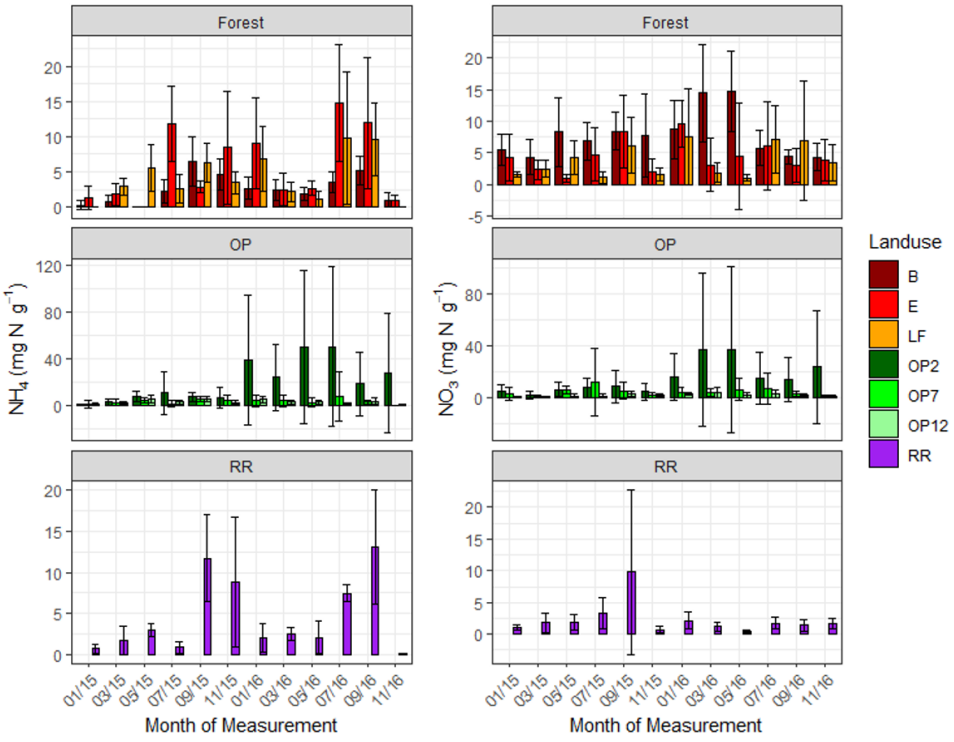
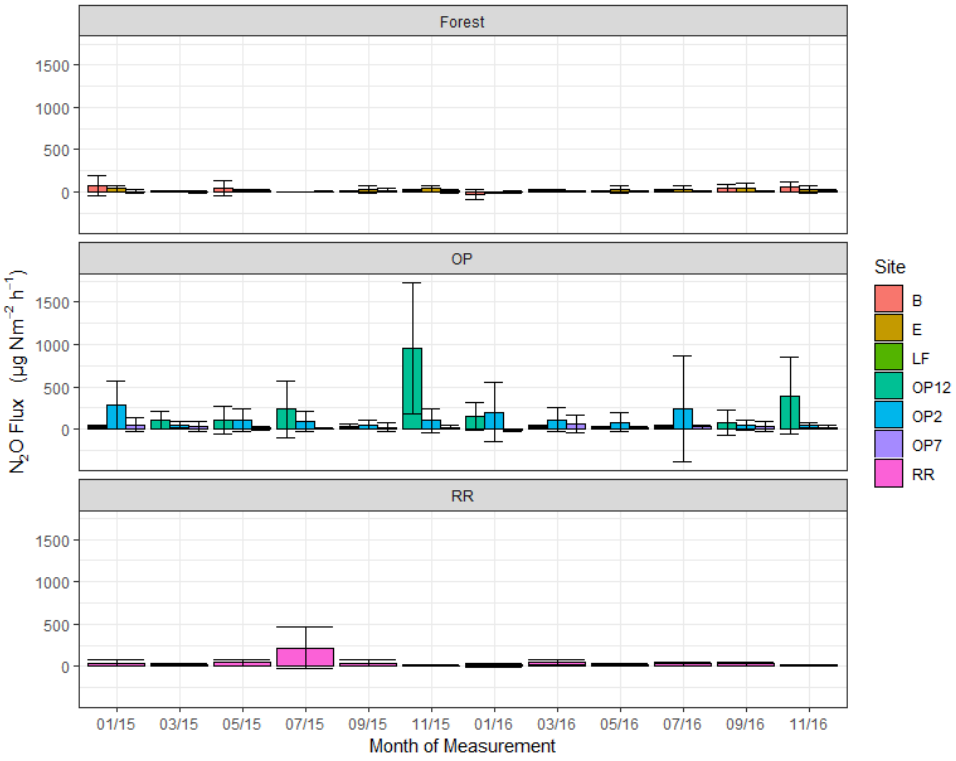


Figure 3. Mean mineral N as KCl extractable NH_4^+ (a) and NO_3^- (b) from January 2015 - November 2016, every two months (upper panel: B, E, LF = logged forests, middle panel: OP~~1~~2, OP7~~2~~, OP~~7~~12 = oil palm plantations, bottom panel: RR = riparian reserve). Error bars represent standard deviation of the samples around the mean. Please note different y-axis scale for OP.


Forest
OP
RR
1500
1000
500
0
N_2O Flux ($\mu g\ Nm^{-2}\ h^{-1}$)
01/15
03/15
05/15
07/15
09/15
11/15
01/16
03/16
05/16
07/16
09/16
11/16
Month of Measurement
Site
B
E
LF
OP12
OP2
OP7
RR

978

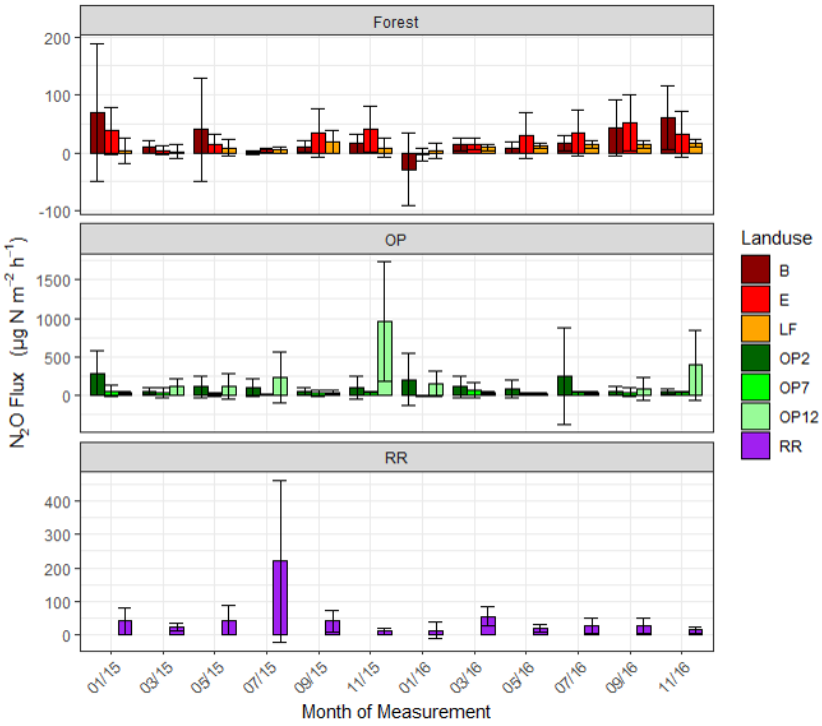
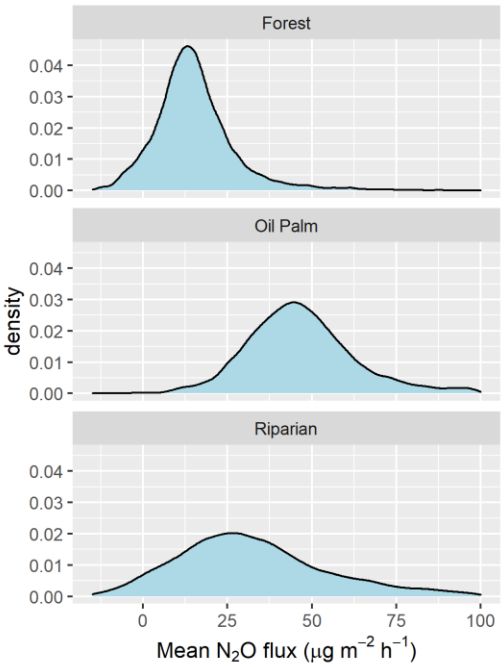


Figure 4. a) Nitrous oxide (N_2O-N) fluxes in µg m^{-2} h^{-1} from January 2015 - November 2016, every two months (upper panel: B, E, LF = logged forests, middle panel: OP~~1~~2, OP~~2~~7, OP12~~7~~ = oil palm plantations, bottom panel: RR = riparian reserve). Bars are mean for each site and error bars are standard deviation of number of chambers per site. Please note different y-axis scales for each land-use.


Forest
Oil Palm
Riparian
density
0.04
0.03
0.02
0.01
0.00
0
25
50
75
100
Mean N2O flux (μg m−2 h−1)

984

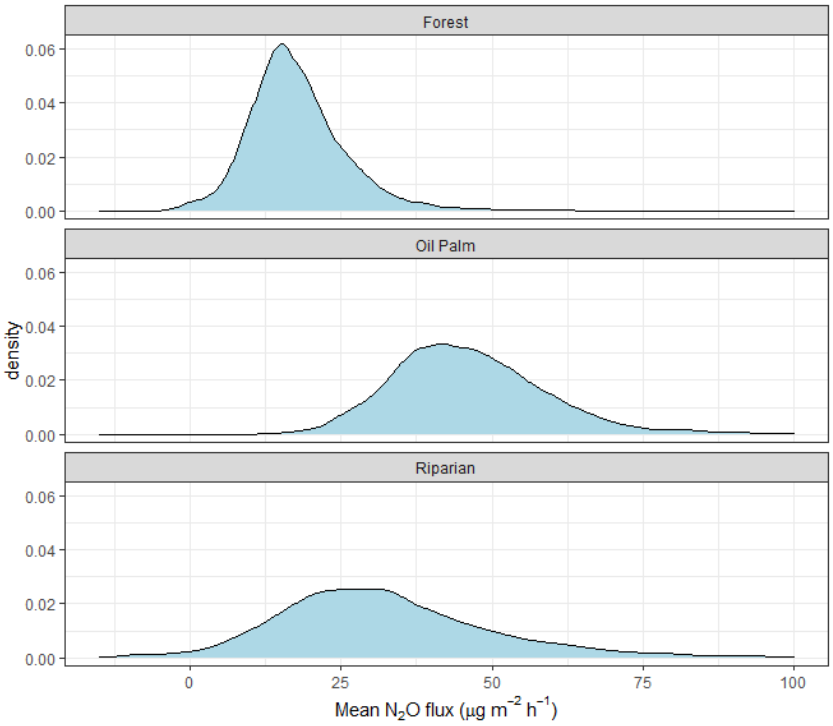
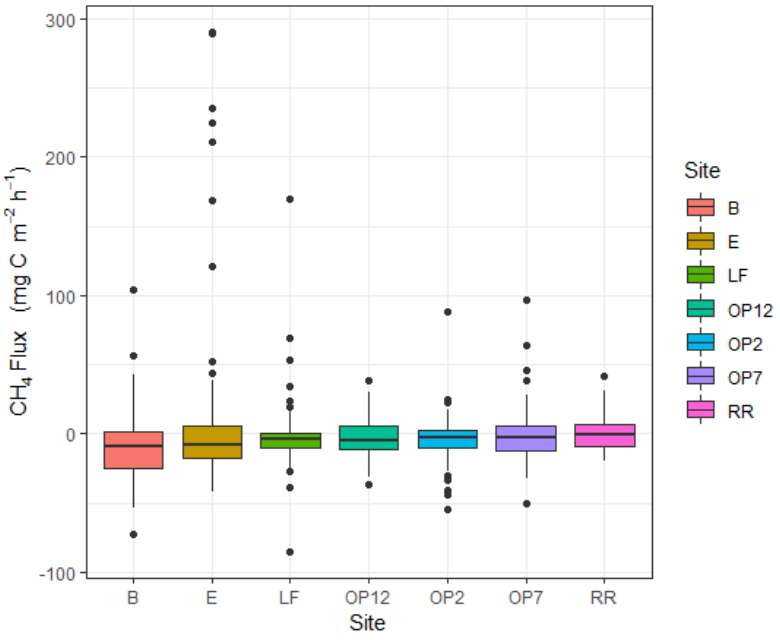


Figure 4. b) Posterior probability density of the mean nitrous oxide flux from each land-use, estimated by the Bayesian GLMM described in the text.


300
200
100
0
-100
CH_4 Flux (mg C m^{-2} h^{-1})
B
E
LF
OP12
OP2
OP7
RR
Site
Site
B
E
LF
OP12
OP2
OP7
RR

988

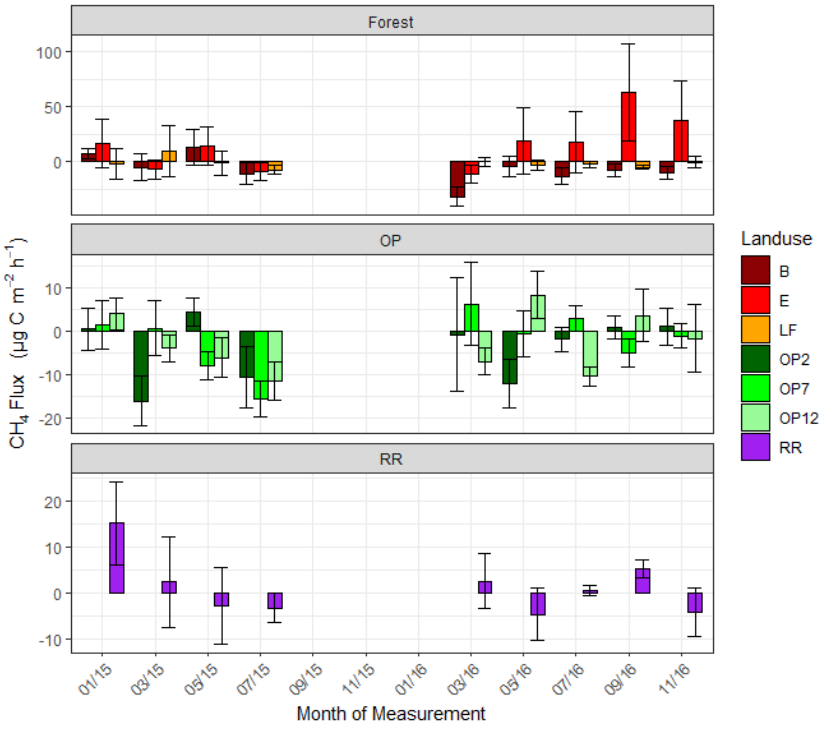
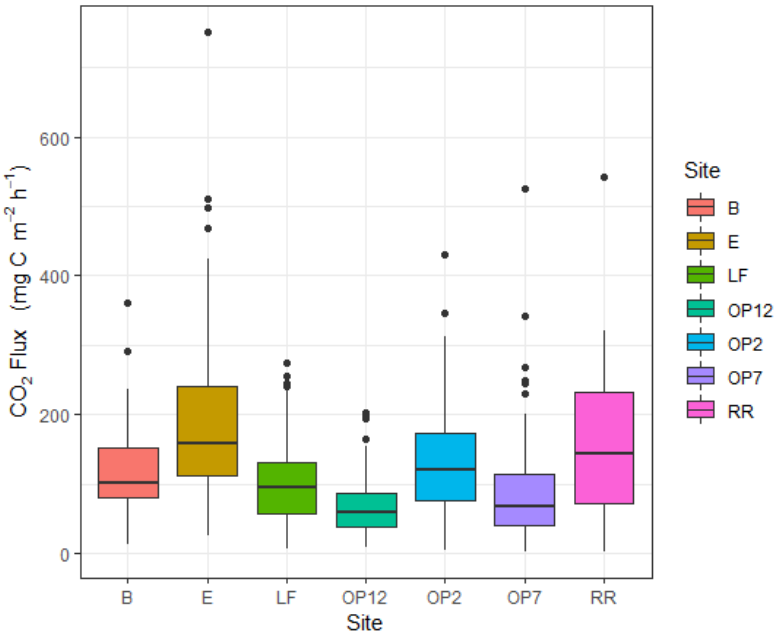


Figure 5. Methane (CH_4-C) fluxes in µg m^{-2} h^{-1} fluxes in µg m^{-2} h^{-1} from January 2015 - November 2016, every two months (upper panel: B, E, LF = logged forests, middle panel: OP2, OP7, OP12 = oil palm plantations, bottom panel: RR = riparian reserve). Bars are mean for each site and error bars are standard deviation of number of chambers per site. Please note different y-axis scales for each land-use. Due to technical issues data is missing for 09/15 to 01/16.

~~from the different sites from January 2015 – November 2016, every two months (B, E, LF = logged forests, OP12, OP2, OP7 = oil palm plantations, RR = riparian reserve). The ends of the box are the upper and lower quartiles, so the box spans the interquartile range. The median is marked by a horizontal line inside the box. The whiskers are the two lines outside the box that extend to the highest and lowest observations with outliers marked with an asterisk (*).~~



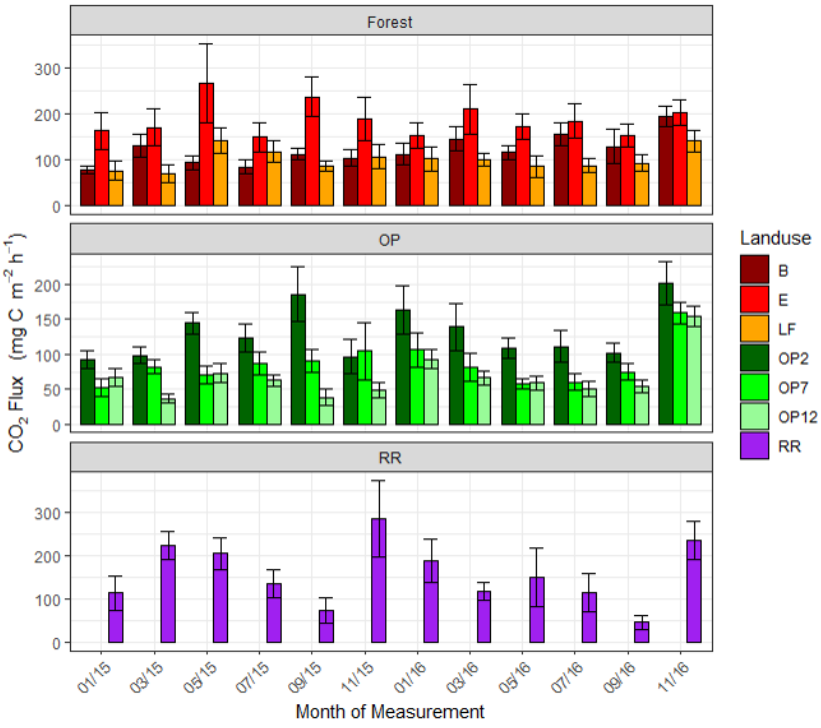
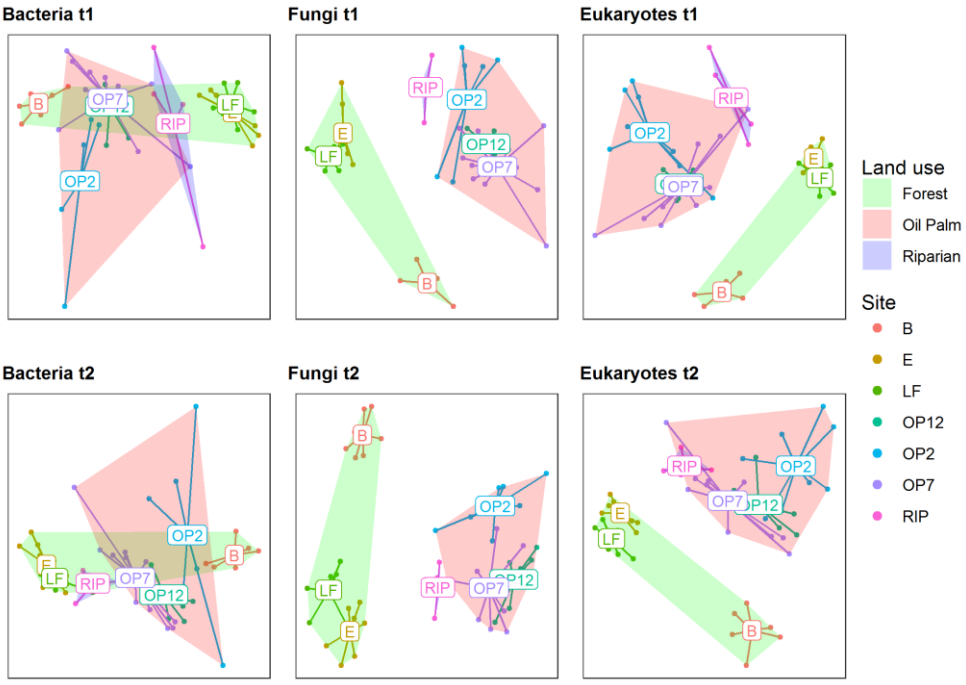


Figure 6. Soil respiration (CO_2-C) ~~fluxes~~ rates in mg m^{-2} h^{-1} fluxes in µg m^{-2} h^{-1} from January 2015 - November 2016, every two months (upper panel: B, E, LF = logged forests, middle panel: OP2, OP7, OP12 = oil palm plantations, bottom panel: RR = riparian reserve). Bars are mean for each site and error bars are standard deviation of number of chambers per site. Please note different y-axis scale for OP.

~~from January 2015 - November 2016, every two months (B, E, LF = logged forests, OP12, OP2, OP7 = oil palm plantations, RR = riparian reserve). The ends of the box are the upper and lower quartiles, so the~~

box spans the interquartile range. The median is marked by a horizontal line inside the box. The whiskers are the two lines outside the box that extend to the highest and lowest observations with outliers marked with an asterisk (*).


Bacteria t1
Fungi t1
Eukaryotes t1
Bacteria t2
Fungi t2
Eukaryotes t2
Land use
Forest
Oil Palm
Riparian
Site
B
E
LF
OP12
OP2
OP7
RIP

1012

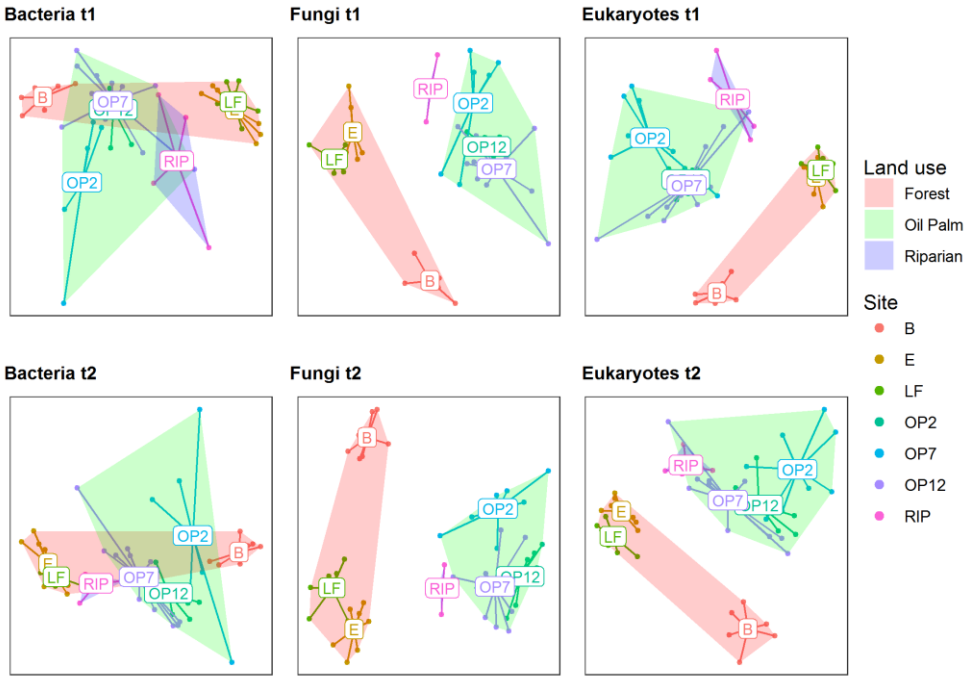


Figure 7. 2D Non metric multidimensional scaling ordination plots of bacteria, fungal and eukaryotic communities from two samples dates March 2016 (upper panel, t1) and November 2016 (lower panel, t2). Coloured points designate replicates from each site (B, E, LF = logged forests, OP~~1~~2, OP7~~2~~, OP12~~7~~ = oil palm plantations, RIP = riparian reserve), as indicated in the legend with additional site centroids denoted on the plots. In addition, hulls indicate broad land-use categories as indicated in the legend.

Supplementary information

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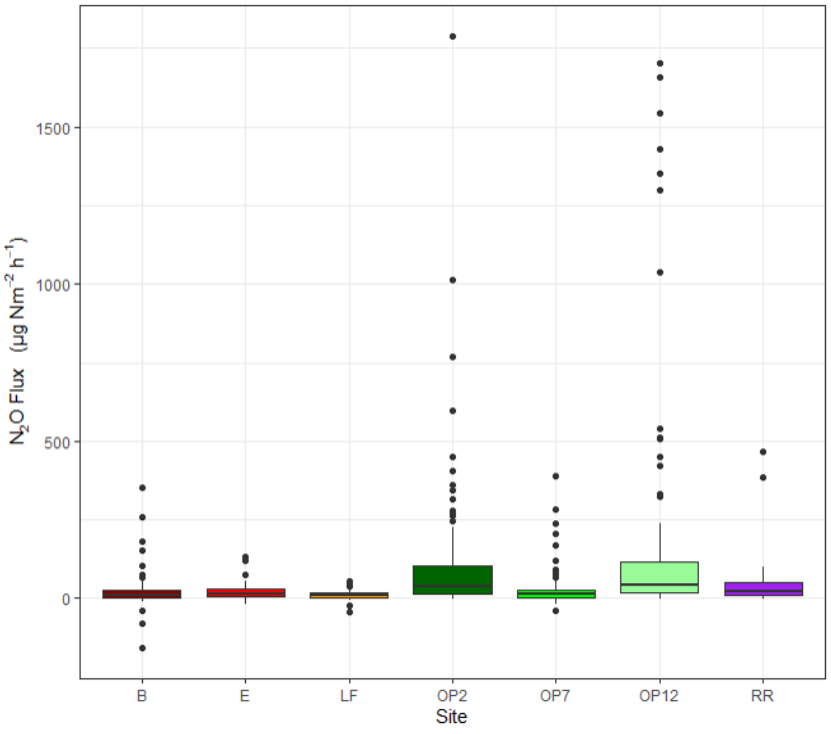

Figure S1. Nitrous oxide (N_2O-N) fluxes in µg m^{-2} h^{-1} from January 2015 - November 2016, every two months (B, E, LF = logged forests, OP2, OP7, OP12 = oil palm plantations, RR = riparian reserve). The ends of the box are the upper and lower quartiles, so the box spans the interquartile range. The median is marked by a horizontal line inside the box. The whiskers are the two lines outside the box that extend to the highest and lowest observations with outliers marked with an asterisk (*).

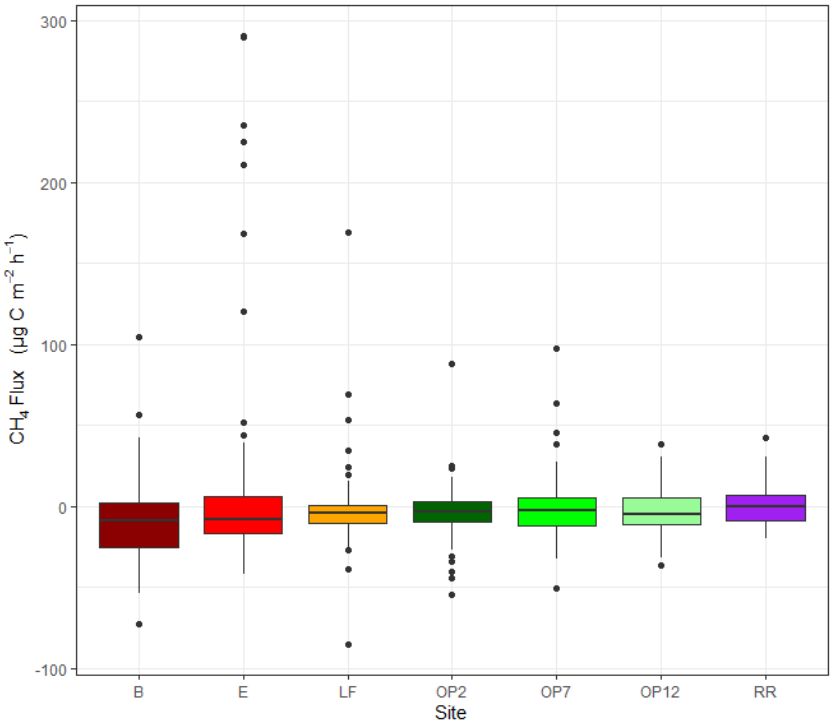

Figure S2. Methane (CH_4-C) fluxes in µg m^{-2} h^{-1} from January 2015 - November 2016, every two months (B, E, LF = logged forests, OP2, OP7, OP12 = oil palm plantations, RR = riparian reserve). The ends of the box are the upper and lower quartiles, so the box spans the interquartile range. The median is marked by a horizontal line inside the box. The whiskers are the two lines outside the box that extend to the highest and lowest observations with outliers marked with an asterisk (*).

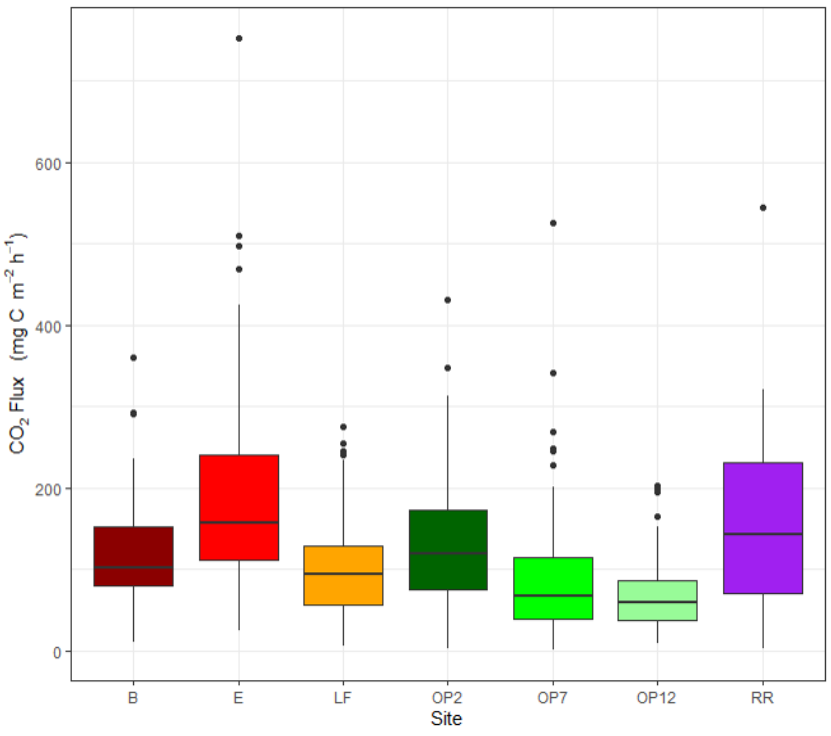

Figure S3. Soil respiration (CO_2-C) rates in mg m^{-2} h^{-1} from January 2015 - November 2016, every two months (B, E, LF = logged forests, OP2, OP7, OP12 = oil palm plantations, RR = riparian reserve). The ends of the box are the upper and lower quartiles, so the box spans the interquartile range. The median is marked by a horizontal line inside the box. The whiskers are the two lines outside the box that extend to the highest and lowest observations with outliers marked with an asterisk (*).

~~marked by a horizontal line inside the box. The whiskers are the two lines outside the box that extend to the highest and lowest observations with outliers marked with an asterisk (*).~~

Table S1. Relationships between environmental variables and microbial community structure, determined by linear fitting of vectors to the NMDS ordination axis scores at sample t2 (see Fig 7). Significance of fits is displayed as ***p<=0.001, **p<=0.01, and *p<=0.05.

	Bacteria (16S)				Fungi (ITS)				Eukaryotes (18S)			
	NMDS1	NMDS2	r^2	p	NMDS1	NMDS2	r^2	p	NMDS1	NMDS2	r^2	p
pH	0.95	-0.30	0.85	***	-0.74	0.67	0.67	***	0.76	0.65	0.73	***
Soil Moisture (%)	0.98	0.22	0.17	*	-0.79	0.61	0.02		0.71	0.71	0.17	*
Bulk Density	-0.72	-0.69	0.14	*	0.91	0.42	0.51	***	-0.82	0.58	0.46	***
N %	0.90	0.43	0.15	*	-0.91	-0.42	0.50	***	0.85	-0.53	0.45	***
C %	0.96	0.30	0.09		-0.93	-0.38	0.28	***	0.77	-0.63	0.32	***
Temperature	-0.53	-0.85	0.43	***	0.81	0.58	0.69	***	-0.89	0.46	0.72	***
Land Use (factor centroids)			0.22	***			0.53	***			0.49	***
Forest	0.21	0.07			-0.27	-0.11			0.24	-0.12		
Oil Palm	-0.21	-0.03			0.18	0.06			-0.19	0.05		
Riparian	0.20	-0.22			-0.04	0.25			0.04	0.33		

~~**Table S1. Relationships between environmental variables and microbial community structure, determined by linear fitting of vectors to the NMDS ordination axis scores at sample t2 (see fig 7). Significance of fits is displayed as ***p<=0.001, **p<=0.01, and *p<=0.05.**~~

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