Temperature response of *ex-situ* greenhouse gas emissions from tropical peatlands: interactions between forest type and peat moisture conditions

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Abstract

Climate warming is likely to increase carbon dioxide (CO_2) and methane (CH_4) emissions from tropical wetlands by stimulating microbial activity, but the magnitude of temperature response of these CO_2 and CH_4 emissions, as well as variation in temperature response among forest types, is poorly understood. This limits the accuracy of predictions of future ecosystem feedbacks on the climate system, which is a serious knowledge gap as these tropical wetland ecosystems represent a very large source of greenhouse gas emissions (e.g. two-thirds of CH_4 emissions from natural wetlands are estimated to be from tropical systems). In this study, we experimentally manipulated temperatures and moisture conditions in peat collected from different forest types in lowland neotropical peatlands in Panama and measured how this impacted *ex-situ* CO_2 and CH_4 emissions. The greatest temperature response was found for anaerobic CH_4 production (Q_{10} = 6.8), and CH_4 consumption (mesic conditions, Q_{10} = 2.7), while CO_2 production showed a weaker temperature response (Q_{10} < 2) across the three moisture treatments. The greatest temperature response of CO_2 production was found under flooded oxic conditions. Net emissions of CO_2 and CH_4 were greatest from palm forest under all moisture treatments. Furthermore, the temperature response of CH_4 emissions differed among dominant vegetation types with the strongest response at palm forest sites where fluxes increased from 42 ± 25 to 2166 ± 842 ng CH_4 g^{-1} h^{-1} as temperatures were raised from 20 to 35 °C. We conclude that CH_4 fluxes are likely to be more strongly impacted by higher temperatures than CO_2 fluxes but that responses may differ substantially among forest types. Such differences in temperature response among forest types (e.g. palm vs evergreen broad leaved forest types) need to be

considered when predicting ecosystem greenhouse gas responses under future climate change scenarios.

Introduction

Global atmospheric methane (CH_4) and carbon dioxide (CO_2) concentrations are increasing as a consequence of human activities such as fossil fuel burning and land use change (IPCC 2013). The resulting climatic changes may further increase greenhouse gas (GHG) emissions from terrestrial biomes, creating a positive feedback loop resulting in additional climate warming; however, such feedbacks will differ among ecosystems. Wetlands are important components of the global carbon cycle and exchange large quantities of CH_4 and CO_2; indeed, they are recognised as the largest individual natural source of atmospheric CH_4, a potent GHG (e.g. Lelieveld et al. 1998; Bridgham et al., 2013; IPCC 2013).

Two thirds of wetland CH_4 emissions are estimated to originate from natural tropical ecosystems in Southeast Asia, Africa and the Neotropics (Melton et al., 2013). These wetlands are also large emitters of CO_2, estimated at 4540 ± 1480 Tg CO_2 year^{-1} (Sjögersten et al., 2014). Furthermore, tropical peatlands acts as globally important stores of carbon (C) (Page et al., 2011). The CO_2 and CH_4 emissions of tropical peatlands are regulated by water table/redox state (Jauhiainen et al., 2005; Hoyos-Santillán, 2014), quantity and quality of litter inputs (Wright et al., 2011; Sjögersten et al., 2014; Hoyos-Santillán et al., 2015) and temperature (Hirano et al., 2009). However, despite the significance of tropical wetlands in the global carbon cycle, the temperature response of GHG emissions from tropical peatlands is largely unknown (see Hirano et al., 2009), limiting our ability to predict climate change responses of their CO_2 and CH_4 emissions despite their high emissive potential (Bridgham et al., 2013).

This is a critical knowledge gap as we do not know if the wealth of data exploring temperature responses of CH_4 and CO_2 fluxes from higher latitude ecosystems can be transferred to tropical systems. It is for example plausible that tropical wetland microbial communities are adapted to higher temperatures, rendering them less sensitive to elevated temperatures than those in higher latitudes. Alternatively, differences in soil organic matter chemistry between high and low latitude wetlands may result is substantial differences in the temperature response of decomposition and release of GHGs (Lloyd and Taylor, 1994; Bosatta and Ågren, 1999; Fierer et al., 2005).

Tropical peatlands are under threat from climate change, which could substantially affect their water balance, and resultant CO_2 and CH_4 emissions (Furukawa et al., 2005; Li et al., 2007; Hooijer et al., 2010; Laiho, 2006; IPCC 2013). With regards to climate change, current predictions indicate air temperatures in the neotropics and Southeast Asia will be 3-4°C higher by 2100 and 5-7 °C higher by 2200 (IPCC, 2013). To date precipitation changes in the Amazon region have been associated with wetter wet seasons and drier dry season but there are no strong overall trends for the region (Almeida et al, 2017). In the future precipitation in the neotropics is predicted to decrease by ca. 10% by 2100 (ca. 350 mm less per year) and by 20-40% by 2200 (up to 1400 mm less per year) under the Intergovernmental Panel on Climate Change (IPCC) scenario RCP 8.5 (IPCC, 2013) although, model predictions of changes in precipitation patterns are more uncertain than the temperature predictions and patterns varies between inland and coastal areas (Chao et al., 2008; Oueslati et al., 2016). Together these changes are predicted to result in drier soils (IPCC, 2013). Increased temperature can be expected to increase microbial

100 decomposition rates directly (Hirano et al., 2009), while lower water tables could
101 result in large increases in soil CO_2 losses to the atmosphere and reduced CH_4
102 emissions (Jauhiainen et al., 2005; Couwenberg et al., 2010).
103
104 The “carbon-quality temperature hypothesis” postulates that the temperature
105 sensitivity of decomposition processes increases with the complexity (recalcitrance)
106 of soil organic matter, because larger activation energies are required for its
107 catabolism under aerobic conditions (Lloyd and Taylor, 1994; Bosatta and Ågren,
108 1999; Fierer et al., 2005). In the context of tropical peatlands, this would suggest that
109 climate change could result in decomposition of recalcitrant organic matter as
110 temperatures increase. Furthermore, it is plausible that the dominance of palms and
111 evergreen broad leaved trees in tropical peatlands result in substantially different soil
112 organic matter chemistry (Hoyos-Santillan et al., 2015) compared to higher latitude
113 wetlands where peat formation is often driven by graminoid and moss litter inputs
114 (Turetsky et al., 2014) which is likely to affect the temperature response of peat
115 decomposition. For example, recalcitrant lignin and long chain fatty acids from wood
116 and evergreen leaf litter inputs, respectively, represent a large component of litter
117 inputs in tropical peatlands (Sjogersten et al., 2014). According to the carbon-quality
118 temperature hypothesis this would suggest that soil organic matter in tropical
119 peatland may be more responsive to elevated temperature than higher latitude
120 ecosystems.
121
122 Water logging and anaerobic conditions have been shown to affect the temperature
123 response of C mineralisation strongly: CH_4 production in both subtropical and high
124 latitude wetlands appears to be more sensitive to temperature than either aerobic or

anaerobic CO_2 production (Dunfield et al., 1993; van Hulzen et al., 1999; Inglett et al., 2012; Treat et al., 2014). When comparing the relative impact of temperature on CH_4 production and oxidation, CH_4 oxidation does not appear to increase with temperature as rapidly as CH_4 production (Dunfield et al., 1993; Inglett et al., 2012), so higher temperatures may increase net CH_4 emissions. It is important to consider temperature response in the context of moisture status as soils are predicted to come drier in the tropics in response to climate change as there are strong links between moisture conditions/water tables position and GHG emissions (Jauihianen et al., 2005; Couwenberg et al., 2010)..

The aim of this study is therefore to investigate how increasing peat temperatures and changes in moisture levels of neotropical peatlands may interact to control *ex situ* CO_2 and CH_4 emissions. To achieve this we ran controlled experiments with peat from lowland neotropical peatlands to determine the temperature responses for *ex situ* CO_2 and CH_4 fluxes under both aerobic and anaerobic conditions. The experiment consisted of incubating peat at a range of temperatures and moisture states. As these peatlands are heterogeneous with regards to vegetation and soil nutrient status (Troxler et al., 2007; Sjogersten et al., 2011) we investigated the impact of moisture and temperature treatments on CO_2 and CH_4 emissions from peat samples extracted from four forest types commonly found in peatlands in the neotropics (Phillips et al., 1997; Nahlik and Mitch 2011; Roucoux et al., 2013): palm, mixed, hardwood and stunted forest.

Methods

Study area

150 The San San Pond Sak wetland complex is a 164 km^2 mosaic of freshwater and
151 marine-influenced wetlands in Bocas del Toro Province on the Caribbean coast of
152 western Panama (Cohen and Stack, 1996). Recognised internationally as a largely
153 pristine wetland of special scientific interest (Ramsar site #611), San San Pond Sak
154 includes the significant 80 km^2 Changuinola peat deposit, an ombrotrophic domed
155 peatland to the south east of Changuinola river (Phillips et al., 1997). The oldest
156 deposits in the Changuinola peatland are estimated to have been formed 4000–4500
157 years ago and are >8 m deep in the central areas (Phillips et al., 1997). Peat at the
158 edges of the peatland is younger and *ca*. 2 m deep.
159
160 Seven distinct phasic plant communities cover the peatland (Phillips et al., 1997).
161 Starting from the periphery, these communities have been designated as (i)
162 *Rhizophora mangle* mangrove swamp, (ii) mixed back mangrove swamp, (iii) *Raphia*
163 *taedigera* palm forest swamp, (iv) mixed forest swamp (consisting of both palm and
164 evergreen broadleaved hardwood trees), (v) *Campnosperma panamensis* forest
165 swamp, (vi) sawgrass/stunted forest swamp and (vii) *Myrica-Cyrilla* bog-plain. In this
166 study we focused on (iii) to (vi) of these phasic communities as these represent the
167 dominant forest types in the peatland. For simplicity we denote these as palm forest,
168 mixed forest, hardwood forest, and stunted forest throughout the paper. The forest is
169 mainly unaffected by human activities although occasional small scale selective
170 logging is evident in areas close to the coast and rivers. Nutrient levels in the peat and
171 plant tissue vary greatly among vegetation communities and are generally low in the
172 interior and higher towards the edge of the peatland (Troxler, 2007; Sjögersten et al.,
173 2011). The low nutrient content in the interior is reflected by reduced microbial activity,
174 with higher microbial biomass C:N and C:P ratios and up-regulation of the activity of

extracellular enzymes involved in nutrient acquisition (Sjögersten et al., 2011; Cheesman et al., 2012). Furthermore, *in situ* (i.e. measurement in the field) CO_2 and CH_4 fluxes along this vegetation transect did not appear to reflect peat nutrient availability (Wright *et al.,* 2013), while laboratory incubations (*ex situ*) of drained surface peat samples show lower CO_2 production in substrates from the interior than sites closer to the edge of the peatland (Sjögersten et al., 2011).

A weather station in the nearby town of Bocas del Toro, Isla Colon, *ca*. 10 km from the peatland, shows the area has a mean annual temperature of 25.9°C with low intra-annual variability, and recorded a mean annual precipitation of 3092 mm between 2003 and 2011 (Hoyos- Santillán et al., 2015). Rainfall is continuous throughout the year with no pronounced dry season, although there are two distinct periods of lower rainfall (February–March and September–October). Water tables in these peatlands are dynamic and mainly fluctuate around ± 0.2 m from the surface, with water tables increasing rapidly after intense rainfall events and dropping to or below the surface in between rainfall events (Wright et al., 2013; S. Sjögersten, pers. obs.). During occasional, prolonged dry (i.e. no rainfall) periods, the water table can drop as low as -40 cm (Hoyos-Santillán 2014). Conversely, high rainfall events can cause the water tables to rise above the peat surface (normally no more than ca. 10-20 cm). Mean peat temperature 10 cm below the surface is *ca*. 25°C and shows little intra-annual variation (Wright *et al.*, 2013).

Field sampling strategy

For the sampling campaign we established four transects (ca. 1 km) (Fig. 1). Transects were selected following assessment of satellite imagery of the study area; in each

case there was evidence of vegetation transition from the coast or river inlets towards the interior of the peatland. Along these transects we collected peat samples for the incubation study from palm forest (n=6 sites), mixed forest (n=9), hardwood forest (n=3) and stunted forest (n=3), i.e. 21 sites in total. More detailed description of these four forest types are in Sjögersten et al. (2011). Note that not all forest types occurred along all transects. At a subset of sites denoted 'major sites' (Fig. 1), we carried out a more detailed site characterisation including *in situ* CO_2 and CH_4 surface exchange measurements to serve as background data for the incubation study.

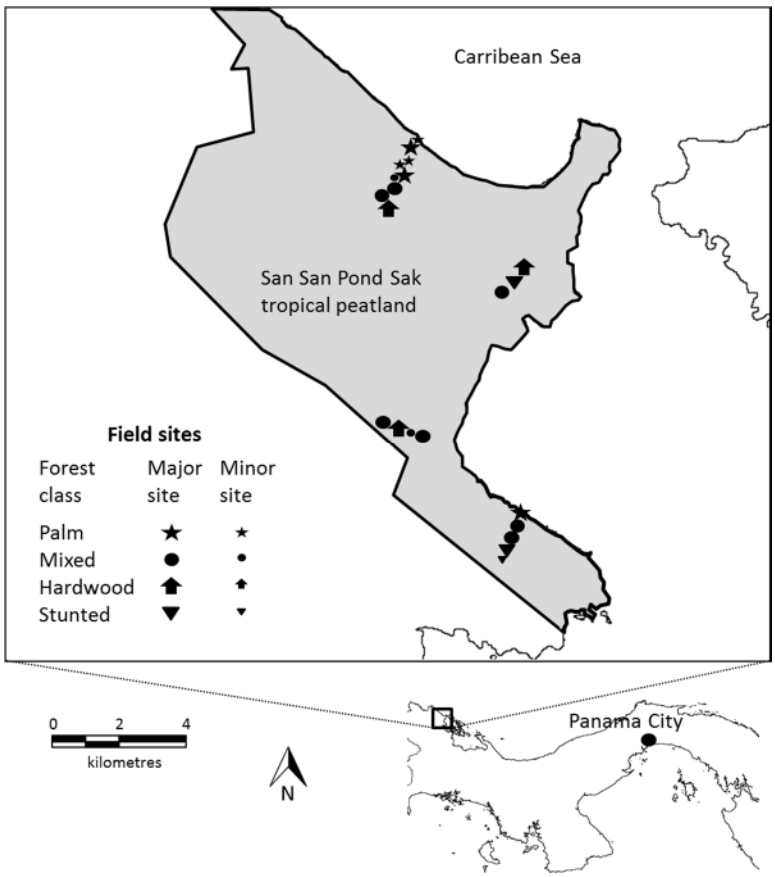


Figure 1. Map of the San San Pond Sak peatland showing the sampling sites used in the field campaign.

Collection and analysis of field gas samples

At the major sites we established 5×5 m plots using a set of random coordinates. Within each plot we made a visual assessment of the proportion of the area covered by standing water (done independently by two people). The depth of pools of standing water relative to the peat surface was determined in three random locations within the plot. Air and peat temperature (at 10 cm depth) was measured.

As part of the site characterisation the *in situ* net exchange surface fluxes of CO_2 and CH_4 were determined at the major sites; however, as gas sampling was carried out at only one time point, these data only give a snapshot of *in situ* fluxes and should be interpreted carefully. Gas samples were collected from the four corners of the 5×5 m plots using the closed static chamber technique (Denmead, 2008). Gas sampling was made between 10 a.m. and 4 p.m. concurrently with other plot characterisation measurements. The chamber volume was 9 dm^3 and the exchange surface 0.07 m^2. To avoid root and soil disturbance the chambers was sealed to the water logged peat surface by gently placing them into the peat or floating them on the water surface when the sampling location was flooded. Air samples were collected through a Suba-Seal® valve (Sigma-Aldrich, St-Louis, USA) using a hypodermic needle and 20 mL a syringe. Samples of 20 mL were collected after 1, 3, 5 and 7 min and injected into evacuated 12 mL Exetainer serum vials(Labco, Ceredigion, UK) giving a slight over-pressure in the vial to allow for leak detection. Samples were collected by a team member reaching over the sampling chamber from ca 1 m distance. There was no movement around the chamber during the sampling period.

All gas samples were analysed by gas chromatography (GC 2014, Shimadzu, Milton Keynes, UK) using a 1 mL sampling loop and a molecular sieve column (12 m, 0.53

mm internal diameter); CO_2 concentration was determined by thermal conductivity and CH_4 by flame ionisation. Fluxes of CO_2 and CH_4 were calculated using the ideal gas law for sampling points which met the assumption of linear (or near linear) gas accumulation during the closure period (Wright et al., 2013).

At all plots a peat sample from 0-10 cm depth, ca. 5×5x5 cm volume, was collected for incubation experiments and chemical characterisation. Peat depth was measured by pushing 2 cm diameter connecting rods through the peat (low density 0.1 g cm^{-3}) as far as the underlying marine sediments (clay or sand; higher density > 1 g cm^{-3}). The accuracy of this method was tested by comparison with depths determined using a Russian peat borer for a subset of sites; this indicated that the rods were accurate, although depths might be overestimated in areas where a transition occurs from peat to soft organic rich marine clay sediments (error estimated at 0-100 cm based on peat core data (Hoyos-Santillán, 2014, Sjogersten et al., unpublished data)).

Peat chemical characterisation

The collected peat samples were analysed for total elements and extractable nutrients. Peat samples were transported to the laboratory (approx. 4 h), stored at -20°C and shipped frozen to the UK to avoid depletion of labile substrates during storage. We acknowledge that the freezing may have impacted on activity of the microbial community; however, comparisons of microbial enzyme activities in tropical forest soils do not suggest that freezing has a negative impact on the activities of enzymes involved in microbial C acquisition, compared to storage at room temperature (Turner and Romero 2010). Prior to analysis, peats were thawed at 4°C.

After thawing, roots were removed by hand with tweezers prior to analysis but fine roots inevitably remained in some samples. Moisture content was determined by drying subsamples of peat at 105°C for 24 h. Peat pH and conductivity were determined using a glass electrode and a portable conductivity meter (Hanna Instruments), respectively, in a 1:2 ratio of fresh peat to deionized water.

Dissolved organic C and nitrogen (N) fractions were extracted by shaking 40 g of fresh soil in 75 mL of 0.5 M K_2SO_4 for 1 h. Extracts were centrifuged (8000*g*, 15 min) and dissolved C and N were determined after a five-fold dilution by automated combustion and gas chromatography on a TOC-VCSH analyzer (Shimadzu UK Ltd, Milton Keynes, UK), coupled with a total N measuring unit (TNM-1, Shimadzu UK Ltd, Milton Keynes, UK). The fulvic:humic acid ratio and the related degree of humification in dissolved organic matter were estimated by spectrophotometric analysis (Grayson and Holden 2012). Porewater samples were passed through cellulose filters (Whatman Grade 1, 11 µm) and absorbance was measured at 465 and 665 nm (U-2010, Hitachi UV-VIS Spectrophotometer). The absorbance values were then used to estimate the E_{465}/E_{665} index (Uyguner and Bekbolet 2005) where a greater ratio indicates more labile constituents. Ammonium in the K_2SO_4 (see above) extracts was determined by colorimetry at 635 nm following reaction with phenol and hypochlorite. Readily-exchangeable phosphate was determined by extraction with anion exchange membranes (AEM) using a method based on that described by Myers et al. (1999). Peat (20 g fresh weight) was shaken for 24 h with 80 ml deionized water and five anion-exchange resin strips (1 x 4 cm; manufactured by BDH Prolabo and distributed by VWR International, Lutterworth, Leicestershire, UK). The strips were rinsed in deionized water and the phosphate recovered by shaking

for 1 h in 50 ml of 0.25 M H_2SO_4. Multi-element analysis of diluted solutions was undertaken by ICP-MS (Thermo-Fisher Scientific iCAP-Q; Thermo Fisher Scientific, Bremen, Germany). The instrument was run using standard mode (STD) in which the collision cell is evacuated. Samples were introduced from an autosampler (Cetac ASX-520) incorporating an ASXpress™ rapid uptake module through a PEEK nebulizer (Burgener Mira Mist). Internal standards were introduced to the sample stream on a separate line via the ASXpress unit and included Ge (10 µg L^{-1}), Rh (10 µg L^{-1}) and Ir (5 µg L^{-1}) in 2% trace analysis grade (Fisher Scientific, UK) HNO3. External multi-element calibration standards (Claritas-PPT grade CLMS-2 from SPEX Certiprep Inc., Metuchen, NJ, USA) included Ag, Al, As, Ba, Be, Cd, Ca, Co, Cr, Cs, Cu, Fe, K, Li, Mg, Mn, Mo, Na, Ni, P, Pb, Rb, S, Se, Sr, Tl, U, V and Zn, in the range 0 – 100 µg L-1 (0, 20, 40, 100 µg L-1). Phosphorus also utilized in-house standard solutions (KH_2PO_4). In-sample switching was used to measure P in STD mode. Sample processing was undertaken using Qtegra™ software (Thermo-Fisher Scientific) utilizing external cross-calibration between pulse-counting and analogue detector modes when required. Loss on ignition (LOI) was determined as mass loss following ignition for 7 h at 550 °C (Heiri et al., 2001).

Incubation procedures

The collected peat samples were also measured for ex situ GHG fluxes under three moisture treatments: flooded anaerobic, flooded oxic, and mesic conditions The anaerobic treatment models long-term raised water tables. The flooded oxic treatment models oxygenated high water table conditions (e.g. following rainfall). The mesic treatment reflects low surface moisture during periods of low rainfall when water tables drop. Each of these treatment was placed to four different temperatures:

20, 25, 30 and 35°C (reflecting the *in situ* annual air temperature range incremented by 5°C to reflect climate warming predictions IPCC (2014)). The assumption made here are that peat temperatures will increase to the same extent as air temperatures.

For the incubation, 100 ml serum bottles were filled with 5 g of field moist peat from each peat sample collected from the peat surface (0-10 cm). For the anaerobic treatment 10 ml of deionised water was added to the peat and the peat water mixture was bubbled with N_2 vigorously to create oxygen-free conditions and to fill the head space with N_2 (Hoyos-Santillán et al., 2016). The bottles were then capped using black butyl stoppers and crimped, and the bottles were placed in four different incubators set at the required temperature. The peat mesocosms were then left in the incubator for three weeks to allow the microbial communities to acclimatise, after this time a 5 ml gas sample was taken from the bottle and analysed for CO_2 and CH_4 using a GC (see above) to assess anaerobic gas production. This sampling was repeated after one week.

For the flooded oxygenated treatment the head space was aerated and then shaken for ca 1 minute to encourage O_2 mixing. This procedure was repeated daily for a week to stimulate aerobic heterotrophic activity while the bottles were kept in their respective incubators (modified from Hoyos-Santillán et al. (2016)). At the end of the week, aerobic CO_2 and CH_4 production rates were assessed. This was done by first bubbling air with known CO_2 and CH_4 concentrations (127 ± 1.9 and 1.5 ± 0.1 ppm, for CO_2 and CH_4, respectively) through the peat for 1 minute. After flushing, the headspace bottles were capped using butyl stoppers. The bottles were immediately returned to their incubators for ca. 1 hour (Dunfield et al., 1993; Inglett al., 2012)

after which a 5 ml gas sample was taken from each bottle for determination of CH_4 and CO_2. Gas fluxes were calculated using the concentration difference between the initial head space concentrations compared to those after one hour's incubation.

The mesic moisture treatment involved incubation of the bottles at 30 °C to allow moisture to evaporate from the bottles, reflecting natural evaporation conditions during low rainfall periods. The evaporation rate differed among samples and, rather than letting the peat dry for a set time, we regularly checked the peat moisture status visually, and conditions were considered mesic when there was no 'free' water visible in the bottles' peat but the peat was still moist. The gravimetric moisture content used for the mesic incubations ranged between 300 and 800% (dry weight basis), reflecting the high and variable water absorption capacity of the peat. After mesic conditions were achieved, the bottles were covered in parafilm and placed back in their respective temperature incubators for two weeks to equilibrate. CO_2 and CH_4 production rates were assessed by bubbling air with known CO_2 and CH_4 concentrations following the same procedure as described in the section above.

Data analysis

At the end of the temperature incubations Q_{10} values was calculated in the instances when exponential growth models fitted the GHG flux data (Lloyd and Taylor 1994). The Q_{10} value describes the increase in respiration rates with a 10 °C increase in temperature and was calculated using eq.1 with *k* being the rate constant

$$Q_{10} = e^{10k}. \quad (1)$$

Analyses of variance on the impact of the treatments on GHG fluxes were performed using the Residual Maximum Likelihood method (REML). We ran mixed linear models to tease apart the impact of forest type, temperature and moisture regime on the CO_2 and CH_4 fluxes. In the model forest type, temperature and moisture treatment were used as fixed effects, and transect and site as random effects. The CH_4 fluxes were log-transformed prior to analysis. Differences in site properties were analysed using REML with forest type as fixed effect and site as random effect.

We investigated the relationship between temperature and gas fluxes using regression analysis. Where required, the flux data were log-transformed to meet normality assumptions. Normal distributions, homogeneity and homeoscedacity of residuals were checked using QQ-plots and scatter-plots for all statistical models. Statistical analyses were performed in GenStat (*VSN International*, 2011).

Results

Site and chemical properties

All of the plots had a peat depth of > 2 m with the shallowest peats found in palm sites, which were at the edges of the peatland, and the deepest peats in the hardwood and stunted forest (Table 1). The physiochemical properties indicated that all sites, apart from one hardwood site, were characterised by fresh water conditions and that the peat was acid (Table 1): pH ranged between 3.5 and 4.5 and the conductivity ranged between ca. 100 and 700 $\mu S\ cm^{-1}$. The peat in all plots was highly organic with high LOI (> 80%).

The palm sites had the greatest DON concentrations and subsequently the lowest C:N ratio in the porewater, while neither NH_4^+ nor resin P differed among forest types. At palm sites the low C:N ratio in the peat solution together with a high E_{465}:E_{665} ratio suggest a large pool of less decomposed C in the dissolved fraction.

The *in situ* surface emissions of CO_2 were lowest at the palm sites (< 400 mg m^{-2} h^{-1}), with the highest (> 700 mg m^{-2} h^{-1}) fluxes at the stunted forest sites. The *in situ* CH_4 surface emissions ranged between 1.3 ± 0.5 and 32 ± 23.7 mg m^{-2} h^{-1} (Table 1). During sampling, water level was close to the surface at all sites. Specifically, at palm sites ca. 90% of the surface was covered by water while the surface water coverage at mixed forest sites was ca. 50%.

Table 1. Peat properties measure *in situ* or from peat samples collected from the peat surface in different forest types during the field campaign. Mean and standard error of the mean are shown. *** $P<0.001$, * $P<0.05$, $P < 0.1$. Note that some of the measurements were only carried out at the major sites.

	Palm		**Mixed**		**Hardwood**		**Stunted**	
ALL SITES								
Peat depth (m)	2.2	±0.2	3.0	±0.3	4.0	±1.0	3.8	±0.8
pH	4.34	±0.14	4.28	±0.27	4.24	±0.75	3.65	±0.05
Conductivity (μS)	135	±17	110.3	±18	718	±604	94	±10
LOI (%)	87.7	±2.6	85.60	±4.8	84.4	±12.2	94.4	±1.4
DOC (mg C g^{-1})	10.7	±2.9	5.8	±2.4	6.3	±5.6	1.7	±0.5
DON (mg N g^{-1}) *	7.2	±2.0	2.2	±1.2	2.3	±2.1	0.2	±0.1
NH_4^+ (μg N g^{-1})	40.9	±13.3	54.5	±10.9	25.8	±10.2	28.7	±6.2

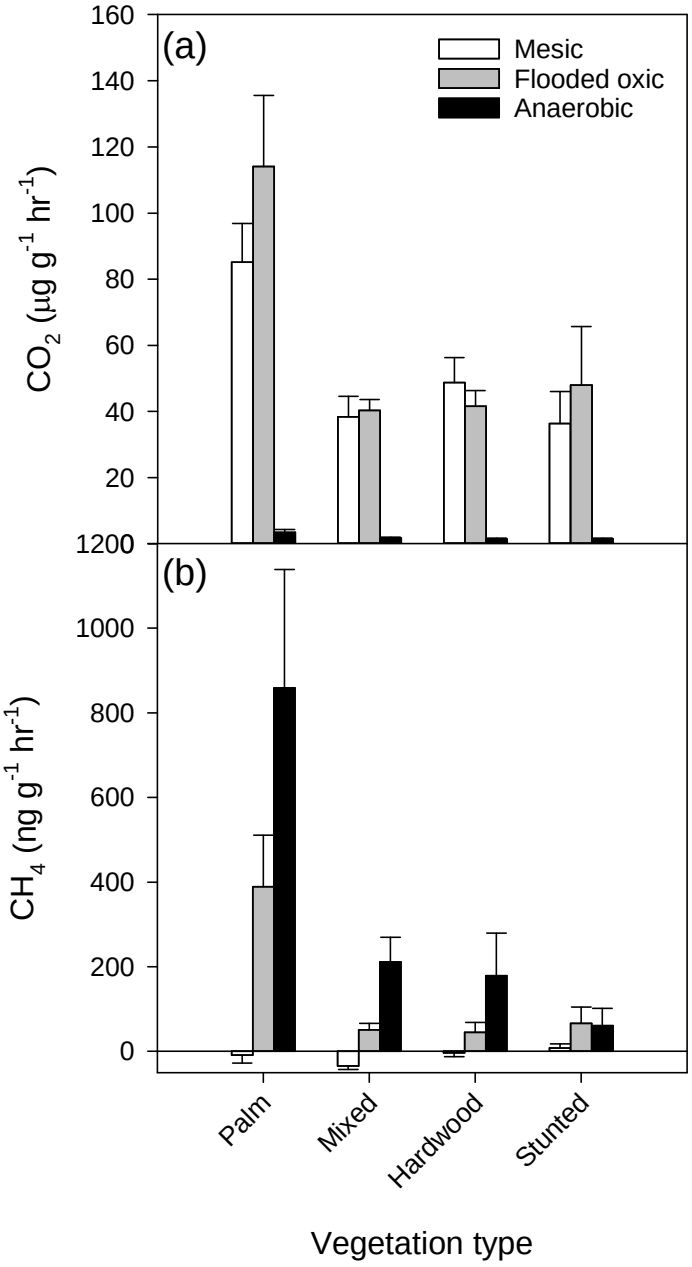
PO_4^{3-}(μg P g^{-1})	0.9	±0.4	3.9	±1.9	2.7	±2.3	4.3	±0.4
E_{465}/E_{665}	5.2	±1.8	3.7	±1.2	4.7	±1.9	2.3	±0.5
C/N[a] ***	1.9	±0.4	3.6	±0.4	3.6	±0.8	7.0	±0.4
MAJOR SITES								
In situ CO_2 (mg m^{-2} h^{-1})	369.4	±57.9	575	±85	527	±20	753.0	±186.3
In situ CH_4 (mg m^{-2} h^{-1})	1.3	±0.5	1.3	±1.2	20.0	±17.1	32.0	±23.7
T_{soil} (°C)	24.4	±0.7	24.9	±0.3	24.4	±0.3	25.1	±0.3
T_{air} (°C)	24.7	±1.1	25.4	±0.7	25.1	±0.8	27.8	±0.7
Standing water (% area)	90	±5	50	±13	70	±17	70	±7
Depth of surface water pools (cm)	12.4	±1.9	13.3	±3.9	18.2	±6.3	8.1	±0.6

[a]Elemental ratio in the dissolved fraction

405

406 *Gas fluxes from incubated samples*

407 In contrast to the *in situ* flux measurement, maximum *ex situ* basal respiration of CO_2
408 and CH_4 from the surface peat samples were found at palm sites (Fig. 2 a and b,
409 Table 2). For CH_4 emissions the mixed and hardwood forest had moderately high
410 emissions, while the lowest emissions were from the stunted forest.



411

412 Figure 2. Fluxes of (a) CO_2 and (b) CH_4 from surface peat reflecting *ex situ* basal respiration
413 from four forest types. The errors shown are standard error of the mean, *n* = 6 for palm
414 forest, *n* = 9 for mixed forest, *n* = 3 for hardwood forest and *n* =3 for student forest.

415

416 Table 2. Statistics describing treatment effects of forest type (Forest), moisture (M) and
417 temperature (T) (fixed effects) on CO_2 and CH_4 fluxes from the laboratory incubations. CO_2
418 and CH_4 fluxes were log-transformed to meet the normality assumption. Significant effects
419 are in bold.

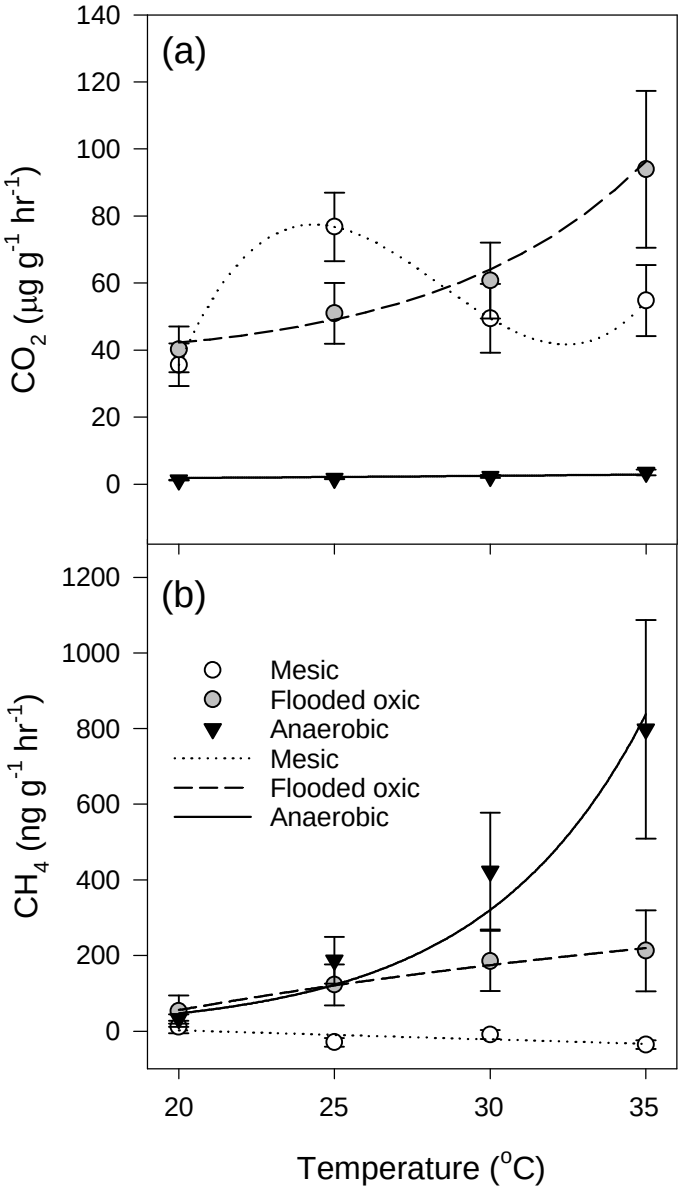
VARIATE	FIXED EFFECT	Wald statistic	*n.d.f.*[a]	*F-value*	*d.d.f.*[b]	*P*	*SED*
Log CO_2							
	Forest	**16.25**	**3**	**5.41**	**16.2**	**<0.01**	**9.6**
	M	**1750.63**	**3**	**583.54**	**253.1**	**<0.001**	**6.1**
	T	**69.1**	**3**	**23.03**	**253.1**	**<0.001**	**6.1**
	Forest × M	10.21	9	1.13	253.1	0.3	13.8
	Forest × T	9.63	9	1.07	253.1	0.3	13.8
	M × T	**29.77**	**9**	**3.31**	**253.1**	**<0.001**	**12.2**
	Forest × M × T	18.16	27	0.67	253.1	0.9	25.0
Log CH_4							
	Forest	9.48	3	3.13	15.8	0.055	135.6
	M	**121.36**	**3**	**40.45**	**254**	**<0.001**	**78.9**
	T	**52.82**	**3**	**17.61**	**254**	**<0.001**	**78.9**
	Forest × M	**33.48**	**9**	**3.72**	**254.1**	**<0.001**	**177.4**
	Forest × T	**26.81**	**9**	**2.98**	**254.1**	**<0.01**	**177.4**
	M × T	**51.86**	**9**	**5.76**	**254**	**<0.001**	**147.7**
	Forest × M × T	35.21	27	1.3	254.1	0.2	308.2

[a]numerator degrees of freedom

[b]denominator degrees of freedom

The moisture treatments strongly influenced CO_2 production, with comparable fluxes for the mesic and the oxic-flooded treatments, while fluxes were an order of magnitude lower in the anaerobic treatment (Fig. 2a, Table 2). For all forest types, CO_2 emissions increased exponentially with temperature in the flooded anaerobic and flooded oxic incubation, with CO_2 emissions being most temperature sensitive under the flooded oxic treatment with a Q_{10} of 3.8 (Fig. 3a and 4a, Table 3). The temperature response was lowest for the mesic conditions during which the CO_2 emissions peaked at 25°C and then dropped as temperatures increased. Note that peat moisture levels in the mesic treatment were slightly elevated in the 25°C treatment compared to the other temperatures possibly (moisture content were 435±38, 970±100, 471±42, 606±74.7 in the 20, 25, 30 and 35°C treatments,

434 respectively. Variation in peat moisture levels within the mesic treatment was not
435 significantly related to either CO_2 or CH_4 fluxes ($P > 0.05$) and addition peat moisture
436 as a covariate in the statistical models did not alter the temperature response of the
437 CO_2 or CH_4 fluxes.
438



439

440 Figure 3. Temperature response of (a) CO_2 fluxes and (b) CH_4 fluxes from the laboratory
441 surface peat incubations, combining data from vegetation types. Means and standard error

or the means are shown; lines are significant best fit regression models, of which exponential models were used for the Q_{10} calculations in Table 3.

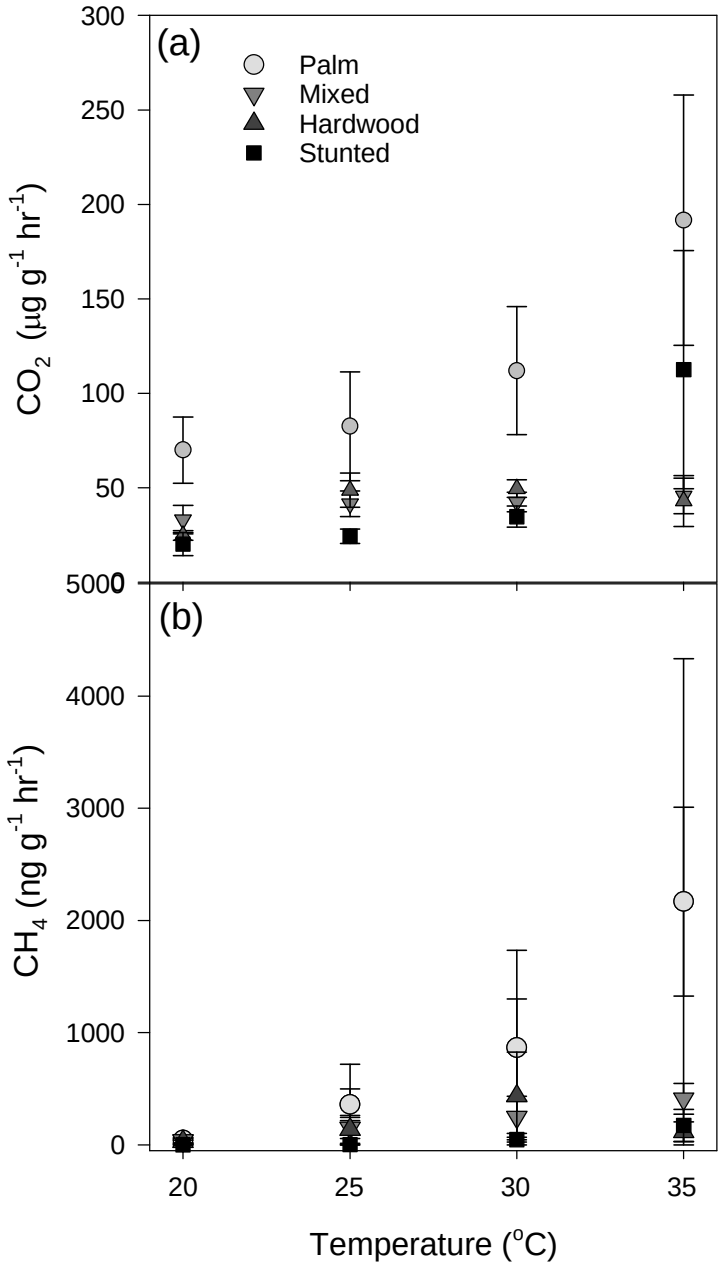


Figure 4. Temperature response of (a) CO_2 fluxes from surface peat under flooded oxic conditions and (b) anaerobic CH_4 fluxes from laboratory incubations of peat from different

449 forest types. Mean and standard error of the mean are shown. n = 6 for palm forest, n = 9 for
450 mixed forest, n = 3 for hardwood forest and n =3 for student forest.
451
452
453
454
455 Table 3. Q_{10} (± SE) for the significant exponential models shown in Figure 3. Q_{10} is
456 calculated using $Q_{10}=e^{(10*k)}$.
457

	CO_2			CH_4		
Moisture regime	**Best fit model**	**Q_{10}**		**Best fit model**	**Q_{10}**	
Mesic	Cubic polynomial	n/a		Exponential growth*	2.7	1.1
Flooded oxic	Exponential growth	1.8	± 1.0	ns	n/a	
Anaerobic	Exponential growth	1.3	± 1.0	Exponential growth	6.8	± 1.0

458 *Note that this relationship corresponds to CH_4 uptake, i.e. increasing negative fluxes with
459 higher temperature (Figure 3 b).
460
461 CH_4 emissions from peat were greatest under anaerobic conditions followed by the
462 oxic flooded and mesic treatment (Fig. 2b, Table 2). Palm, mixed and hardwood
463 forest had higher CH_4 emissions under anaerobic conditions, while peat from stunted
464 forest sites was less responsive to the moisture treatments as indicated by the
465 significant interaction between forest type and moisture treatment (Fig. 2b, Table 2).
466 CH_4 was also emitted under flooded oxic conditions, but emissions dropped
467 substantially under this treatment in the peat from the palm, mixed and hardwood
468 forest sites. The net CH_4 uptake under mesic conditions was highest at the mixed
469 forest sites.

Anaerobic CH_4 production increased exponentially with temperature (Q_{10} > 6; Fig. 3b, Table 3), while temperature responses of CH_4 fluxes were weaker in the flooded oxic and mesic redox treatments, resulting in a significant Moisture×Temperature interaction (Table 2). This might be due to increased CH_4 consumption rates under oxic conditions as indicated by the negative CH_4 flux from the mesic samples, particularly at higher temperatures (Fig. 3b). The temperature response of CH_4 fluxes was most pronounced in peat from palm forests (Fig. 4b, Table 2).

Discussion

The Q_{10} values for CO_2 emissions were in the lower range of those previously reported for aerobic decomposition in peats from higher latitude wetlands (range of Q_{10} 1–16; Moore and Dalva 1993; McKenzie et al., 1998; Inglett et al., 2012) and anaerobic CO_2 production found in subtropical peat (range 1.3–2.5; Inglett et al., 2012). As expected, the temperature response of CO_2 production was highest (Q_{10} of 1.8) when neither O_2 nor water availability limited decomposition, showing that both anoxia and moisture deficiency limit the temperature response of CO_2 production. The low temperature response of CO_2 emissions from tropical peats is an important finding as it indicates that the temperature response of heterotrophic decomposition in tropical wetland systems may be lower than in higher latitudes. This suggests that tropical systems may be less sensitive to rising temperatures with regards to CO_2 emission compared to colder wetlands. Similar low temperature responses of CO_2 production by microbial communities has been reported from well drained tropical lowland forest soils in Peru (Nottingham et al., 2015) and in Hawaii (Selmantz et al., 2016). We speculate that the lower temperature response of the

heterotrophic microbial community is linked to adaptations to the prevailing high temperatures in tropical environments. Indeed, lower temperature responses for tropical microbial communities have been linked to the generally high optimum temperatures (ca 25°C of microbial biomass, CO_2 production and enzyme activities (Menichetti et al., 2015).

The high CO_2 emissions in both oxic treatments (mesic and flooded oxygenated) (Fig 2a) suggest that, in addition to water table drawdown (resulting in mesic surface condition), oxygen inputs with rainfall and from roots (Armstrong et al., 2006) may be strong drivers of aerobic decomposition processes below the water table. For example, the high *in situ* CO_2 emissions from tropical peatlands during periods of high rainfall (Wright et al., 2013) could be linked to inputs of oxygen via rainwater boosting heterotrophic respiration. With regards to the high CO_2 production from palm forest peat, relative to the other forest types, across all the moisture treatments, this may be due to greater amounts of higher quality – as indicated by the low C:N ratio in the peat solution (Table 1) – and quantity of substrates driven by the large total plant biomass at palm sites (Sjögersten et al., 2011). The strong difference in CO_2 emissions among vegetation types (i.e. higher at palm sites, Table 2 and Fig 4) implicates the dominant vegetation as an important driver of microbial processes. Indeed, at our study site, specific microbial assemblages have been found to be associated with different dominate vegetation types (Troxler et al., 2012) indicating microbial adaptations to the prevailing litter inputs (Austin and Vivanco 2008; Kaiser et al., 2014).

519 In contrast to the CO_2 emissions, anaerobic CH_4 production was highly temperature
520 sensitive (Q_{10} = 6.1) and in the upper range of Q_{10} values reported for higher latitude
521 peatlands (2 to 16; Dunfield et al., 1993; Turetsky et al., 2014). This clearly shows
522 that the methanogenic microbial communities in tropical peatlands does not have
523 lower temperature responses than those found in regions with colder climates.
524 Furthermore, it indicates the potential for strong increases in CH_4 emissions from
525 tropical wetlands in response to the higher temperatures associated with climate
526 change. Given the current high CH_4 emissions from tropical wetlands (Melton et al.,
527 2013) driven by large inputs of labile substrate from the vegetation (Sjögersten et
528 al., 2014; Hoyos-Santillan et al., 2015 and 2016), such increases would have the
529 potential to create strong positive feedbacks on the climate system. Furthermore,
530 anaerobic CH_4 fluxes increased to a much greater extent than net CH_4 uptake from
531 the mesic treatment (Q_{10} = 2.7) as temperatures increased suggesting that
532 increasing CH_4 production in response to higher temperatures would not be abated
533 by increases in CH_4 uptake. Similar contrasting temperature responses of CH_4
534 production and consumption have been shown for a range of higher latitude
535 peatlands (Turetsky et al., 2014). The net impact on CH_4 fluxes in the field will be
536 modulated by the position of the water table and hence the zone in which CH_4
537 uptake occurs (Jauhiainen et al., 2005). Indeed, during periods of drought and low
538 water tables the peatland system investigated here can act as a CH_4 sink (Wright et
539 al., 2013). Therefore, if climate change results in lower water tables due to increased
540 evapotranspiration and/or reduced precipitation (IPCC 2013), conditions during
541 which CH_4 uptake dominates may persist for longer time periods. Furthermore, the
542 lower CH_4 production in the flooded oxic moisture treatment (Fig. 2b) indicates that
543 high oxygen inputs (e.g. from rainfall or roots Hoyos-Santillán et al., 2016) can

reduce CH_4 emissions by more than half, even when the peat remains completely waterlogged.

The controls posed by forest type on both anaerobic CH_4 production and its temperature response, i.e. greatest at palm sites (Fig 4b, Table 2), may be driven by greater labile substrate availability at palm sites (Wright et al., 2011). Our findings of contrasting temperature responses of CH_4 emissions among forest types in the tropics mirrors findings in higher latitude systems, where nutrient status and vegetation litter inputs have been shown to alter the temperature response of CH_4 emissions (Turetsky et al., 2014). Together, these findings implicate substrate quality (governed by vegetation litter inputs) as a critical control of the temperature response of CH_4 emissions across different latitudes. However, our data does not support the notion of more recalcitrant substrates driving greater temperature responses in tropical peatlands as postulated by the carbon quality hypothesis. Indeed, the Q_{10} value of 1.8 that we found for CO_2 production under oxic flooded conditions (Table 3) is comparable for Q_{10} values for aerobic heterotrophic CO_2 productions reported across a wide range of ecosystems (Davidson et al., 2006). The differential temperature response of anaerobic CH_4 emissions among forest types indicates that climate warming impacts on emissions may differ substantially among areas covered by contrasting forest types, and also points towards the possibility of using vegetation type as a predictor for the responsiveness of CH_4 emissions of different wetland areas to climate warming.

When comparing the magnitude of the overall response of CO_2 and CH_4 fluxes to variation in soil moisture condition, temperature and forest type (significant or near

569 significant main effects Table 2) the shift from anaerobic to mesic conditions created
570 the greatest change in emissions (high CO_2 fluxes from mesic and flooded oxic
571 treatments and high CH_4 fluxes from the two flooded treatments; Fig. 2) as expected.
572 This compares to variation in field GHG emissions in response to fluctuating water
573 tables in tropical peatlands in SE Asia (Jauihianen et al., 2005; Couwenberg et al.,
574 2010). Under high emission condition (Fig 2 a and b) variation in forest type
575 substantially modified emission rates (CO_2 fluxes from palm forest were 2-3 times
576 higher than the other three forest types while CH_4 fluxes were ca. 4 times higher at
577 palm forests). The CO_2 and CH_4 fluxes were 3 and 8 times higher, respectively,
578 when comparing the 35 and 20 °C temperature treatment (flooded oxic and
579 anaerobic treatments CO_2 and CH_4 fluxes, respectively). Together these findings
580 suggests that GHG emissions from tropical peatlands are controlled by a range of
581 strongly interacting factors.
582
583 In this study we investigated the temperature response of GHG production under
584 controlled laboratory conditions to improve our understanding of the relative
585 importance of different peat properties and moisture conditions for the temperature
586 response of GHG fluxes from tropical peatlands as discussed above. However, the
587 laboratory incubations we used in this study does not account for several important
588 drivers of GHG emissions which may extert strong controls of GHG fluxes from
589 tropical peatlands. For example, it is likely that labile C and oxygen input from roots
590 into the peat matrix control variation in GHG emissions among different forest types
591 (Joabson et al., 1999, Strom et al., 2005, Hoyos-Santillán et al., 2016b).
592 Furthermore, in our study we did not consider peat physical properties which is
593 known to impact GHG fluxes as microagregates may maintain peat CH_4 production

also during periods of low water tables (Dunfield et al., 1997). In temperate soil systems processes of microbial acclimation/adaptation to elevated temperature have been shown to dampen temperature responses over time (Bradford et al., 2007; Kaiser et al., 2014). Such processes is important to consider in the context of our study as its short term nature does not allow us to evaluate what the long term *in situ* microbial responses to elevated peat temperatures, both with regards to activity levels and shifts in community composition, may be. Although, our findings cannot be used to quantify how *in situ* GHG fluxes will be affected by climate change, they suggest potential for strong temperature responses of GHG fluxes also in the tropics and the importance of exploring such temperature responses in the context of peat moisture conditions and forest type.

The greater temperature response of CH_4 fluxes than that of CO_2 fluxes suggests that climate warming may increase CH_4 emissions to a greater extent than CO_2 emissions under flooded conditions providing substrate does not limit production. Based on the temperature relationships shown here (Fig. 3), assuming no microbial acclimation/adaptation to higher temperatures and that increased air temperatures would result in parallel increases in surface peat temperatures, a 3 °C warming by 2100, as predicted under the RPC8.5 scenario (IPCC 2013), would generate a ca. 80 % increase in CH_4 emissions from these ecosystems. However, if water tables drop, as discussed above, temperature-driven increases in emissions will be strongly modulated, and potentially mitigated against, by shifts in the moisture regime as methane oxidation processes as well as CO_2 production under mesic peat conditions also respond strongly to increasing temperatures.

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