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Interactions between labile carbon, temperature and land use regulate carbon dioxide and methane production in tropical peat

Authors: N. T. Girkin^{a*}, S. Dhandapani^{a,b,c,d}, S., Evers^{b,c}, N. Ostle^e, B. L. Turner^f, S. Sjögersten^a

- a. School of Biosciences, University of Nottingham, Nottingham, NG7 2RD, UK.
- b. School of Natural sciences and Psychology, Liverpool John Moores University, Liverpool, UK.
- c. TROCARI (Tropical Catchment Research Initiative), Malaysia
- d. Crops For the Future, Semenyih, Malaysia.
- e. Lancaster Environment Centre, University of Lancaster, LA1 4YQ, UK
- f. Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama

* Corresponding author: Nicholas.girkin@gmail.com

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Abstract

1 Tropical peatlands are a significant carbon store and contribute to global carbon dioxide (CO₂) and methane (CH₄)
2 emissions. Tropical peatlands are threatened by both land use and climate change, including 3 – 4°C predicted
3 warming by 2100 and the alteration of regional precipitation patterns. Plant communities in tropical peatlands can
4 regulate greenhouse gas (GHG) fluxes through labile carbon inputs, but the extent to which these inputs regulate
5 the temperature response of CO₂ and CH₄ production in tropical peat remains unclear. We conducted an anoxic
6 incubation experiment using three peat types derived from contrasting botanical origins to assess how carbon
7 addition affects the temperature response (Q₁₀) of CO₂ and CH₄ production. Peats from a forested peatland in
8 Panama and Malaysia, and a converted oil palm and pineapple intercropping system in Malaysia differed
9 significantly in terms of redox potential, total carbon and carbon: nitrogen ratios. The production of CO₂ and CH₄
10 varied significantly among peat types and increased with increasing temperature. Carbon addition further
11 increased gas fluxes, but did not influence the Q₁₀ for CO₂ or CH₄ production. These findings demonstrate that
12 CO₂ and CH₄ production in tropical peats are sensitive to warming, that potential emissions vary among
13 contrasting peat types, but that the effect of root inputs in altering Q₁₀ appears to be limited.

14 **Introduction**

15 Global atmospheric concentrations of carbon dioxide (CO₂) and methane (CH₄) are increasing, driven by
16 anthropogenic activities and accelerating climate change (IPCC, 2013). Tropical peatlands represent an important
17 component of the carbon cycle, being an important source of both CO₂ and CH₄ and a major store of carbon.
18 Indeed, tropical peatlands account for 11% of total peatland area but 15-19% of peat carbon stocks worldwide,
19 equivalent to approximately 104.7 Gt C, with significant deposits reported throughout the tropics in Central and
20 South America, Central Africa, and Southeast Asia (Dargie et al., 2017; Page et al., 2011).

21
22 Greenhouse gas (GHG) emissions from tropical peatlands are strongly regulated by peat temperature, with
23 increased temperature associated with greater fluxes *in situ* (Jauhiainen et al., 2014). This is particularly important
24 in the context of predicted climate change for tropical peatlands globally. Current estimates of air temperature
25 changes in the Neotropics and Southeast Asia are for 3 – 4°C warming by 2100 (IPCC, 2013). Previous *ex situ*
26 studies have demonstrated that the temperature response of tropical peats to warming is not linear (Sjögersten et
27 al., 2018), meaning that relatively small increases in temperature have the potential to dramatically increase
28 emissions.

29
30 In addition to changing regional climate patterns, many tropical peatlands are under significant threat from
31 changes in land use. In Southeast Asia, the drainage, deforestation and expansion of plantation agriculture has the
32 potential to significantly alter the balance of emissions from peatland sites (Hergoualc'h and Verchot, 2014).
33 Conversion to plantation agriculture has previously been shown to significantly alter organic matter properties
34 (Cooper et al., 2019; Tonks et al., 2017). In turn, this may affect the response of these ecosystems to environmental
35 change, including to elevated temperatures and altered patterns of precipitation. Differences in organic matter
36 properties between contrasting vegetation types have also been reported in Neotropical systems (Girkin et al.,
37 2019; Hoyos-Santillan et al., 2015; Upton et al., 2018).

38
39 Root exudates represent an important plant carbon input which, depending on their composition, can contribute
40 significantly to net greenhouse gas emissions in tropical peats even at relatively low addition rates (Girkin et al.,
41 2018a, 2018b). Root respiration, which includes microbial use of exudates, can be the dominant driver of CO₂
42 fluxes *in situ* in tropical peatlands (Girkin et al., 2018c; Melling et al., 2013). Emissions of both CO₂ and CH₄ are
43 also driven by the decomposition of peat organic matter, with the extent of production determined by substrate

44 quality (Bridgham and Richardson, 1992; Hoyos-Santillan et al., 2015). Under low oxygen to anoxic conditions
45 that can predominate in peatlands, methanogenic archaea produce CH₄ through the reduction of acetate
46 (acetoclastic methanogenesis), the reduction of CO₂ and H₂ (hydrogenotrophic methanogenesis), or the cleavage
47 of methylated organic compounds (Holmes et al., 2015; Kolton et al., 2019; Le Mer and Roger, 2001). These
48 pathways are strongly influenced by prevalent environmental conditions *in situ*, including substrate and nutrient
49 availability, microbial community structure, water table depth, and temperature (Couwenberg et al., 2009;
50 Gorham, 1991; Le Mer and Roger, 2001).

51

52 The temperature sensitivity of soil respiration under aerobic conditions increases with the recalcitrance of organic
53 matter due to the higher activation energies required (Fierer et al., 2005; Lloyd and Taylor, 1994). Tropical (and
54 some temperate) peats have been shown to have a lower carbohydrate content and a higher proportion of aromatic
55 compounds compared to boreal peatlands (Hodgkins et al., 2018), therefore requiring higher energy yield terminal
56 electron acceptors to drive decomposition, which are likely less available in the low oxygen to anaerobic
57 conditions of peatlands (Keiluweit et al., 2016). The degradation of root exuded labile carbon compounds, which
58 can include a range of organic acids, sugars and amino acids, are likely to therefore have a lower sensitivity than
59 other organic matter components, the oxidation of which may be coupled to lower yielding terminal electron
60 acceptors (Davidson and Janssens, 2006; Keiluweit et al., 2016). Previous *ex situ* studies of the response of tropical
61 peat have not accounted for the influence of continuous low input rates of labile carbon (Sjögersten et al., 2018),
62 for example low concentrations of glucose, a common component of plant root exudate profiles (Smith, 1976).

63

64 Developing an understanding of temperature sensitivity of peat and soils is important in accurately assessing
65 future changes in the global carbon cycle in response to rises in temperature. Strong responses of greenhouse gas
66 production to increased temperature, and greater temperature sensitivity with increasing carbon substrate
67 recalcitrance are predicted by kinetic theory (Davidson and Janssens, 2006) and supported by some experimental
68 data (Conant et al., 2008). Decomposition of recalcitrant peatland carbon (particularly highly aromatic tropical
69 peat) may also be subject to thermodynamic limitation due to a shortage of terminal electron acceptors (Beer and
70 Blodau, 2007). Previous studies in mineral soils have reported an increase in the temperature sensitivity of aerobic
71 respiration on the addition of labile carbon (Gershenson et al., 2009; Nianpeng et al., 2013; Song et al., 2010),
72 most likely because microbial respiration in these soils was limited by carbon lability. High latitude peatlands
73 have previously been demonstrated to have high temperature sensitivity for CH₄ production (Bergman et al.,

74 1998). Increased temperatures have also been shown to result in substantial changes in microbial community
75 structure, possibly resulting in changes in methanogenic pathways (Lupascu et al., 2012). However, it is unclear
76 how this applies in tropical peatlands with high organic matter content (> 60%), but a high aromatic content, and
77 how responses vary between dominant vegetation types with different litter inputs (Upton et al., 2018, Cooper et
78 al., 2019), and under waterlogged and low oxygen conditions (Wright et al., 2013).

79

80 In this study, we assessed the response of CO₂ and CH₄ production of three tropical peats to elevated temperatures
81 and carbon addition, in the form of glucose. Based on the strong role of organic matter quality in regulating
82 greenhouse gas emissions we predicted that i) basal CO₂ and CH₄ production would differ among peat types, and
83 ii) temperature sensitivity would differ among peat types. As labile carbon can be rapidly depleted during
84 decomposition, and peat is predominantly composed of recalcitrant biomolecules, we also hypothesised that iii)
85 glucose addition would increase Q₁₀ for all peat types due to waterlogged, low oxygen conditions, and strong
86 substrate limitation resulting in thermodynamic limitation.

87

88 **Methods**

89 **Study sites**

90 This study was conducted using peat samples collected from sites in Panama and Malaysia between May 2016
91 and July 2017. Panamanian peat samples were collected in May 2016 from the 80 km² ombrotrophic peatland at
92 Changuinola, part of the San San Pond Sak freshwater and marine wetland located in Bocas del Toro province
93 (Figure 1a). The site was located approximately 600 m from the coast (09° 18' 13.00"N, 82° 21' 13.80"W) in a
94 mixed forest stand. The central peat dome is approximately 8 m deep and was initiated approximately 4000–5000
95 years ago (Phillips et al., 1997). The site features seven distinct plant phasic communities beginning with a
96 *Rhizophora mangle* mangrove swamp on the coastal margins, which is succeeded by palm swamp dominated by
97 *Raphia taedigera*, a mixed forest stand, a monodominant *Camposperma panamensis* forest stand, and a *Myrica-*
98 *Cyrtilla* bog-plain (Phillips et al., 1997). This vegetation gradient is matched by a pronounced decrease in nutrient
99 availability, particularly phosphorus (Cheesman et al., 2012; Sjögersten et al., 2011). The microbial community
100 throughout the peatland is dominated by *Acidobacteria*, with precise community composition clustered by
101 phosphorus availability (Troxler et al., 2012). Sampling was conducted in the mixed forest stand dominated by *C.*
102 *panamensis*, *R. taedigera*, and *Symphonia globulifera*.

103

104 The Malaysian forested peatland site is located in Terengganu state, in northeastern Peninsular Malaysia. The site
105 is approximately 8.42 km² and, and is 11.3 km from the coast, located in Kampung Mat Jintan (5°25'16.2"N,
106 102°55'46.2"E) in the boundary between Kula Nerus and Setiu districts (Figure 1b). The forest vegetation
107 comprised trees that were up to 40 m tall and with a diameter-at-breast-height (DBH) of 40 - 50 cm. Common
108 species included *Antisoptera* sp., *Shorea* sp., *Calophyllum sclerophyllum*, *Calophyllum* sp., *Blumeodendron*
109 *tokbrai*, *Durio carinatus*, *Gonostylus bancanus*, *Elateriospermum tapos*, and *Syzygium* sp. Both *Macaranga*
110 *pruinosa* and *M. gigantean* were present on the forest edges. *Pandanus helicopus* and *Nepenthes ampullaria* were
111 common understory species. Peat depth was approximately 2 m.

112

113 The Malaysian oil palm and pineapple intercropping site is located in Selangor State, approximately 14 km from
114 the west coast of Peninsular Malaysia (3°25'20.6"N, 101°19'56.6"E). The site is surrounded by recently planted
115 (2014) 2nd generation oil palm mono-cropping and is drained by two drainage ditches along the borders at opposite
116 sides of the site (Dhandapani et al., 2019b). During sampling the site was not flooded, although the peat was moist,
117 with high gravimetric moisture content.

118

119 At each site, three 10 × 10 × 10 cm bulk peat samples were collected using a hand trowel, excluding any recent
120 surface litter. Samples were shipped to the University of Nottingham and kept at 4°C for one month prior to
121 analysis.

122

123 **Experimental design**

124 Peat samples (20 g) from each site, were placed in stainless steel chambers (0.6 dm³) with polypropylene lids and
125 a silicon ring seal. Two holes were drilled in the lids and fitted with three-way stopcock valves silicon-sealed in
126 place. The gas-tightness of chambers was tested by closing all valves and submersing in water, and through
127 flushing the chamber with N₂ and observing for changes in headspace CO₂ and CH₄ concentrations over time prior
128 to adding peat. Each peat sample was mixed with 20 ml of deionised water to mimic *in situ* flooded conditions.
129 Chambers were flushed with N₂ to displace accumulated headspace gases for two minutes and were placed in
130 incubators set at 25, 30 and 35°C for acclimation of microbial communities for seven weeks following sample
131 storage and preparation. temperatures were selected to represent broad scale warming of peatlands in the Central
132 Americas and in Southeast Asia (IPCC, 2013). Chambers were subsequently opened to displace accumulated

133 headspace gases, flushed again with N₂ for two minutes and sealed. Overall conditions most closely match the
134 flooded oxic conditions outlined in Sjogersten et al. (2018), namely, water saturated with low oxygen, but not
135 entirely anoxic, mostly closely resembling peat *in situ* conditions in the 0 – 10 cm horizon (Girkin, 2018; Hoyos-
136 Santillan et al., 2016).

137

138 Glucose solutions were prepared for an input rate equivalent to 0.1 mg C g⁻¹ soil per day. This addition rate
139 represents a relatively low daily addition rate for plant carbon inputs (Grayston and Campbell, 1996). Solutions
140 were adjusted to a pH of 5.5 using HCl sterilised, and stored at 4°C prior to addition. Oxygen was not removed
141 from exudate solutions prior to addition to better mimic the combined inputs of oxygen and labile carbon at the
142 root-peat interface (Hoyos-Santillan et al., 2016).

143

144 During headspace sampling, chambers were connect to a Los Gatos ultraportable greenhouse gas analyser (San
145 Jose, California), sampling at 0.5 Hz. Fluxes were subsequently measured over 90 seconds, with measurement
146 occurring immediately prior to glucose addition, and at 6, 24, 72 and 120 hours following the first addition.
147 Glucose (or deionised water) was added to each chamber at the rate of 1 ml per day. Gas concentrations were
148 adjusted for incubation temperature (25 – 35°C), as well tube and optical bench volume, according to the ideal
149 gas law. The rate of potential gas production, expressed as µg CO₂ g⁻¹ hr⁻¹ or µg CH₄ g⁻¹ hr⁻¹, was calculated
150 assuming a linear accumulation rate of gases in the headspace (Hogg et al., 1992).

151

152 Q₁₀, describing the temperature sensitivity of CO₂ and CH₄ production was calculated as:

$$153 \quad Q_{10} = 10^{(m \times 10)}$$

154 Where m is the regression slope of a log₁₀ CO₂ or CH₄ flux versus temperature plot.

155

156 **Peat characterisation**

157 Sub-samples from each site were used to characterise peat physiochemical properties. Gravimetric water content
158 was determined by analysis of the mass of water lost from 10 g fresh peat oven dried at 105°C for 24 hours.
159 Organic matter content was determined as the mass lost after ignition for 7 hours at 550°C. Total carbon (C) and
160 total nitrogen (N) content were determined from 0.2 g of dry, homogenised peat combusted using a total element
161 analyser (Flash EA 1112, CE Instruments, Wigan, UK). pH and redox potential were measured using a Hanna

162 209 meter coupled with pH and redox probes following one week acclimation but prior to beginning the
163 experiment. After measurement, chambers were flushed with N₂ and resealed.

164

165 **Statistical analysis**

166 Differences in CO₂ and CH₄ production and Q_{10S} were tested using the restricted maximum likelihood method
167 (REML), including site, temperature and presence/absence of glucose as fixed effects and sample replicate as a
168 random effect. CO₂ and CH₄ fluxes were log-transformed to meet test assumptions. Significance was assessed at
169 $p < 0.05$. All statistical analyses were conducted using Genstat v17.

170

171 **Results**

172 **Peat biochemical properties**

173 Peats were acidic ($pH < 5$), with high gravimetric moisture and organic matter contents. These properties were
174 not significantly different among peat types ($p > 0.05$). There was, however, a significant difference in redox
175 potential among sites ($p = 0.003$), with substantially lower redox potential in the Malaysian primary forest peats
176 compared to the Panamanian forest or intercropping site (Table 1). Total carbon was also significantly different
177 among sites ($p = 0.021$), and was greatest in pineapple intercropping sites. Total nitrogen did not differ
178 significantly among peat types ($p = 0.134$). C:N was significantly different among peat types ($p = 0.003$), and was
179 lowest in Panamanian forest peat but broadly comparable between Malaysian peats.

180

181 **Basal peat CO₂ and CH₄ production**

182 Mean basal CO₂ production varied between 69.0 – 77.7 $\mu\text{g CO}_2 \text{ g}^{-1} \text{ hr}^{-1}$ (Figure 2) but did not differ significantly
183 among peat types ($p = 0.151$). CH₄ production, however, varied significantly among peat types ($p = 0.02$). The
184 magnitude of CH₄ production compared to CO₂ was considerably lower, ranging from 0.06 – 0.08 $\mu\text{g CH}_4 \text{ g}^{-1} \text{ hr}^{-1}$.
185 Greatest CO₂ and CH₄ production occurred in Malaysian primary forest peats, with the most variable production
186 occurring in peats from the intercropping sites.

187

188 **Temperature and labile carbon sensitivity**

189 Temperature strongly influenced CO₂ fluxes, with increased production relative to basal rates for all sites at both
190 30°C and 35°C ($p < 0.001$). Glucose addition significantly increased CO₂ production ($p < 0.001$), with a significant

191 (p < 0.001) interaction between glucose addition and peat type, with a 178% increase in mean fluxes from
192 Malaysian primary forest peats, but only 34% for the Panamanian mixed forest peat.

193

194 CH₄ production increased significant with temperature (p < 0.001), with mean production increasing at both 30
195 and 35°C (Figure 3b,d,f). Glucose addition increased mean CH₄ fluxes by 11% (p = 0.034). There was also a
196 significant interaction between glucose addition and peat type (p < 0.001). In Malaysian forest and Panamanian
197 forest peats, there were 5 and 7% declines in mean CH₄ fluxes respectively on glucose addition, but there was a
198 56% increase in mean fluxes for the intercropping site.

199

200 There were no significant differences in temperature sensitivity (Q₁₀) of CO₂ or CH₄ production in the presence or
201 absence of glucose (p > 0.05, Table 2), between sites (p > 0.05), or in the interaction between treatment and sites
202 (p > 0.05).

203

204 **Discussion**

205 Warming promoted CO₂ and CH₄ production in all peat types, in common with previous studies in both temperate
206 and boreal (Dunfield et al., 1993, Inglett et al., 2012), and tropical peats (Sjögersten et al., 2018), as well as drained
207 lowland tropical soils from Peru (Nottingham et al., 2015). Previously, it has been proposed that heterotrophic
208 microbial communities in tropical peat respond weakly to warming primarily due to adaptation to high peat
209 temperatures, and because optimal temperature for respiration and methanogenesis is approximately 25°C (Kolton
210 et al., 2019; Menichetti et al., 2015; Sjögersten et al., 2018). Q₁₀ for both CO₂ (1.07 – 2.25) and CH₄ (1.10 – 2.39)
211 production were relatively low in our study, particularly when compared to 6.1 for anaerobic CH₄ production
212 reported for Panamanian peats (Sjögersten et al., 2018), although they are closer to the 2.2 – 3.7 reported from
213 studies of CH₄ production in Central Kalimantan, Indonesia (Brady, 1997; Hirano et al., 2009; Jauhiainen et al.,
214 2014), and 1.8 under flooded oxic conditions from Panamanian peats (Sjögersten et al., 2018). Previous studies
215 have reported a higher temperature sensitivity of CH₄ production than CO₂ production, although we found no
216 supporting evidence for this (Table 2) (Sjögersten et al., 2018, and references therein). These results have clear
217 implications in assessing the impact of future environmental change on gaseous carbon emissions from tropical
218 peatlands: warming peat will result in increased CO₂ and CH₄ emissions from flooded, low oxygen peats.

219

220 Although there was no difference in basal CO₂ production (from unamended peats at 25°C), or in temperature
221 sensitivity among peat types, both CO₂ and CH₄ fluxes varied significantly among sites across the three
222 temperatures. While organic matter content was similar among peat types, there were significant differences in
223 total carbon and C:N, likely reflecting contrasting aboveground vegetation and management practices. Previous
224 work in Malaysia (Tonks et al., 2017, Cooper et al., 2019) and Panama (Hoyos-Santillan et al., 2015, Upton et al.,
225 2018, Girkin et al., 2019) has demonstrated substantial differences in organic matter properties between
226 contrasting plant functional types and land uses, driven by differences in plant litter inputs and decomposition
227 rates. While various studies have assessed the impacts of land use change on organic matter properties (Cooper et
228 al., 2019; Könönen et al., 2018; Tonks et al., 2017), there is limited data available regarding the role of
229 intercropping systems on organic matter properties, meaning differences in responses cannot be readily ascribed
230 to contrasts in organic matter properties alone. The low CH₄ fluxes from the Malaysian intercropping system may
231 reflect significant depletion of labile carbon (Cooper et al., 2019), but could also be driven by a poorly adapted
232 methanogenic community, or a highly active methanotrophic community under partially aerobic conditions
233 (Andersen et al., 2013), as well as a redox potential c. 300 mV.

234

235 Changes in CO₂ and CH₄ production in response to glucose addition varied between peat types. At 35°C, CH₄
236 fluxes were greater from unamended Panamanian and Malaysian forest peats compared to carbon amended peats,
237 implying that labile carbon availability was not a limiting factor for production at this temperature. Similarly, CO₂
238 production in peat from the Panamanian primary forest was comparable at 30 – 35°C even with glucose
239 amendment implying an additional limiting factor other than temperature. Rates of CO₂ and CH₄ production in
240 tropical peatlands have previously been reported as lower at low fertility (Sjögersten et al., 2011), with litter
241 decomposition partially constrained by nutrient availability (Hoyos Santillan et al., 2018). The higher response of
242 the Malaysian intercropping peat to glucose addition may reflect the effects of management practices, specifically
243 fertiliser addition. This may substantially alter the temperature sensitivity of the system by alleviating inorganic
244 nitrogen (NH₄⁺/NO₂⁻/NO₃⁻) limitation (Liu et al., 2016; Wang et al., 2010), although in this study only total peat
245 nitrogen was assessed and this did not differ significantly between peat types. The lack of significant difference
246 in temperature sensitivity of CO₂ and CH₄ production with glucose addition may be because despite an increase
247 in carbon lability, unamended peats still had sufficient available carbon for respiration due to high organic matter
248 content (Dai et al., 2017). Alternatively, the system is thermodynamically limited due to a shortage of high energy
249 terminal electron acceptors necessary for the decomposition of recalcitrant aromatic carbon which is likely under

250 the low oxygen conditions (Hodgkins et al., 2018; Kolton et al., 2019), and with the relatively low concentration
251 glucose additions being rapidly consumed (Girkin et al., 2018a).

252

253 Fully understanding the impact of increased temperature on fluxes *in situ* is more complex due to the additional
254 regulatory roles of microtopography (Jauhiainen et al., 2005), water table changes (Wright et al., 2013), plant
255 inputs of oxygen (Hoyos-Santillan et al., 2016), and small scale heterogeneity of peat organic matter properties
256 (Girkin et al., 2019). In temperate peatlands, vegetation cover has been shown to also have a significant impact
257 on the temperature sensitivity of GHG production (Leroy et al., 2017). Increasing atmospheric CO₂ has been found
258 to increase rates of root exudation in wetland ecosystems (Sánchez-Carrillo et al., 2018) and increases in
259 temperature have also been reported to enhance rates of root exudation in some tree species (Uselman et al., 2000),
260 and alter the composition of exudate profiles (Badri and Vivanco, 2009; Vančura, 1967), both known to be critical
261 regulators of GHG emissions and peat properties (Girkin et al., 2018a & 2018b). As a consequence, the true
262 response of *in situ* net emissions of GHGs will comprise components driven by both the temperature sensitivity
263 of the peat itself, and any changes in root inputs.

264

265 Taken together, our results demonstrate that increased temperatures will substantially increase CO₂ and CH₄
266 production in tropical peats, regardless of current land cover. As a consequence, predicted warming for Central
267 America and Southeast Asia will be associated with substantial increases in gaseous carbon emissions (IPCC,
268 2013). However, the extent of this increase is likely to be lower than the response of higher latitude peatlands for
269 which higher Q₁₀s have been reported, including 2.4 – 5.8 for a *Sphagnum* peatland (Lupascu et al., 2012) and 2.5
270 – 35 (Bergman et al., 1998). Differences in fluxes between peat types are likely driven by contrasts in organic
271 matter properties (Cooper et al., 2019) and/or nutrient availability (Hoyos Santillan et al., 2018; Sjögersten et al.,
272 2011) and microbial community structure and function. Processes that alter organic matter properties, for example
273 the conversion of pristine forest to oil palm, or the use of intercropping species, will further affect fluxes. In
274 addition, our findings demonstrate that the temperature sensitivity of CO₂ and CH₄ production is not affected by
275 labile carbon addition. This is important because plants can input significant quantities of labile carbon which are
276 not accounted for in the majority of studies of GHG temperature sensitivity.

277

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286

287 **References**

- 288 Andersen, R., Chapman, S.J., Artz, R.R.E., 2013. Microbial communities in natural and disturbed peatlands: A
289 review. *Soil Biology & Biochemistry* 57, 979–994. doi:10.1016/j.soilbio.2012.10.003
- 290 Badri, D. V, Vivanco, J.M., 2009. Regulation and function of root exudates. *Plant Cell and Environment* 32, 666–
291 681. doi:DOI 10.1111/j.1365-3040.2009.01926.x
- 292 Beer, J., Blodau, C., 2007. Transport and thermodynamics constrain belowground carbon turnover in a northern
293 peatland. *Geochimica et Cosmochimica Acta*. doi:10.1016/j.gca.2007.03.010
- 294 Bergman, I., Svensson, B.H., Nilsson, M., 1998. Regulation of methane production in a swedish acid mire by pH,
295 temperature and substrate. *Soil Biology and Biochemistry*. doi:10.1016/S0038-0717(97)00181-8
- 296 Brady, M.A., 1997. Organic matter dynamics of coastal peat deposits in Sumatra, Indonesia. Department of
297 Forestry. University of British Columbia.
- 298 Bridgman, S.D., Richardson, C.J., 1992. Mechanisms controlling soil respiration (CO₂ and CH₄) in southern
299 peatlands. *Soil Biology & Biochemistry* 24, 1089–1099.
- 300 Cheesman, A.W., Turner, B.L., Reddy, K.R., 2012. Soil Phosphorus Forms along a Strong Nutrient Gradient in a
301 Tropical Ombrotrophic Wetland. *Soil Science Society of America Journal* 76, 1496–1506.
302 doi:10.2136/sssaj2011.0365
- 303 Conant, R.T., Drijber, R.A., Haddix, M.L., Parton, W.J., Paul, E.A., Plante, A.F., Six, J., Steinweg, M.J., 2008.
304 Sensitivity of organic matter decomposition to warming varies with its quality. *Global Change Biology*.
305 doi:10.1111/j.1365-2486.2008.01541.x
- 306 Cooper, H. V., Vane, C.H., Evers, S., Aplin, P., Girkin, N.T., Sjögersten, S., 2019. From peat swamp forest to oil
307 palm plantations: The stability of tropical peatland carbon. *Geoderma* 342, 109–117.

308 Couwenberg, J., Dommain, R., Joosten, H., 2009. Greenhouse gas fluxes from tropical peatlands in south-east
309 Asia. *Global Change Biology* 16, 1715–1732. doi:10.1111/j.1365-2486.2009.02016.x

310 Dai, S.S., Li, L.J., Ye, R., Zhu-Barker, X., Horwath, W.R., 2017. The temperature sensitivity of organic carbon
311 mineralization is affected by exogenous carbon inputs and soil organic carbon content. *European Journal of*
312 *Soil Biology*. doi:10.1016/j.ejsobi.2017.06.010

313 Dargie, G.C., Lewis, S.L., Lawson, I.T., Mitchard, E.T.A., Page, S.E., Bocko, Y.E., Ifo, S.A., 2017. Age, extent
314 and carbon storage of the central Congo Basin peatland complex. *Nature*. doi:10.1038/nature21048

315 Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to
316 climate change. *Nature*. doi:10.1038/nature04514

317 Dhandapani, S., Ritz, K., Evers, S., Sjögersten, S., 2019a. Environmental impacts as affected by different oil palm
318 cropping systems in tropical peatlands. *Agriculture, Ecosystems and Environment*.
319 doi:10.1016/j.agee.2019.02.012

320 Dhandapani, S., Ritz, K., Evers, S., Yule, C.M., Sjögersten, S., 2019b. Are secondary forests second-rate?
321 Comparing peatland greenhouse gas emissions, chemical and microbial community properties between
322 primary and secondary forests in Peninsular Malaysia. *Science of the Total Environment*.
323 doi:10.1016/j.scitotenv.2018.11.046

324 Fierer, N., Craine, J.M., Mclauchlan, K., Schimel, J.P., 2005. Litter quality and the temperature sensitivity of
325 decomposition. *Ecology*. doi:10.1890/04-1254

326 Gershenson, A., Bader, N.E., Cheng, W., 2009. Effects of substrate availability on the temperature sensitivity of
327 soil organic matter decomposition. *Global Change Biology*. doi:10.1111/j.1365-2486.2008.01827.x

328 Girkin, N.T., 2018. Tropical forest greenhouse gas emissions: root regulation of soil processes and fluxes.
329 University of Nottingham.

330 Girkin, N.T., Turner, B.L., Ostle, N., Craigan, J., Sjögersten, S., 2018a. Root exudate analogues accelerate CO₂
331 and CH₄ production in tropical peat. *Soil Biology and Biochemistry* 117, 48–55.
332 doi:10.1016/j.soilbio.2017.11.008

333 Girkin, N.T., Turner, B.L., Ostle, N., Sjögersten, S., 2018b. Composition and concentration of root exudate
334 analogues regulate greenhouse gas fluxes from tropical peat. *Soil Biology and Biochemistry* 127, 280–285.
335 doi:S0038071718303444

336 Girkin, N.T., Turner, B.L., Ostle, N., Sjögersten, S., 2018c. Root-derived CO₂ flux from a tropical peatland.
337 *Wetlands Ecology and Management* 26, 985–991. doi:10.1007/s11273-018-9617-8

338 Girkin, N.T., Vane, C.H., Cooper, H. V., Moss-Hayes, V., Craigon, J., Turner, B.L., Ostle, N., Sjögersten, S.,
339 2019. Spatial variability of organic matter properties determines methane fluxes in a tropical forested
340 peatland. *Biogeochemistry* 142, 231–245.

341 Gorham, E., 1991. Northern Peatlands - Role in the Carbon-Cycle and Probable Responses to Climatic Warming.
342 *Ecological Applications* 1, 182–195. doi:Doi 10.2307/1941811

343 Grayston, S.J., Campbell, C.D., 1996. Functional biodiversity of microbial communities in the rhizospheres of
344 hybrid larch (*Larix eurolepis*) and Sitka spruce (*Picea sitchensis*). *Tree Physiology* 16, 1031–1038.

345 Hergoualc'h, K., Verchot, L. V, 2014. Greenhouse gas emission factors for land use and land-use change in
346 Southeast Asian peatlands. *Mitigation and Adaptation Strategies for Global Change* 19, 789–807. doi:DOI
347 10.1007/s11027-013-9511-x

348 Hirano, T., Jauhiainen, J., Inoue, T., Takahashi, H., 2009. Controls on the Carbon Balance of Tropical Peatlands.
349 *Ecosystems* 12, 873–887. doi:DOI 10.1007/s10021-008-9209-1

350 Hodgkins, S.B., Richardson, C.J., Dommain, R., Wang, H., Glaser, P.H., Verbeke, B., Winkler, B.R., Cobb, A.R.,
351 Rich, V.I., Missilmani, M., Flanagan, N., Ho, M., Hoyt, A.M., Harvey, C.F., Vining, S.R., Hough, M.A.,
352 Moore, T.R., Richard, P.J.H., De La Cruz, F.B., Toufaily, J., Hamdan, R., Cooper, W.T., Chanton, J.P.,
353 2018. Tropical peatland carbon storage linked to global latitudinal trends in peat recalcitrance. *Nature*
354 *Communications*. doi:10.1038/s41467-018-06050-2

355 Hogg, E.H., Liefers, V.J., Wein, R.W., 1992. Potential Carbon Losses from Peat Profiles - Effects of
356 Temperature, Drought Cycles, and Fire. *Ecological Applications* 2, 298–306. doi:Doi 10.2307/1941863

357 Holmes, M.E., Chanton, J.P., Tfaily, M.M., Ogram, A., 2015. CO₂ and CH₄ isotope compositions and production
358 pathways in a tropical peatland. *Global Biogeochemical Cycles* 29, 1–18. doi:10.1002/2014GB004951

359 Hoyos-Santillan, J., Craigon, J., Lomax, B.H., Lopez, O.R., Turner, B.L., Sjögersten, S., 2016. Root oxygen loss
360 from *Raphia taedigera* palms mediates greenhouse gas emissions in lowland neotropical peatlands. *Plant*
361 *and Soil* 404, 47–60. doi:10.1007/s11104-016-2824-2

362 Hoyos-Santillan, J., Lomax, B.H., Large, D., Turner, B.L., Boom, A., Lopez, O.R., Sjögersten, S., 2015. Getting
363 to the root of the problem: litter decomposition and peat formation in lowland Neotropical peatlands.
364 *Biogeochemistry* 126, 115–129. doi:10.1007/s10533-015-0147-7

365 Hoyos Santillan, J., Lomax, B.H., Turner, B.L., Sjögersten, S., 2018. Nutrient limitation or home field advantage:
366 Does microbial community adaptation overcome nutrient limitation of litter decomposition in a tropical
367 peatland? *Journal of Ecology* 00, 1–12.

368 IPCC, 2013. Climate Change 2013: The Physical Science Basis, Climate Change 2013: The Physical Science
369 Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on
370 Climate Change. doi:10.1017/CBO9781107415324

371 Jauhiainen, J., Kerojoki, O., Silvennoinen, H., Limin, S., Vasander, H., 2014. Heterotrophic respiration in drained
372 tropical peat is greatly affected by temperature—a passive ecosystem cooling experiment. *Environmental*
373 *Research Letters* 9. doi:Artn 105013Doi 10.1088/1748-9326/9/10/105013

374 Jauhiainen, J., Takahashi, H., Heikkinen, J.E.P., Martikainen, P.J., Vasander, H., 2005. Carbon fluxes from a
375 tropical peat swamp forest floor. *Global Change Biology*. doi:10.1111/j.1365-2486.2005.001031.x

376 Keiluweit, M., Nico, P.S., Kleber, M., Fendorf, S., 2016. Are oxygen limitations under recognized regulators of
377 organic carbon turnover in upland soils? *Biogeochemistry*. doi:10.1007/s10533-015-0180-6

378 Kolton, M., Marks, A., Wilson, R.M., Chanton, J.P., Kostka, J.E., 2019. Impact of warming on greenhouse gas
379 production and microbial diversity in anoxic peat from a Sphagnum-dominated bog (Grand Rapids,
380 Minnesota, United States). *Frontiers in Microbiology*. doi:10.3389/fmicb.2019.00870

381 Könönen, M., Jauhiainen, J., Straková, P., Heinonsalo, J., Laiho, R., Kusin, K., Limin, S., Vasander, H., 2018.
382 Deforested and drained tropical peatland sites show poorer peat substrate quality and lower microbial
383 biomass and activity than unmanaged swamp forest. *Soil Biology and Biochemistry*.
384 doi:10.1016/j.soilbio.2018.04.028

385 Le Mer, J., Roger, P., 2001. Production, oxidation, emission and consumption of methane by soils: A review.
386 *European Journal of Soil Biology* 37, 25–50.

387 Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Hu, Z., Laggoun-Défarge, F., 2017. Vegetation
388 composition controls temperature sensitivity of CO₂ and CH₄ emissions and DOC concentration in
389 peatlands. *Soil Biology and Biochemistry*. doi:10.1016/j.soilbio.2017.01.005

390 Liu, Q., Wang, R., Li, R., Hu, Y., Guo, S., 2016. Temperature sensitivity of soil respiration to nitrogen
391 fertilization: Varying effects between growing and non-growing seasons. *PLoS ONE*.
392 doi:10.1371/journal.pone.0168599

393 Lloyd, J., Taylor, J., 1994. On the temperature dependence of soil respiration. *Functional Ecology*.
394 doi:10.2307/2389824

395 Lupascu, M., Wadham, J.L., Hornibrook, E.R.C., Pancost, R.D., 2012. Temperature Sensitivity of Methane
396 Production in the Permafrost Active Layer at Stordalen, Sweden: a Comparison with Non-permafrost
397 Northern Wetlands. *Arctic Antarctic and Alpine Research* 44, 469–482. doi:10.1657/1938-4246-44.4.469

398 Melling, L., Tan, C.S.Y., Goh, K.J., Hatano, R., 2013. Soil Microbial and Root Respirations from Three
399 Ecosystems in Tropical Peatland of Sarawak, Malaysia. *Journal of Oil Palm Research* 25, 44–57.

400 Menichetti, L., Reyes Ortigoza, A.L., García, N., Giagnoni, L., Nannipieri, P., Renella, G., 2015. Thermal
401 sensitivity of enzyme activity in tropical soils assessed by the Q10 and equilibrium model. *Biology and*
402 *Fertility of Soils*. doi:10.1007/s00374-014-0976-x

403 Nianpeng, H., Ruomeng, W., Yang, G., Jingzhong, D., Xuefa, W., Guirui, Y., 2013. Changes in the temperature
404 sensitivity of SOM decomposition with grassland succession: Implications for soil C sequestration. *Ecology*
405 *and Evolution*. doi:10.1002/ece3.881

406 Page, S.E., Rieley, J.O., Banks, C.J., 2011. Global and regional importance of the tropical peatland carbon pool.
407 *Global Change Biology*. doi:10.1111/j.1365-2486.2010.02279.x

408 Phillips, S., Rouse, G.E., Bustin, R.M., 1997. Vegetation zones and diagnostic pollen profiles of a coastal peat
409 swamp, Bocas del Toro, Panama. *Palaeogeography, Palaeoclimatology, Palaeoecology* 128, 301–338.

410 Sánchez-Carrillo, S., Álvarez-Cobelas, M., Angeler, D.G., Serrano-Grijalva, L., Sánchez-Andrés, R., Cirujano,
411 S., Schmid, T., 2018. Elevated Atmospheric CO₂ Increases Root Exudation of Carbon in Wetlands: Results
412 from the First Free-Air CO₂ Enrichment Facility (FACE) in a Marshland. *Ecosystems*. doi:10.1007/s10021-
413 017-0189-x

414 Sjögersten, S., Aplin, P., Gauci, V., Peacock, M., Siegenthaler, A., Turner, B.L., 2018. Temperature response of
415 ex-situ greenhouse gas emissions from tropical peatlands: Interactions between forest type and peat moisture
416 conditions. *Geoderma*. doi:10.1016/j.geoderma.2018.02.029

417 Sjögersten, S., Cheesman, A.W., Lopez, O., Turner L., B., 2011. Biogeochemical processes along a nutrient
418 gradient in a tropical ombrotrophic peatland. *Biogeochemistry* 104, 147–163. doi:DOI 10.1007/s10533-
419 010-9493-7

420 Smith, W.H., 1976. Character and Significance of Forest Tree Root Exudates. *Ecology* 57, 324–331. doi:Doi
421 10.2307/1934820

422 Song, M., Jiang, J., Cao, G., Xu, X., 2010. Effects of temperature, glucose and inorganic nitrogen inputs on carbon
423 mineralization in a Tibetan alpine meadow soil. *European Journal of Soil Biology*.
424 doi:10.1016/j.ejsobi.2010.09.003

425 Tonks, A.J., Aplin, P., Beriro, D.J., Cooper, H., Evers, S., Vane, C.H., Sjögersten, S., 2017. Impacts of conversion
426 of tropical peat swamp forest to oil palm plantation on peat organic chemistry, physical properties and
427 carbon stocks. *Geoderma* 289, 36–45. doi:10.1016/j.geoderma.2016.11.018

428 Troxler, T.G., Ikenaga, M., Scinto, L., Boyer, J.N., Condit, R., Perez, R., Gann, G.D., Childers, D.L., 2012.
429 Patterns of Soil Bacteria and Canopy Community Structure Related to Tropical Peatland Development.
430 Wetlands 32, 769–782. doi:10.1007/s13157-012-0310-z

431 Upton, A., Vane, C.H., Girkin, N., Turner, B.L., Sjögersten, S., 2018. Does litter input determine carbon storage
432 and peat organic chemistry in tropical peatlands? Geoderma 326, 76–87.
433 doi:10.1016/j.geoderma.2018.03.030

434 Uselman, S.M., Qualls, R.G., Thomas, R.B., 2000. Effects of increased atmospheric CO₂, temperature, and soil
435 N availability on root exudation of dissolved organic carbon by a N-fixing tree (*Robinia pseudoacacia* L.).
436 Plant and Soil. doi:Doi 10.1023/A:1004705416108

437 Vančura, V., 1967. Root exudates of plants - III. Effect of temperature and “cold shock” on the exudation of
438 various compounds from seeds and seedlings of maize and cucumber. Plant and Soil.
439 doi:10.1007/BF01376325

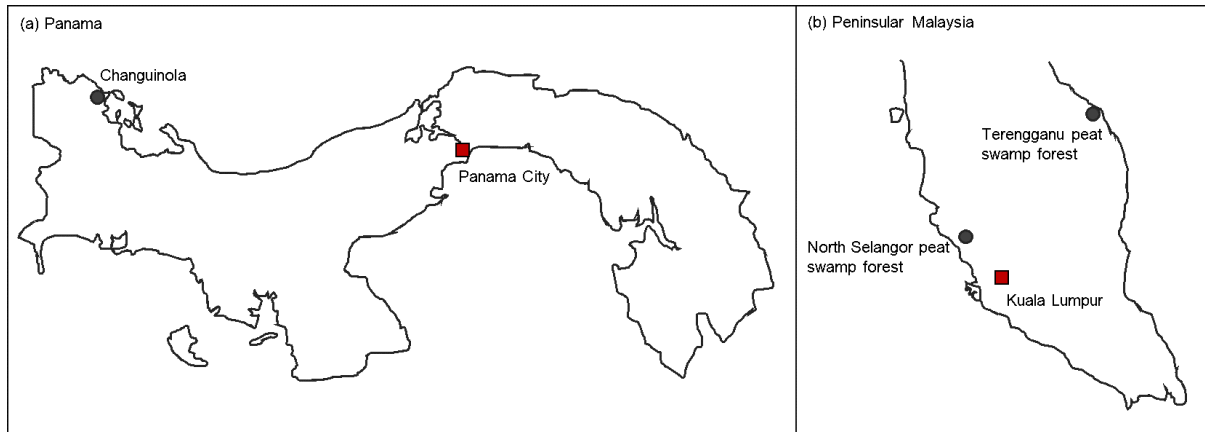
440 Wang, X., Li, X., Hu, Y., Lv, J., Sun, J., Li, Z., Wu, Z., 2010. Effect of temperature and moisture on soil organic
441 carbon mineralization of predominantly permafrost peatland in the Great Hing’an Mountains, Northeastern
442 China. Journal of Environmental Sciences. doi:10.1016/S1001-0742(09)60217-5

443 Wright, E.L., Black, C.R., Turner, B.L., Sjögersten, S., 2013. Environmental controls of temporal and spatial
444 variability in CO₂ and CH₄ fluxes in a neotropical peatland. Global Change Biology.
445 doi:10.1111/gcb.12330

446

447 **List of tables and figures**

448



449

450 Figure 1: Study site locations in (a) Panama: Changuinola, Bocas del Toro province. (b) Malaysia: Kampung Raja

451 Musa, North Selangor and Kampung Mat Jintan, Terengganu,

452

453 Table 1: Peat properties for Panamanian and Malaysian forested peatlands, and converted Malaysian oil palm with

454 pineapple intercropping. Means \pm one SE (n = 3). (^a Phillips et al., 1997; ^b Isla Colon, STRI Environmental

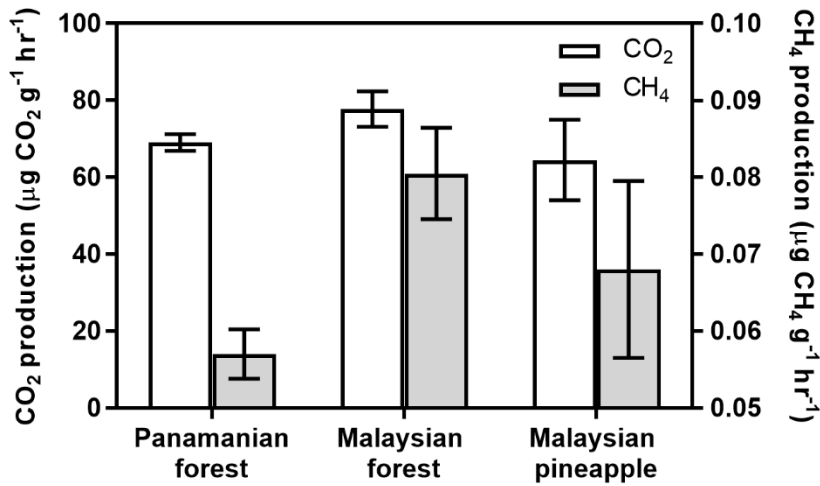
455 Monitoring; ^c (Wright et al., 2013); ^d (Dhandapani et al., 2019b); ^e (Dhandapani et al., 2019a); ^f (Global

456 Environment Centre, 2014).

	Panamanian forest	Malaysian forest	Malaysian intercropping	p-value
Peat depth (m)	5 ^a	2 ^d	3 ^e	-
pH	4.0 \pm 0.01	4.4 \pm 0.4	4.2 \pm 0.1	0.457
Redox potential (mV)	303.7 \pm 6.9	185.3 \pm 21.2	294.3 \pm 3.5	0.001
Moisture content (%)	77.00 \pm 9.5	90.4 \pm 0.2	77.2 \pm 1.2	0.225
Organic matter content (%)	93.8 \pm 1.4	78.9 \pm 11.8	86.3 \pm 2.5	0.378
C (%)	43.8 \pm 3.9	51.3 \pm 0.6	59.4 \pm 2.8	0.021
N (%)	2.6 \pm 0.4	1.9 \pm 0.1	2.3 \pm 0.05	0.134
C:N	17 \pm 1.0	26.9 \pm 1.3	25 \pm 1.7	0.003
Peat temperature (°C)	23.9 \pm 0.1	27.3 \pm 0.1	27.7 \pm 0.5	-
Air temperature (°C)	26.3	26.8	26.6	-
Mean annual rainfall (mm)	3206 ^b	1000 ^d	1359- 2480 ^f	-
Water table range (cm)	-20 – 20 ^c	5 – 10 ^d	-150 – -50 ^f	-

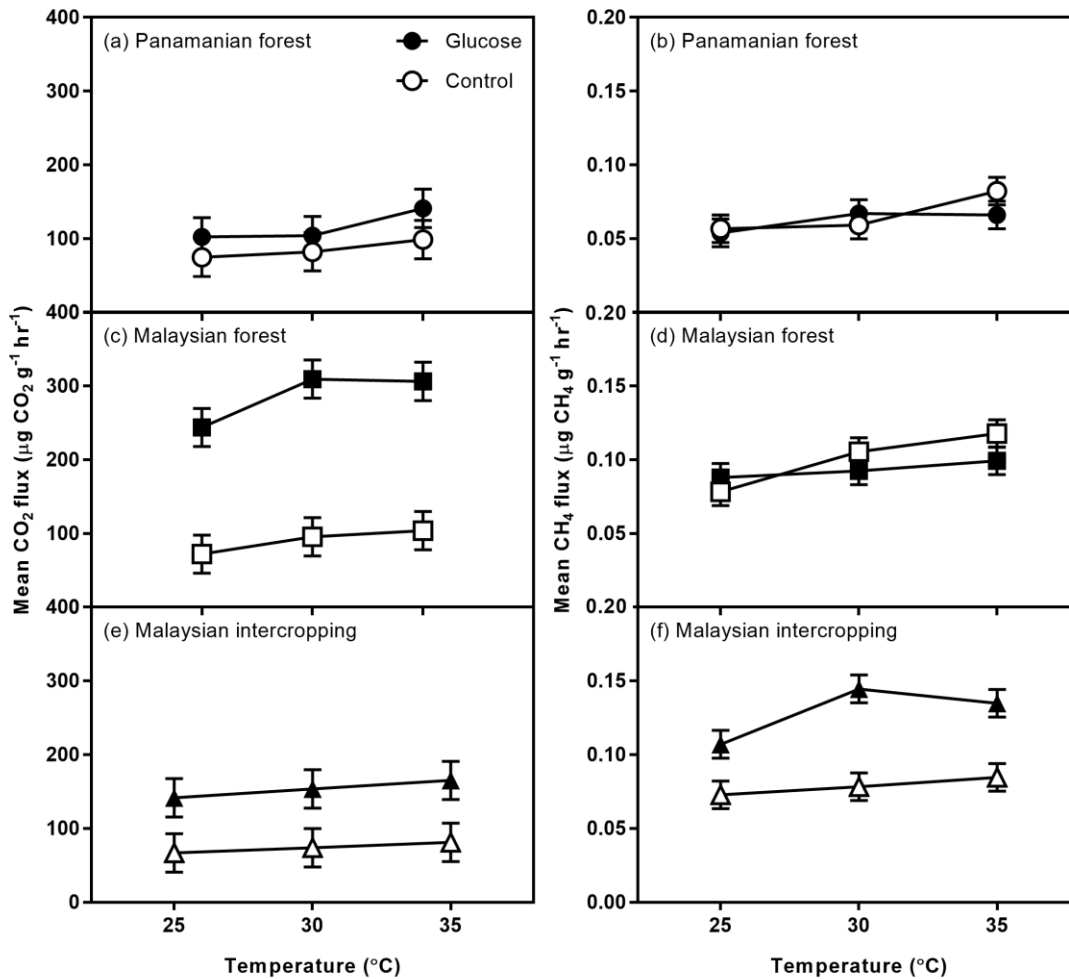
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460 Figure 2: *Ex situ* basal CO₂ and CH₄ fluxes at 25°C and in the absence of glucose. Means ± one SE (n = 3).



461

462 Figure 3: Mean CO₂ and CH₄ fluxes for (a-b) Panamanian forest, (c-d) Malaysian forest, (e-f) Malaysian pineapple

463 intercropping. Means ± one SE (n = 3).

464 Table 2: Q₁₀ for Panamanian and Malaysian forests, and Malaysian pineapple intercropping sites in the presence
 465 and absence of glucose. Mean ± one SE (n = 3).

Site	Glucose	CO ₂		CH ₄	
		Q ₁₀	R ²	Q ₁₀	R ²
Panamanian forest	+	1.3 ± 0.4	0.67	1.1 ± 0.04	0.48
	-	1.5 ± 0.2	0.78	1.5 ± 0.3	0.74
Malaysian forest	+	1.4 ± 0.1	0.31	1.2 ± 0.1	0.50
	-	1.3 ± 0.01	0.80	1.5 ± 0.3	0.57
Malaysian intercropping	+	1.2 ± 0.04	0.83	1.3 ± 0.2	0.04
	-	1.3 ± 0.3	0.81	1.3 ± 0.2	0.68

466