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

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Key words: Climate change, Carbon dioxide, Methane, Peatland, Moisture status, Temperature response, Tropical

24 **Abstract**

25 Climate warming is likely to increase carbon dioxide (CO₂) and methane (CH₄)
26 emissions from tropical wetlands by stimulating microbial activity, but the magnitude
27 of temperature response of these CO₂ and CH₄ emissions, as well as variation in
28 temperature response among forest types, is poorly understood. This limits the
29 accuracy of predictions of future ecosystem feedbacks on the climate system, which
30 is a serious knowledge gap as these tropical wetland ecosystems represent a very
31 large source of greenhouse gas emissions (e.g. two-thirds of CH₄ emissions from
32 natural wetlands are estimated to be from tropical systems). In this study, we
33 experimentally manipulated temperatures and moisture conditions in peat collected
34 from different forest types in lowland neotropical peatlands in Panama and measured
35 how this impacted *ex-situ* CO₂ and CH₄ emissions. The greatest temperature
36 response was found for anaerobic CH₄ production (Q₁₀ = 6.8), and CH₄ consumption
37 (mesic conditions, Q₁₀ = 2.7), while CO₂ production showed a weaker temperature
38 response (Q₁₀ < 2) across the three moisture treatments. The greatest temperature
39 response of CO₂ production was found under flooded oxic conditions. Net emissions
40 of CO₂ and CH₄ were greatest from palm forest under all moisture treatments.
41 Furthermore, the temperature response of CH₄ emissions differed among dominant
42 vegetation types with the strongest response at palm forest sites where fluxes
43 increased from 42 ± 25 to 2166 ± 842 ng CH₄ g⁻¹ h⁻¹ as temperatures were raised
44 from 20 to 35 °C. We conclude that CH₄ fluxes are likely to be more strongly
45 impacted by higher temperatures than CO₂ fluxes but that responses may differ
46 substantially among forest types. Such differences in temperature response among
47 forest types (e.g. palm vs evergreen broad leaved forest types) need to be

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

50

51 **Introduction**

52 Global atmospheric methane (CH₄) and carbon dioxide (CO₂) concentrations are
53 increasing as a consequence of human activities such as fossil fuel burning and land
54 use change (IPCC 2013). The resulting climatic changes may further increase
55 greenhouse gas (GHG) emissions from terrestrial biomes, creating a positive
56 feedback loop resulting in additional climate warming; however, such feedbacks will
57 differ among ecosystems. Wetlands are important components of the global carbon
58 cycle and exchange large quantities of CH₄ and CO₂; indeed, they are recognised as
59 the largest individual natural source of atmospheric CH₄, a potent GHG (e.g.
60 Lelieveld et al. 1998; Bridgham et al., 2013; IPCC 2013).

61

62 Two thirds of wetland CH₄ emissions are estimated to originate from natural tropical
63 ecosystems in Southeast Asia, Africa and the Neotropics (Melton et al., 2013).
64 These wetlands are also large emitters of CO₂, estimated at 4540 ± 1480 Tg CO₂
65 year⁻¹ (Sjögersten et al., 2014). Furthermore, tropical peatlands acts as globally
66 important stores of carbon (C) (Page et al., 2011). The CO₂ and CH₄ emissions of
67 tropical peatlands are regulated by water table/redox state (Jauhiainen et al., 2005;
68 Hoyos-Santillán, 2014), quantity and quality of litter inputs (Wright et al., 2011;
69 Sjögersten et al., 2014; Hoyos-Santillán et al., 2015) and temperature (Hirano et al.,
70 2009). However, despite the significance of tropical wetlands in the global carbon
71 cycle, the temperature response of GHG emissions from tropical peatlands is largely
72 unknown (see Hirano et al., 2009), limiting our ability to predict climate change
73 responses of their CO₂ and CH₄ emissions despite their high emissive potential
74 (Bridgham et al., 2013).

75 This is a critical knowledge gap as we do not know if the wealth of data exploring
76 temperature responses of CH₄ and CO₂ fluxes from higher latitude ecosystems can
77 be transferred to tropical systems. It is for example plausible that tropical wetland
78 microbial communities are adapted to higher temperatures, rendering them less
79 sensitive to elevated temperatures than those in higher latitudes. Alternatively,
80 differences in soil organic matter chemistry between high and low latitude wetlands
81 may result in substantial differences in the temperature response of decomposition
82 and release of GHGs (Lloyd and Taylor, 1994; Bosatta and Ågren, 1999; Fierer et
83 al., 2005).

84

85 Tropical peatlands are under threat from climate change, which could substantially
86 affect their water balance, and resultant CO₂ and CH₄ emissions (Furukawa et al.,
87 2005; Li et al., 2007; Hooijer et al., 2010; Laiho, 2006; IPCC 2013). With regards to
88 climate change, current predictions indicate air temperatures in the neotropics and
89 Southeast Asia will be 3-4°C higher by 2100 and 5-7 °C higher by 2200 (IPCC,
90 2013). To date precipitation changes in the Amazon region have been associated
91 with wetter wet seasons and drier dry season but there are no strong overall trends
92 for the region (Almeida et al, 2017). In the future precipitation in the neotropics is
93 predicted to decrease by ca. 10% by 2100 (ca. 350 mm less per year) and by 20-
94 40% by 2200 (up to 1400 mm less per year) under the Intergovernmental Panel on
95 Climate Change (IPCC) scenario RCP 8.5 (IPCC, 2013) although, model predictions
96 of changes in precipitation patterns are more uncertain than the temperature
97 predictions and patterns varies between inland and coastal areas (Chao et al., 2008;
98 Oueslati et al., 2016). Together these changes are predicted to result in drier soils
99 (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 CO₂ losses to the atmosphere and reduced CH₄
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: CH₄ production in both subtropical and high
124 latitude wetlands appears to be more sensitive to temperature than either aerobic or

125 anaerobic CO₂ production (Dunfield et al., 1993; van Hulzen et al., 1999; Inglett et
126 al., 2012; Treat et al., 2014). When comparing the relative impact of temperature on
127 CH₄ production and oxidation, CH₄ oxidation does not appear to increase with
128 temperature as rapidly as CH₄ production (Dunfield et al., 1993; Inglett et al., 2012),
129 so higher temperatures may increase net CH₄ emissions. It is important to consider
130 temperature response in the context of moisture status as soils are predicted to
131 come drier in the tropics in response to climate change as there are strong links
132 between moisture conditions/water tables position and GHG emissions (Jauhiainen
133 et al., 2005; Couwenberg et al., 2010)..

134

135 The aim of this study is therefore to investigate how increasing peat temperatures
136 and changes in moisture levels of neotropical peatlands may interact to control *ex*
137 *situ* CO₂ and CH₄ emissions. To achieve this we ran controlled experiments with
138 peat from lowland neotropical peatlands to determine the temperature responses for
139 *ex situ* CO₂ and CH₄ fluxes under both aerobic and anaerobic conditions. The
140 experiment consisted of incubating peat at a range of temperatures and moisture
141 states. As these peatlands are heterogeneous with regards to vegetation and soil
142 nutrient status (Troxler et al., 2007; Sjogersten et al., 2011) we investigated the
143 impact of moisture and temperature treatments on CO₂ and CH₄ emissions from peat
144 samples extracted from four forest types commonly found in peatlands in the
145 neotropics (Phillips et al., 1997; Nahlik and Mitch 2011; Roucoux et al., 2013): palm,
146 mixed, hardwood and stunted forest.

147

148 **Methods**

149 *Study area*

150 The San San Pond Sak wetland complex is a 164 km² 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 km² 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) *Camposperma 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

175 extracellular enzymes involved in nutrient acquisition (Sjögersten et al., 2011;
176 Cheesman et al., 2012). Furthermore, *in situ* (i.e. measurement in the field) CO₂ and
177 CH₄ fluxes along this vegetation transect did not appear to reflect peat nutrient
178 availability (Wright *et al.*, 2013), while laboratory incubations (*ex situ*) of drained
179 surface peat samples show lower CO₂ production in substrates from the interior than
180 sites closer to the edge of the peatland (Sjögersten et al., 2011).

181

182 A weather station in the nearby town of Bocas del Toro, Isla Colon, ca. 10 km from the
183 peatland, shows the area has a mean annual temperature of 25.9°C with low intra-
184 annual variability, and recorded a mean annual precipitation of 3092 mm between
185 2003 and 2011 (Hoyos- Santillán et al., 2015). Rainfall is continuous throughout the
186 year with no pronounced dry season, although there are two distinct periods of lower
187 rainfall (February–March and September–October). Water tables in these peatlands
188 are dynamic and mainly fluctuate around ± 0.2 m from the surface, with water tables
189 increasing rapidly after intense rainfall events and dropping to or below the surface in
190 between rainfall events (Wright et al., 2013; S. Sjögersten, pers. obs.). During
191 occasional, prolonged dry (i.e. no rainfall) periods, the water table can drop as low as
192 -40 cm (Hoyos-Santillán 2014). Conversely, high rainfall events can cause the water
193 tables to rise above the peat surface (normally no more than ca. 10-20 cm). Mean peat
194 temperature 10 cm below the surface is ca. 25°C and shows little intra-annual variation
195 (Wright *et al.*, 2013).

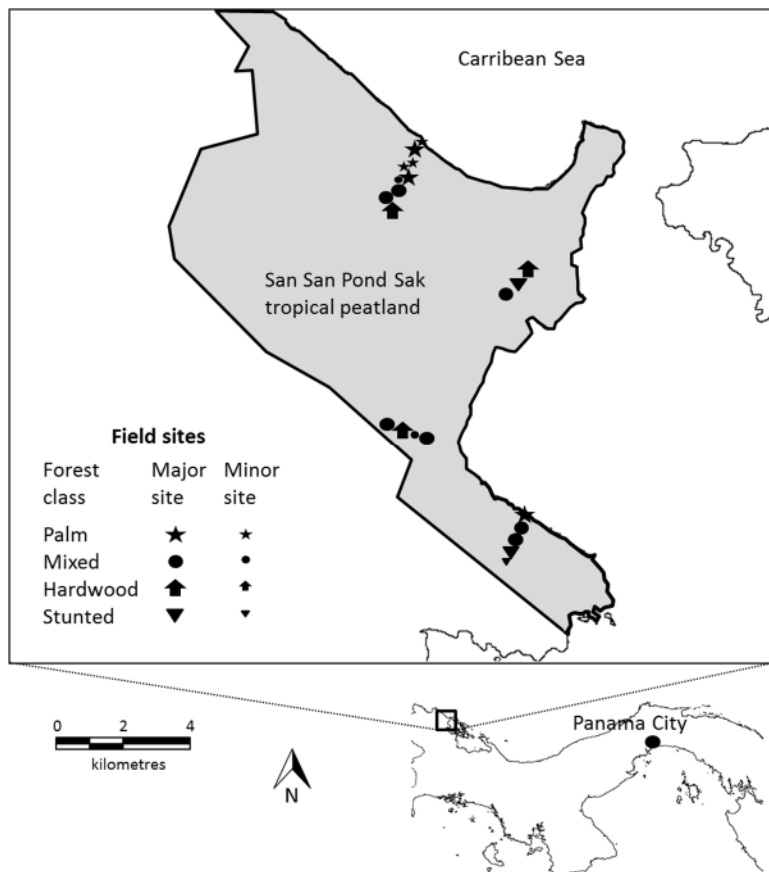
196

197 *Field sampling strategy*

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

200 case there was evidence of vegetation transition from the coast or river inlets towards
201 the interior of the peatland. Along these transects we collected peat samples for the
202 incubation study from palm forest (n=6 sites), mixed forest (n=9), hardwood forest
203 (n=3) and stunted forest (n=3), i.e. 21 sites in total. More detailed description of these
204 four forest types are in Sjögersten et al. (2011). Note that not all forest types occurred
205 along all transects. At a subset of sites denoted 'major sites' (Fig. 1), we carried out a
206 more detailed site characterisation including *in situ* CO₂ and CH₄ surface exchange
207 measurements to serve as background data for the incubation study.

208



209

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

212

213 *Collection and analysis of field gas samples*

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

219

220 As part of the site characterisation the *in situ* net exchange surface fluxes of CO₂ and
221 CH₄ were determined at the major sites; however, as gas sampling was carried out at
222 only one time point, these data only give a snapshot of *in situ* fluxes and should be
223 interpreted carefully. Gas samples were collected from the four corners of the 5×5 m
224 plots using the closed static chamber technique (Denmead, 2008). Gas sampling was
225 made between 10 a.m. and 4 p.m. concurrently with other plot characterisation
226 measurements. The chamber volume was 9 dm³ and the exchange surface 0.07 m².
227 To avoid root and soil disturbance the chambers was sealed to the water logged peat
228 surface by gently placing them into the peat or floating them on the water surface when
229 the sampling location was flooded. Air samples were collected through a Suba-Seal®
230 valve (Sigma-Aldrich, St-Louis, USA) using a hypodermic needle and 20 mL a syringe.
231 Samples of 20 mL were collected after 1, 3, 5 and 7 min and injected into evacuated
232 12 mL Exetainer serum vials(Labco, Ceredigion, UK) giving a slight over-pressure in
233 the vial to allow for leak detection. Samples were collected by a team member reaching
234 over the sampling chamber from ca 1 m distance. There was no movement around
235 the chamber during the sampling period.

236

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

239 mm internal diameter); CO₂ concentration was determined by thermal conductivity and
240 CH₄ by flame ionisation. Fluxes of CO₂ and CH₄ were calculated using the ideal gas
241 law for sampling points which met the assumption of linear (or near linear) gas
242 accumulation during the closure period (Wright et al., 2013).

243

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

254

255 *Peat chemical characterisation*

256 The collected peat samples were analysed for total elements and extractable
257 nutrients. Peat samples were transported to the laboratory (approx. 4 h), stored at -
258 20°C and shipped frozen to the UK to avoid depletion of labile substrates during
259 storage. We acknowledge that the freezing may have impacted on activity of the
260 microbial community; however, comparisons of microbial enzyme activities in tropical
261 forest soils do not suggest that freezing has a negative impact on the activities of
262 enzymes involved in microbial C acquisition, compared to storage at room
263 temperature (Turner and Romero 2010). Prior to analysis, peats were thawed at 4°C.

264 After thawing, roots were removed by hand with tweezers prior to analysis but fine
265 roots inevitably remained in some samples. Moisture content was determined by
266 drying subsamples of peat at 105°C for 24 h. Peat pH and conductivity were
267 determined using a glass electrode and a portable conductivity meter (Hanna
268 Instruments), respectively, in a 1:2 ratio of fresh peat to deionized water.
269
270 Dissolved organic C and nitrogen (N) fractions were extracted by shaking 40 g of
271 fresh soil in 75 mL of 0.5 M K₂SO₄ for 1 h. Extracts were centrifuged (8000g, 15 min)
272 and dissolved C and N were determined after a five-fold dilution by automated
273 combustion and gas chromatography on a TOC-VCSH analyzer (Shimadzu UK Ltd,
274 Milton Keynes, UK), coupled with a total N measuring unit (TNM-1, Shimadzu UK
275 Ltd, Milton Keynes, UK). The fulvic:humic acid ratio and the related degree of
276 humification in dissolved organic matter were estimated by spectrophotometric
277 analysis (Grayson and Holden 2012). Porewater samples were passed through
278 cellulose filters (Whatman Grade 1, 11 µm) and absorbance was measured at 465
279 and 665 nm (U-2010, Hitachi UV-VIS Spectrophotometer). The absorbance values
280 were then used to estimate the E₄₆₅/E₆₆₅ index (Uyguner and Bekbolet 2005) where a
281 greater ratio indicates more labile constituents. Ammonium in the K₂SO₄ (see above)
282 extracts was determined by colorimetry at 635 nm following reaction with phenol and
283 hypochlorite. Readily-exchangeable phosphate was determined by extraction with
284 anion exchange membranes (AEM) using a method based on that described by
285 Myers et al. (1999). Peat (20 g fresh weight) was shaken for 24 h with 80 ml
286 deionized water and five anion-exchange resin strips (1 x 4 cm; manufactured by
287 BDH Prolabo and distributed by VWR International, Lutterworth, Leicestershire, UK).
288 The strips were rinsed in deionized water and the phosphate recovered by shaking

289 for 1 h in 50 ml of 0.25 M H₂SO₄. Multi-element analysis of diluted solutions was
290 undertaken by ICP-MS (Thermo-Fisher Scientific iCAP-Q; Thermo Fisher Scientific,
291 Bremen, Germany). The instrument was run using standard mode (STD) in which
292 the collision cell is evacuated. Samples were introduced from an autosampler (Cetac
293 ASX-520) incorporating an ASXpress™ rapid uptake module through a PEEK
294 nebulizer (Burgener Mira Mist). Internal standards were introduced to the sample
295 stream on a separate line via the ASXpress unit and included Ge (10 µg L⁻¹), Rh (10
296 µg L⁻¹) and Ir (5 µg L⁻¹) in 2% trace analysis grade (Fisher Scientific, UK) HNO₃.
297 External multi-element calibration standards (Claritas-PPT grade CLMS-2 from
298 SPEX Certiprep Inc., Metuchen, NJ, USA) included Ag, Al, As, Ba, Be, Cd, Ca, Co,
299 Cr, Cs, Cu, Fe, K, Li, Mg, Mn, Mo, Na, Ni, P, Pb, Rb, S, Se, Sr, Tl, U, V and Zn, in
300 the range 0 – 100 µg L⁻¹ (0, 20, 40, 100 µg L⁻¹). Phosphorus also utilized in-house
301 standard solutions (KH₂PO₄). In-sample switching was used to measure P in STD
302 mode. Sample processing was undertaken using Qtegra™ software (Thermo-Fisher
303 Scientific) utilizing external cross-calibration between pulse-counting and analogue
304 detector modes when required. Loss on ignition (LOI) was determined as mass loss
305 following ignition for 7 h at 550 °C (Heiri et al., 2001).

306

307 *Incubation procedures*

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

314 20, 25, 30 and 35°C (reflecting the *in situ* annual air temperature range incremented
315 by 5°C to reflect climate warming predictions IPCC (2014)). The assumption made
316 here are that peat temperatures will increase to the same extent as air temperatures.

317

318 For the incubation, 100 ml serum bottles were filled with 5 g of field moist peat from
319 each peat sample collected from the peat surface (0-10 cm). For the anaerobic
320 treatment 10 ml of deionised water was added to the peat and the peat water mixture
321 was bubbled with N₂ vigorously to create oxygen-free conditions and to fill the head
322 space with N₂ (Hoyos-Santillán et al., 2016). The bottles were then capped using
323 black butyl stoppers and crimped, and the bottles were placed in four different
324 incubators set at the required temperature. The peat mesocosms were then left in
325 the incubator for three weeks to allow the microbial communities to acclimatise, after
326 this time a 5 ml gas sample was taken from the bottle and analysed for CO₂ and CH₄
327 using a GC (see above) to assess anaerobic gas production. This sampling was
328 repeated after one week.

329

330 For the flooded oxygenated treatment the head space was aerated and then shaken
331 for ca 1 minute to encourage O₂ mixing. This procedure was repeated daily for a
332 week to stimulate aerobic heterotrophic activity while the bottles were kept in their
333 respective incubators (modified from Hoyos-Santillán et al. (2016)). At the end of the
334 week, aerobic CO₂ and CH₄ production rates were assessed. This was done by first
335 bubbling air with known CO₂ and CH₄ concentrations (127 ± 1.9 and 1.5 ± 0.1 ppm,
336 for CO₂ and CH₄, respectively) through the peat for 1 minute. After flushing, the
337 headspace bottles were capped using butyl stoppers. The bottles were immediately
338 returned to their incubators for ca. 1 hour (Dunfield et al., 1993; Inglett al., 2012)

339 after which a 5 ml gas sample was taken from each bottle for determination of CH₄
340 and CO₂. Gas fluxes were calculated using the concentration difference between the
341 initial head space concentrations compared to those after one hour's incubation.

342

343 The mesic moisture treatment involved incubation of the bottles at 30 °C to allow
344 moisture to evaporate from the bottles, reflecting natural evaporation conditions
345 during low rainfall periods. The evaporation rate differed among samples and, rather
346 than letting the peat dry for a set time, we regularly checked the peat moisture status
347 visually, and conditions were considered mesic when there was no 'free' water
348 visible in the bottles' peat but the peat was still moist. The gravimetric moisture
349 content used for the mesic incubations ranged between 300 and 800% (dry weight
350 basis), reflecting the high and variable water absorption capacity of the peat. After
351 mesic conditions were achieved, the bottles were covered in parafilm and placed
352 back in their respective temperature incubators for two weeks to equilibrate. CO₂ and
353 CH₄ production rates were assessed by bubbling air with known CO₂ and CH₄
354 concentrations following the same procedure as described in the section above.

355

356

357 *Data analysis*

358 At the end of the temperature incubations Q₁₀ values was calculated in the instances
359 when exponential growth models fitted the GHG flux data (Lloyd and Taylor 1994).

360 The Q₁₀ value describes the increase in respiration rates with a 10 °C increase in
361 temperature and was calculated using eq.1 with *k* being the rate constant

362

$$363 \quad Q_{10} = e^{10k}. \quad (1)$$

364

365 Analyses of variance on the impact of the treatments on GHG fluxes were performed
366 using the Residual Maximum Likelihood method (REML). We ran mixed linear
367 models to tease apart the impact of forest type, temperature and moisture regime on
368 the CO₂ and CH₄ fluxes. In the model forest type, temperature and moisture
369 treatment were used as fixed effects, and transect and site as random effects. The
370 CH₄ fluxes were log-transformed prior to analysis. Differences in site properties were
371 analysed using REML with forest type as fixed effect and site as random effect.

372

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

378

379 **Results**

380 *Site and chemical properties*

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

388

389 The palm sites had the greatest DON concentrations and subsequently the lowest
 390 C:N ratio in the porewater, while neither NH_4^+ nor resin P differed among forest
 391 types. At palm sites the low C:N ratio in the peat solution together with a high
 392 $E_{465}:E_{665}$ ratio suggest a large pool of less decomposed C in the dissolved fraction.

393

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

400

401 Table 1. Peat properties measure *in situ* or from peat samples collected from the peat
 402 surface in different forest types during the field campaign. Mean and standard error of the
 403 mean are shown. *** $P < 0.001$, * $P < 0.05$, $P < 0.1$. Note that some of the measurements were
 404 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^+ ($\mu\text{g N g}^{-1}$)	40.9 ± 13.3	54.5 ± 10.9	25.8 ± 10.2	28.7 ± 6.2

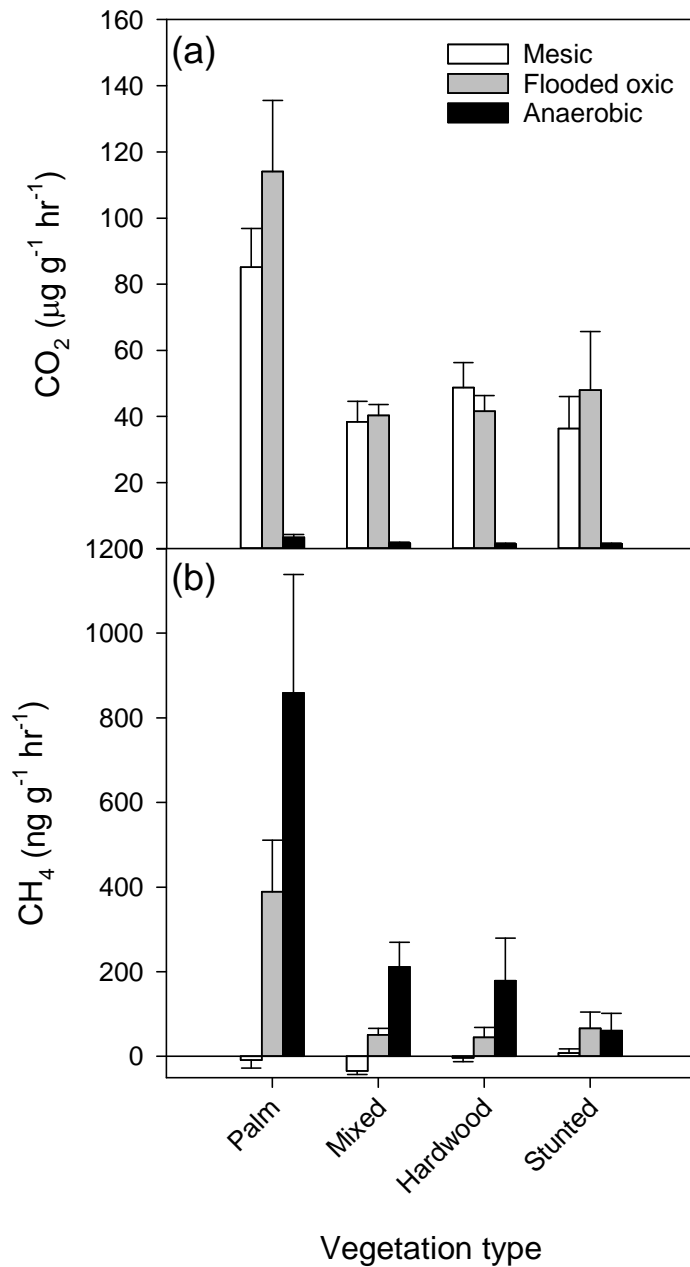
PO ₄ ³⁻ ($\mu\text{g P g}^{-1}$)	0.9 \pm 0.4	3.9 \pm 1.9	2.7 \pm 2.3	4.3 \pm 0.4
E ₄₆₅ /E ₆₆₅	5.2 \pm 1.8	3.7 \pm 1.2	4.7 \pm 1.9	2.3 \pm 0.5
C/N ^a ***	1.9 \pm 0.4	3.6 \pm 0.4	3.6 \pm 0.8	7.0 \pm 0.4
MAJOR SITES				
<i>In situ</i> CO ₂ (mg m ⁻² h ⁻¹)	369.4 \pm 57.9	575 \pm 85	527 \pm 20	753.0 \pm 186.3
<i>In situ</i> CH ₄ (mg m ⁻² h ⁻¹)	1.3 \pm 0.5	1.3 \pm 1.2	20.0 \pm 17.1	32.0 \pm 23.7
T _{soil} (°C)	24.4 \pm 0.7	24.9 \pm 0.3	24.4 \pm 0.3	25.1 \pm 0.3
T _{air} (°C)	24.7 \pm 1.1	25.4 \pm 0.7	25.1 \pm 0.8	27.8 \pm 0.7
Standing water				
(% area)	90 \pm 5	50 \pm 13	70 \pm 17	70 \pm 7
Depth of surface water				
pools (cm)	12.4 \pm 1.9	13.3 \pm 3.9	18.2 \pm 6.3	8.1 \pm 0.6

^aElemental 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 CO₂
408 and CH₄ from the surface peat samples were found at palm sites (Fig. 2 a and b,
409 Table 2). For CH₄ 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) CO₂ and (b) CH₄ 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 CO₂ and CH₄ fluxes from the laboratory incubations. CO₂

418 and CH₄ fluxes were log-transformed to meet the normality assumption. Significant effects

419 are in bold.

VARIATE	FIXED	Wald					
	EFFECT	statistic	<i>n.d.f.</i> ^a	<i>F-value</i>	<i>d.d.f.</i> ^b	<i>P</i>	<i>SED</i>
<i>Log CO₂</i>							
	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
<i>Log CH₄</i>							
	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

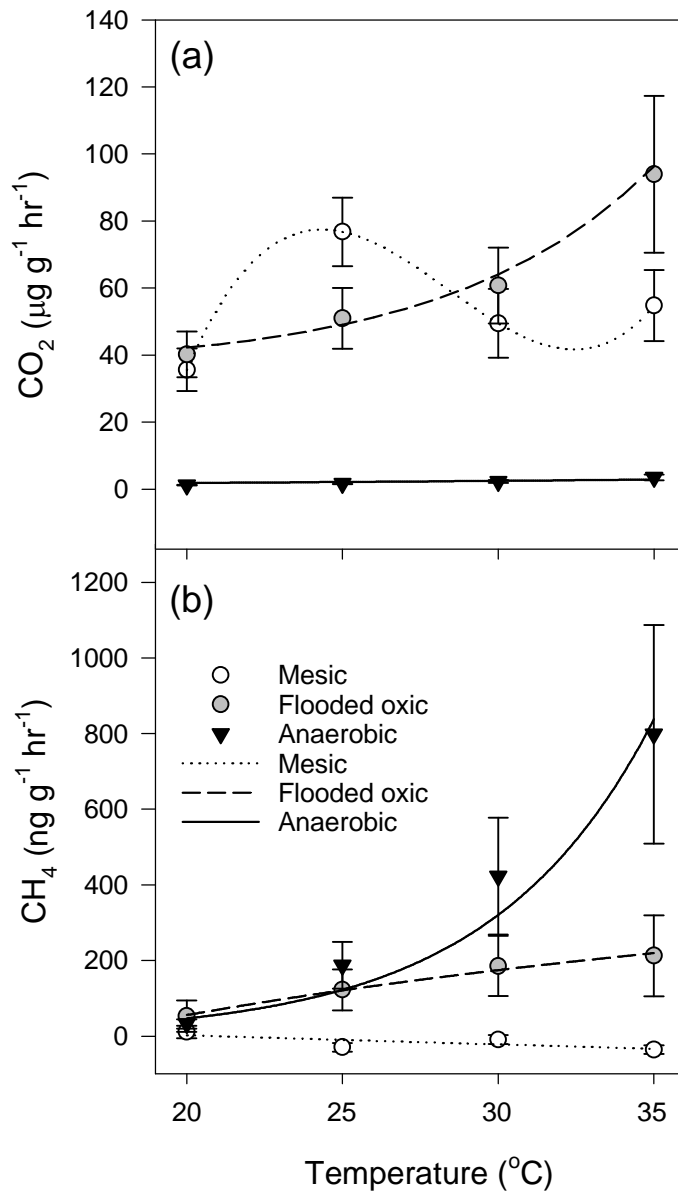
420 ^anumerator degrees of freedom

421 ^bdenominator degrees of freedom

422

423 The moisture treatments strongly influenced CO₂ production, with comparable fluxes
424 for the mesic and the oxic-flooded treatments, while fluxes were an order of
425 magnitude lower in the anaerobic treatment (Fig. 2a, Table 2). For all forest types,
426 CO₂ emissions increased exponentially with temperature in the flooded anaerobic
427 and flooded oxic incubation, with CO₂ emissions being most temperature sensitive
428 under the flooded oxic treatment with a Q₁₀ of 3.8 (Fig. 3a and 4a, Table 3). The
429 temperature response was lowest for the mesic conditions during which the CO₂
430 emissions peaked at 25°C and then dropped as temperatures increased. Note that
431 peat moisture levels in the mesic treatment were slightly elevated in the 25°C
432 treatment compared to the other temperatures possibly (moisture content were
433 435±38, 970±100, 471±42, 606±74.7 in the 20, 25, 30 and 35°C treatments,

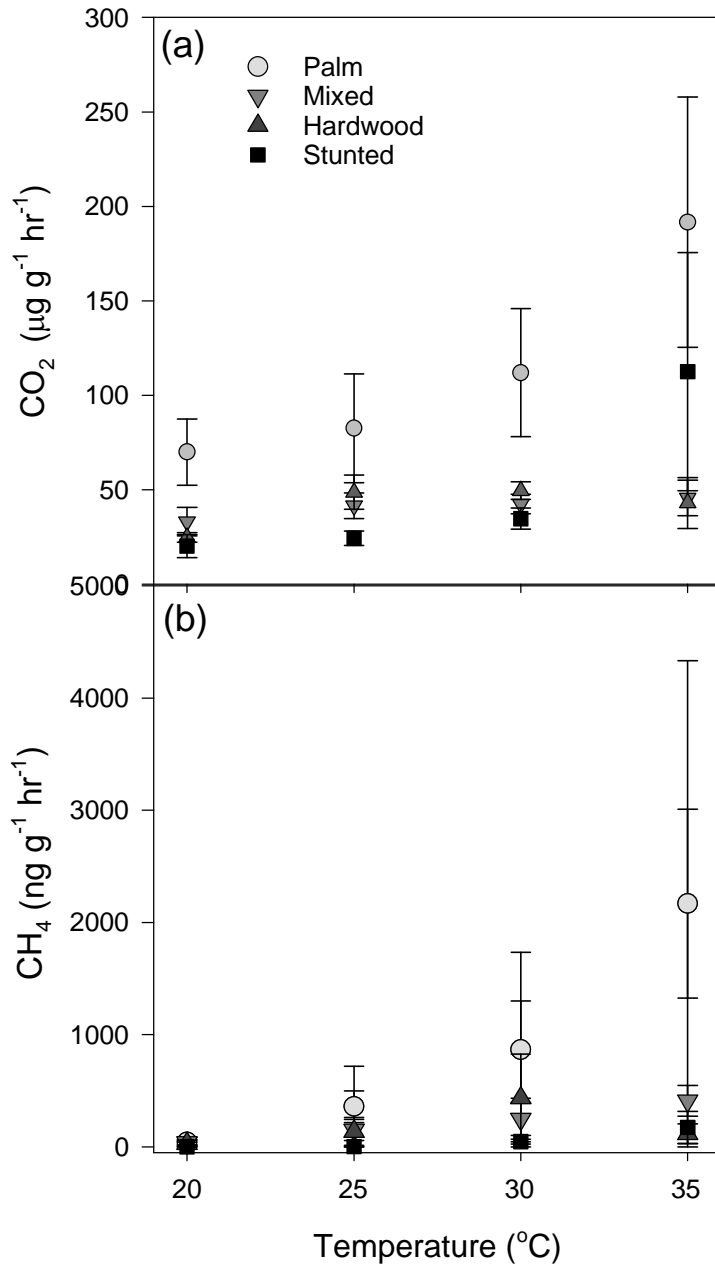
434 respectively. Variation in peat moisture levels within the mesic treatment was not
 435 significantly related to either CO₂ or CH₄ fluxes ($P > 0.05$) and addition peat moisture
 436 as a covariate in the statistical models did not alter the temperature response of the
 437 CO₂ or CH₄ fluxes.
 438



439
 440 Figure 3. Temperature response of (a) CO₂ fluxes and (b) CH₄ fluxes from the laboratory
 441 surface peat incubations, combining data from vegetation types. Means and standard error

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

444



445

446

447 Figure 4. Temperature response of (a) CO₂ fluxes from surface peat under flooded oxic
448 conditions and (b) anaerobic CH₄ 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} (\pm SE) for the significant exponential models shown in Figure 3. Q_{10} is
 456 calculated using $Q_{10}=e^{(10*k)}$.

457

Moisture regime	CO ₂		CH ₄	
	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 \pm 1.0	ns	n/a
Anaerobic	Exponential growth	1.3 \pm 1.0	Exponential growth	6.8 \pm 1.0

458 *Note that this relationship corresponds to CH₄ uptake, i.e. increasing negative fluxes with
 459 higher temperature (Figure 3 b).

460

461 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ uptake under mesic conditions was highest at the mixed
 469 forest sites.

470

471 Anaerobic CH₄ production increased exponentially with temperature ($Q_{10} > 6$; Fig.
472 3b, Table 3), while temperature responses of CH₄ fluxes were weaker in the flooded
473 oxic and mesic redox treatments, resulting in a significant Moisture \times Temperature
474 interaction (Table 2). This might be due to increased CH₄ consumption rates under
475 oxic conditions as indicated by the negative CH₄ flux from the mesic samples,
476 particularly at higher temperatures (Fig. 3b). The temperature response of CH₄
477 fluxes was most pronounced in peat from palm forests (Fig. 4b, Table 2).

478

479 **Discussion**

480 The Q_{10} values for CO₂ emissions were in the lower range of those previously
481 reported for aerobic decomposition in peats from higher latitude wetlands (range of
482 Q_{10} 1–16; Moore and Dalva 1993; McKenzie et al., 1998; Inglett et al., 2012) and
483 anaerobic CO₂ production found in subtropical peat (range 1.3–2.5; Inglett et al.,
484 2012). As expected, the temperature response of CO₂ production was highest (Q_{10}
485 of 1.8) when neither O₂ nor water availability limited decomposition, showing that
486 both anoxia and moisture deficiency limit the temperature response of CO₂
487 production. The low temperature response of CO₂ emissions from tropical peats is
488 an important finding as it indicates that the temperature response of heterotrophic
489 decomposition in tropical wetland systems may be lower than in higher latitudes.
490 This suggests that tropical systems may be less sensitive to rising temperatures with
491 regards to CO₂ emission compared to colder wetlands. Similar low temperature
492 responses of CO₂ production by microbial communities has been reported from well
493 drained tropical lowland forest soils in Peru (Nottingham et al., 2015) and in Hawaii
494 (Selmantz et al., 2016). We speculate that the lower temperature response of the

495 heterotrophic microbial community is linked to adaptations to the prevailing high
496 temperatures in tropical environments. Indeed, lower temperature responses for
497 tropical microbial communities have been linked to the generally high optimum
498 temperatures (ca 25°C of microbial biomass, CO₂ production and enzyme activities
499 (Menichetti et al., 2015).

500

501 The high CO₂ emissions in both oxic treatments (mesic and flooded oxygenated)
502 (Fig 2a) suggest that, in addition to water table drawdown (resulting in mesic surface
503 condition), oxygen inputs with rainfall and from roots (Armstrong et al., 2006) may be
504 strong drivers of aerobic decomposition processes below the water table. For
505 example, the high *in situ* CO₂ emissions from tropical peatlands during periods of
506 high rainfall (Wright et al., 2013) could be linked to inputs of oxygen via rainwater
507 boosting heterotrophic respiration. With regards to the high CO₂ production from
508 palm forest peat, relative to the other forest types, across all the moisture treatments,
509 this may be due to greater amounts of higher quality – as indicated by the low C:N
510 ratio in the peat solution (Table 1) – and quantity of substrates driven by the large
511 total plant biomass at palm sites (Sjögersten et al., 2011). The strong difference in
512 CO₂ emissions among vegetation types (i.e. higher at palm sites, Table 2 and Fig 4)
513 implicates the dominant vegetation as an important driver of microbial processes.
514 Indeed, at our study site, specific microbial assemblages have been found to be
515 associated with different dominate vegetation types (Troxler et al., 2012) indicating
516 microbial adaptations to the prevailing litter inputs (Austin and Vivanco 2008; Kaiser
517 et al., 2014).

518

519 In contrast to the CO₂ emissions, anaerobic CH₄ 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 CH₄ emissions from
525 tropical wetlands in response to the higher temperatures associated with climate
526 change. Given the current high CH₄ 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 CH₄ fluxes increased to a much greater extent than net CH₄ uptake from
531 the mesic treatment ($Q_{10} = 2.7$) as temperatures increased suggesting that
532 increasing CH₄ production in response to higher temperatures would not be abated
533 by increases in CH₄ uptake. Similar contrasting temperature responses of CH₄
534 production and consumption have been shown for a range of higher latitude
535 peatlands (Turetsky et al., 2014). The net impact on CH₄ fluxes in the field will be
536 modulated by the position of the water table and hence the zone in which CH₄
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 CH₄ 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 CH₄ uptake dominates may persist for longer time periods. Furthermore, the
542 lower CH₄ 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

544 reduce CH₄ emissions by more than half, even when the peat remains completely
545 waterlogged.

546

547 The controls posed by forest type on both anaerobic CH₄ production and its
548 temperature response, i.e. greatest at palm sites (Fig 4b, Table 2), may be driven by
549 greater labile substrate availability at palm sites (Wright et al., 2011). Our findings of
550 contrasting temperature responses of CH₄ emissions among forest types in the
551 tropics mirrors findings in higher latitude systems, where nutrient status and
552 vegetation litter inputs have been shown to alter the temperature response of CH₄
553 emissions (Turetsky et al., 2014). Together, these findings implicate substrate quality
554 (governed by vegetation litter inputs) as a critical control of the temperature response
555 of CH₄ emissions across different latitudes. However, our data does not support the
556 notion of more recalcitrant substrates driving greater temperature responses in
557 tropical peatlands as postulated by the carbon quality hypothesis. Indeed, the Q₁₀
558 value of 1.8 that we found for CO₂ production under oxic flooded conditions (Table 3)
559 is comparable for Q₁₀ values for aerobic heterotrophic CO₂ productions reported
560 across a wide range of ecosystems (Davidson et al., 2006). The differential
561 temperature response of anaerobic CH₄ emissions among forest types indicates that
562 climate warming impacts on emissions may differ substantially among areas covered
563 by contrasting forest types, and also points towards the possibility of using
564 vegetation type as a predictor for the responsiveness of CH₄ emissions of different
565 wetland areas to climate warming.

566

567 When comparing the magnitude of the overall response of CO₂ and CH₄ fluxes to
568 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 CO₂ fluxes from mesic and flooded oxic
571 treatments and high CH₄ 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 (Jauhiainen 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 (CO₂ fluxes from palm forest were 2-3 times
576 higher than the other three forest types while CH₄ fluxes were ca. 4 times higher at
577 palm forests). The CO₂ and CH₄ fluxes were 3 and 8 times higher, respectively,
578 when comparing the 35 and 20 °C temperature treatment (flooded oxic and
579 anaerobic treatments CO₂ and CH₄ 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 exert 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 CH₄ production

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

605

606 The greater temperature response of CH₄ fluxes than that of CO₂ fluxes suggests
607 that climate warming may increase CH₄ emissions to a greater extent than CO₂
608 emissions under flooded conditions providing substrate does not limit production.
609 Based on the temperature relationships shown here (Fig. 3), assuming no microbial
610 acclimation/adaptation to higher temperatures and that increased air temperatures
611 would result in parallel increases in surface peat temperatures, a 3 °C warming by
612 2100, as predicted under the RPC8.5 scenario (IPCC 2013), would generate a ca.
613 80 % increase in CH₄ emissions from these ecosystems. However, if water tables
614 drop, as discussed above, temperature-driven increases in emissions will be strongly
615 modulated, and potentially mitigated against, by shifts in the moisture regime as
616 methane oxidation processes as well as CO₂ production under mesic peat conditions
617 also respond strongly to increasing temperatures.

618

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626

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