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

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Abstract

Tropical peatlands are a significant carbon store and contribute to global carbon dioxide (CO_2) and methane (CH_4) emissions. Tropical peatlands are threatened by both land use and climate change, including 3 – 4°C predicted warming by 2100 and the alteration of regional precipitation patterns. Plant communities in tropical peatlands can regulate greenhouse gas (GHG) fluxes through labile carbon inputs, but the extent to which these inputs regulate the temperature response of CO_2 and CH_4 production in tropical peat remains unclear. We conducted an anoxic incubation experiment using three peat types derived from contrasting botanical origins to assess how carbon addition affects the temperature response (Q_{10}) of CO_2 and CH_4 production. Peats from a forested peatland in Panama and Malaysia, and a converted oil palm and pineapple intercropping system in Malaysia differed significantly in terms of redox potential, total carbon and carbon: nitrogen ratios. The production of CO_2 and CH_4 varied significantly among peat types and increased with increasing temperature. Carbon addition further increased gas fluxes, but did not influence the Q_{10} for CO_2 or CH_4 production. These findings demonstrate that CO_2 and CH_4 production in tropical peats are sensitive to warming, that potential emissions vary among contrasting peat types, but that the effect of root inputs in altering Q_{10} appears to be limited.

Introduction

Global atmospheric concentrations of carbon dioxide (CO_2) and methane (CH_4) are increasing, driven by anthropogenic activities and accelerating climate change (IPCC, 2013). Tropical peatlands represent an important component of the carbon cycle, being an important source of both CO_2 and CH_4 and a major store of carbon. Indeed, tropical peatlands account for 11% of total peatland area but 15-19% of peat carbon stocks worldwide, equivalent to approximately 104.7 Gt C, with significant deposits reported throughout the tropics in Central and South America, Central Africa, and Southeast Asia (Dargie et al., 2017; Page et al., 2011).

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

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

Root exudates represent an important plant carbon input which, depending on their composition, can contribute significantly to net greenhouse gas emissions in tropical peats even at relatively low addition rates (Girkin et al., 2018a, 2018b). Root respiration, which includes microbial use of exudates, can be the dominant driver of CO_2 fluxes *in situ* in tropical peatlands (Girkin et al., 2018c; Melling et al., 2013). Emissions of both CO_2 and CH_4 are also driven by the decomposition of peat organic matter, with the extent of production determined by substrate quality (Bridgham and Richardson, 1992; Hoyos-Santillan et al., 2015). Under low oxygen to anoxic conditions that can predominate in peatlands, methanogenic archaea produce CH_4 through the reduction of acetate (acetoclastic methanogenesis), the reduction of CO_2 and H_2 (hydrogenotrophic methanogenesis), or the cleavage of methylated organic compounds (Holmes et al., 2015; Kolton et al., 2019; Le Mer and Roger, 2001). These pathways are strongly influenced by prevalent environmental conditions *in situ*, including substrate and nutrient availability, microbial community structure, water table depth, and temperature (Couwenberg et al., 2009; Gorham, 1991; Le Mer and Roger, 2001).

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

Developing an understanding of temperature sensitivity of peat and soils is important in accurately assessing future changes in the global carbon cycle in response to rises in temperature. Strong responses of greenhouse gas production to increased temperature, and greater temperature sensitivity with increasing carbon substrate recalcitrance are predicted by kinetic theory (Davidson and Jannssens, 2006) and supported by some experimental data (Conant et al., 2008). Decomposition of recalcitrant peatland carbon (particularly highly aromatic tropical peat) may also be subject to thermodynamic limitation due to a shortage of terminal electron acceptors (Beer and Blodau, 2007). Previous studies in mineral soils have reported an increase in the temperature sensitivity of aerobic respiration on the addition of labile carbon (Gershenson et al., 2009; Nianpeng et al., 2013; Song et al., 2010), most likely because microbial respiration in these soils was limited by carbon lability. High latitude peatlands have previously been demonstrated to have high temperature sensitivity for CH_4 production (Bergman et al., 1998). Increased temperatures have also been shown to result in substantial changes in microbial community structure, possibly resulting in changes in methanogenic pathways (Lupascu et al., 2012). However, it is unclear how this applies in tropical peatlands with high organic matter content (> 60%), but a high aromatic content, and how responses vary between dominant vegetation types with different litter inputs (Upton et al., 2018, Cooper et al., 2019), and under waterlogged and low oxygen conditions (Wright et al., 2013).

In this study, we assessed the response of CO_2 and CH_4 production of three tropical peats to elevated temperatures and carbon addition, in the form of glucose. Based on the strong role of organic matter quality in regulating greenhouse gas emissions we predicted that i) basal CO_2 and CH_4 production would differ among peat types, and ii) temperature sensitivity would differ among peat types. As labile carbon can be rapidly depleted during decomposition, and peat is predominantly composed of recalcitrant biomolecules, we also hypothesised that iii) glucose addition would increase Q_{10} for all peat types due to waterlogged, low oxygen conditions, and strong substrate limitation resulting in thermodynamic limitation.

Methods

Study sites

This study was conducted using peat samples collected from sites in Panama and Malaysia between May 2016 and July 2017. Panamanian peat samples were collected in May 2016 from the 80 km^2 ombrotrophic peatland at Changuinola, part of the San San Pond Sak freshwater and marine wetland located in Bocas del Toro province (Figure 1a). The site was located approximately 600 m from the coast (09° 18' 13.00"N, 82° 21' 13.80"W) in a mixed forest stand. The central peat dome is approximately 8 m deep and was initiated approximately 4000–5000 years ago (Phillips et al., 1997). The site features seven distinct plant phasic communities beginning with a *Rhizophora mangle* mangrove swamp on the coastal margins, which is succeeded by palm swamp dominated by *Raphia taedigera*, a mixed forest stand, a monodominant C*ampnosperma panamensis* forest stand, and a *Myrica-Cyrilla* bog-plain (Phillips et al., 1997). This vegetation gradient is matched by a pronounced decrease in nutrient availability, particularly phosphorus (Cheesman et al., 2012; Sjögersten et al., 2011). The microbial community throughout the peatland is dominated by *Acidobacteria*, with precise community composition clustered by phosphorus availability (Troxler et al., 2012). Sampling was conducted in the mixed forest stand dominated by *C. panamensis*, *R. taedigera*, and *Symphonia globulifera*.

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

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

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

Experimental design

Peat samples (20 g) from each site, were placed in stainless steel chambers (0.6 dm^3) with polypropylene lids and a silicon ring seal. Two holes were drilled in the lids and fitted with three-way stopcock valves silicon-sealed in place. The gas-tightness of chambers was tested by closing all valves and submersing in water, and through flushing the chamber with N_2 and observing for changes in headspace CO_2 and CH_4 concentrations over time prior to adding peat. Each peat sample was mixed with 20 ml of deionised water to mimic *in situ* flooded conditions. Chambers were flushed with N_2 to displace accumulated headspace gases for two minutes and were placed in incubators set at 25, 30 and 35°C for acclimation of microbial communities for seven weeks following sample storage and preparation. temperatures were selected to represent broad scale warming of peatlands in the Central Americas and in Southeast Asia (IPCC, 2013). Chambers were subsequently opened to displace accumulated headspace gases, flushed again with N_2 for two minutes and sealed. Overall conditions most closely match the flooded oxic conditions outlined in Sjogersten et al. (2018), namely, water saturated with low oxygen, but not entirely anoxic, mostly closely resembling peat *in situ* conditions in the 0 – 10 cm horizon (Girkin, 2018; Hoyos-Santillan et al., 2016).

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

During headspace sampling, chambers were connect to a Los Gatos ultraportable greenhouse gas analyser (San Jose, California), sampling at 0.5 Hz. Fluxes were subsequently measured over 90 seconds, with measurement occurring immediately prior to glucose addition, and at 6, 24, 72 and 120 hours following the first addition. Glucose (or deionised water) was added to each chamber at the rate of 1 ml per day. Gas concentrations were adjusted for incubation temperature (25 – 35°C), as well tube and optical bench volume, according to the ideal gas law. The rate of potential gas production, expressed as µg CO_2 g^{-1} hr^{-1} or µg CH_4 g^{-1} hr^{-1}, was calculated assuming a linear accumulation rate of gases in the headspace (Hogg et al., 1992).

Q_{10}, describing the temperature sensitivity of CO_2 and CH_4 production was calculated as:

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

Where m is the regression slope of a $\log_{10}$ CO_2 or CH_4 flux versus temperature plot.

Peat characterisation

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

209 meter coupled with pH and redox probes following one week acclimation but prior to beginning the experiment. After measurement, chambers were flushed with N_2 and resealed.

Statistical analysis

Differences in CO_2 and CH_4 production and Q_{10}s were tested using the restricted maximum likelihood method (REML), including site, temperature and presence/absence of glucose as fixed effects and sample replicate as a random effect. CO_2 and CH_4 fluxes were log-transformed to meet test assumptions. Significance was assessed at $p < 0.05$. All statistical analyses were conducted using Genstat v17.

Results

Peat biochemical properties

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

Basal peat CO_2 and CH_4 production

Mean basal CO_2 production varied between 69.0 – 77.7 µg CO_2 g^{-1} hr^{-1} (Figure 2) but did not differ significantly among peat types ($p = 0.151$). CH_4 production, however, varied significantly among peat types ($p = 0.02$). The magnitude of CH_4 production compared to CO_2 was considerably lower, ranging from 0.06 – 0.08 µg CH_4 g^{-1} hr^{-1}. Greatest CO_2 and CH_4 production occurred in Malaysian primary forest peats, with the most variable production occurring in peats from the intercropping sites.

Temperature and labile carbon sensitivity

Temperature strongly influenced CO_2 fluxes, with increased production relative to basal rates for all sites at both 30°C and 35°C ($p < 0.001$). Glucose addition significantly increased CO_2 production ($p < 0.001$), with a significant

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

CH_4 production increased significant with temperature ($p < 0.001$), with mean production increasing at both 30 and 35°C (Figure 3b,d,f). Glucose addition increased mean CH_4 fluxes by 11% ($p = 0.034$). There was also a significant interaction between glucose addition and peat type ($p < 0.001$). In Malaysian forest and Panamanian forest peats, there were 5 and 7% declines in mean CH_4 fluxes respectively on glucose addition, but there was a 56% increase in mean fluxes for the intercropping site.

There were no significant differences in temperature sensitivity (Q_{10}) of CO_2 or CH_4 production in the presence or absence of glucose ($p > 0.05$, Table 2), between sites ($p > 0.05$), or in the interaction between treatment and sites ($p > 0.05$).

Discussion

Warming promoted CO_2 and CH_4 production in all peat types, in common with previous studies in both temperate and boreal (Dunfield et al., 1993, Inglett et al., 2012), and tropical peats (Sjögersten et al., 2018), as well as drained lowland tropical soils from Peru (Nottingham et al., 2015). Previously, it has been proposed that heterotrophic microbial communities in tropical peat respond weakly to warming primarily due to adaptation to high peat temperatures, and because optimal temperature for respiration and methanogenesis is approximately 25°C (Kolton et al., 2019; Menichetti et al., 2015; Sjögersten et al., 2018). Q_{10} for both CO_2 (1.07 – 2.25) and CH_4 (1.10 – 2.39) production were relatively low in our study, particularly when compared to 6.1 for anaerobic CH_4 production reported for Panamanian peats (Sjögersten et al., 2018), although they are closer to the 2.2 – 3.7 reported from studies of CH_4 production in Central Kalimantan, Indonesia (Brady, 1997; Hirano et al., 2009; Jauhiainen et al., 2014), and 1.8 under flooded oxic conditions from Panamanian peats (Sjögersten et al., 2018). Previous studies have reported a higher temperature sensitivity of CH_4 production than CO_2 production, although we found no supporting evidence for this (Table 2) (Sjögersten et al., 2018, and references therein). These results have clear implications in assessing the impact of future environmental change on gaseous carbon emissions from tropical peatlands: warming peat will result in increased CO_2 and CH_4 emissions from flooded, low oxygen peats.

Although there was no difference in basal CO_2 production (from unamended peats at 25°C), or in temperature sensitivity among peat types, both CO_2 and CH_4 fluxes varied significantly among sites across the three temperatures. While organic matter content was similar among peat types, there were significant differences in total carbon and C:N, likely reflecting contrasting aboveground vegetation and management practices. Previous work in Malaysia (Tonks et al., 2017, Cooper et al., 2019) and Panama (Hoyos-Santillan et al., 2015, Upton et al., 2018, Girkin et al., 2019) has demonstrated substantial differences in organic matter properties between contrasting plant functional types and land uses, driven by differences in plant litter inputs and decomposition rates. While various studies have assessed the impacts of land use change on organic matter properties (Cooper et al., 2019; Könönen et al., 2018; Tonks et al., 2017), there is limited data available regarding the role of intercropping systems on organic matter properties, meaning differences in responses cannot be readily ascribed to contrasts in organic matter properties alone. The low CH_4 fluxes from the Malaysian intercropping system may reflect significant depletion of labile carbon (Cooper et al., 2019), but could also be driven by a poorly adapted methanogenic community, or a highly active methanotrophic community under partially aerobic conditions (Andersen et al., 2013), as well as a redox potential c. 300 mV.

Changes in CO_2 and CH_4 production in response to glucose addition varied between peat types. At 35°C, CH_4 fluxes were greater from unamended Panamanian and Malaysian forest peats compared to carbon amended peats, implying that labile carbon availability was not a limiting factor for production at this temperature. Similarly, CO_2 production in peat from the Panamanian primary forest was comparable at 30 – 35°C even with glucose amendment implying an additional limiting factor other than temperature. Rates of CO_2 and CH_4 production in tropical peatlands have previously been reported as lower at low fertility (Sjögersten et al., 2011), with litter decomposition partially constrained by nutrient availability (Hoyos Santillan et al., 2018). The higher response of the Malaysian intercropping peat to glucose addition may reflect the effects of management practices, specifically fertiliser addition. This may substantially alter the temperature sensitivity of the system by alleviating inorganic nitrogen ($NH_4^+/NO_2^-/NO_3^-$) limitation (Liu et al., 2016; Wang et al., 2010), although in this study only total peat nitrogen was assessed and this did not differ significantly between peat types. The lack of significant difference in temperature sensitivity of CO_2 and CH_4 production with glucose addition may be because despite an increase in carbon lability, unamended peats still had sufficient available carbon for respiration due to high organic matter content (Dai et al., 2017). Alternatively, the system is thermodynamically limited due to a shortage of high energy terminal electron acceptors necessary for the decomposition of recalcitrant aromatic carbon which is likely under the lox oxygen conditions (Hodgkins et al., 2018; Kolton et al., 2019), and with the relatively low concentration glucose additions being rapidly consumed (Girkin et al., 2018a).

Fully understanding the impact of increased temperature on fluxes *in situ* is more complex due to the additional regulatory roles of microtopography (Jauhiainen et al., 2005), water table changes (Wright et al., 2013), plant inputs of oxygen (Hoyos-Santillan et al., 2016), and small scale heterogeneity of peat organic matter properties (Girkin et al., 2019). In temperate peatlands, vegetation cover has been shown to also have a significant impact on the temperature sensitivity of GHG production (Leroy et al., 2017). Increasing atmospheric CO_2 has been found to increase rates of root exudation in wetland ecosystems (Sánchez-Carrillo et al., 2018) and increases in temperature have also been reported to enhance rates of root exudation in some tree species (Uselman et al., 2000), and alter the composition of exudate profiles (Badri and Vivanco, 2009; Vančura, 1967), both known to be critical regulators of GHG emissions and peat properties (Girkin et al., 2018a & 2018b). As a consequence, the true response of *in situ* net emissions of GHGs will comprise components driven by both the temperature sensitivity of the peat itself, and any changes in root inputs.

Taken together, our results demonstrate that increased temperatures will substantially increase CO_2 and CH_4 production in tropical peats, regardless of current land cover. As a consequence, predicted warming for Central America and Southeast Asia will be associated with substantial increases in gaseous carbon emissions (IPCC, 2013). However, the extent of this increase is likely to be lower than the response of higher latitude peatlands for which higher Q_{10}s have been reported, including 2.4 – 5.8 for a *Sphagnum* peatland (Lupascu et al., 2012) and 2.5 – 35 (Bergman et al., 1998). Differences in fluxes between peat types are likely driven by contrasts in organic matter properties (Cooper et al., 2019) and/or nutrient availability (Hoyos Santillan et al., 2018; Sjögersten et al., 2011) and microbial community structure and function. Processes that alter organic matter properties, for example the conversion of pristine forest to oil palm, or the use of intercropping species, will further affect fluxes. In addition, our findings demonstrate that the temperature sensitivity of CO_2 and CH_4 production is not affected by labile carbon addition. This is important because plants can input significant quantities of labile carbon which are not accounted for in the majority of studies of GHG temperature sensitivity.

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List of tables and figures

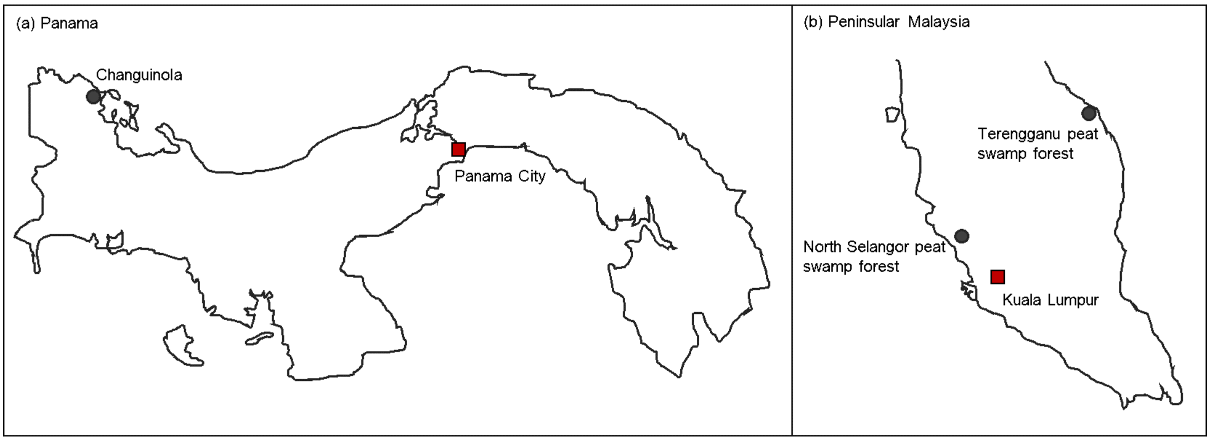

Figure 1: Study site locations in (a) Panama: Changuinola, Bocas del Toro province. (b) Malaysia: Kampung Raja Musa, North Selangor and Kampung Mat Jintan, Terenganu,

Table 1: Peat properties for Panamanian and Malaysian forested peatlands, and converted Malaysian oil palm with pineapple intercropping. Means ± one SE (n = 3). ([a.] Phillips et al., 1997; [b.] Isla Colon, STRI Environmental Monitoring; [c.] (Wright et al., 2013); [d.] (Dhandapani et al., 2019b); [e.] (Dhandapani et al., 2019a); [f.] (Global Environment Centre, 2014).

	Panamanian forest	**Malaysian forest**	**Malaysian intercropping**	**p-value**
Peat depth (m)	5[a]	2[d]	3[e]	-
pH	4.0 ± 0.01	4.4 ± 0.4	4.2 ± 0.1	0.457
Redox potential (mV)	*303.7 ± 6.9*	*185.3 ± 21.2*	*294.3 ± 3.5*	*0.001*
Moisture content (%)	77.00 ± 9.5	90.4 ± 0.2	77.2 ± 1.2	0.225
Organic matter content (%)	93.8 ± 1.4	78.9 ± 11.8	86.3 ± 2.5	0.378
C (%)	*43.8 ± 3.9*	*51.3 ± 0.6*	*59.4 ± 2.8*	*0.021*
N (%)	2.6 ± 0.4	1.9 ± 0.1	2.3 ± 0.05	0.134
C:N	*17 ± 1.0*	*26.9 ± 1.3*	*25 ± 1.7*	*0.003*
Peat temperature (°C)	23.9 ± 0.1	27.3 ± 0.1	27.7 ± 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]	-

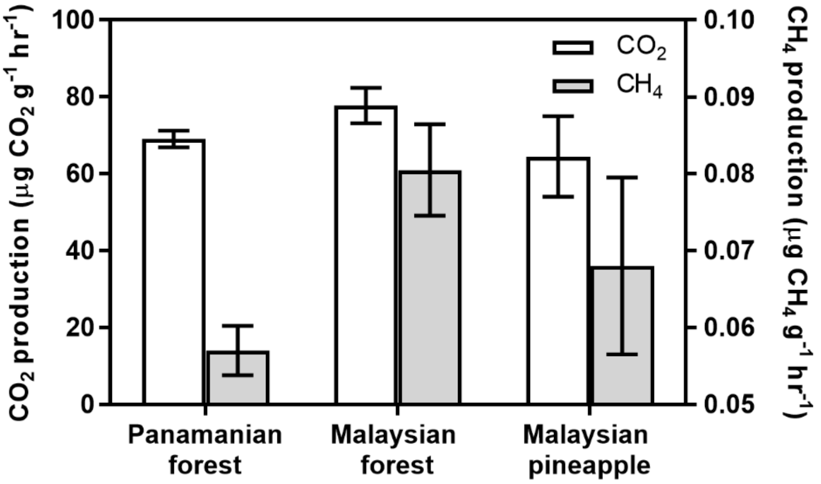

Figure 2: *Ex situ* basal CO$_2$ and CH$_4$ fluxes at 25°C and in the absence of glucose. Means ± one SE (n = 3).

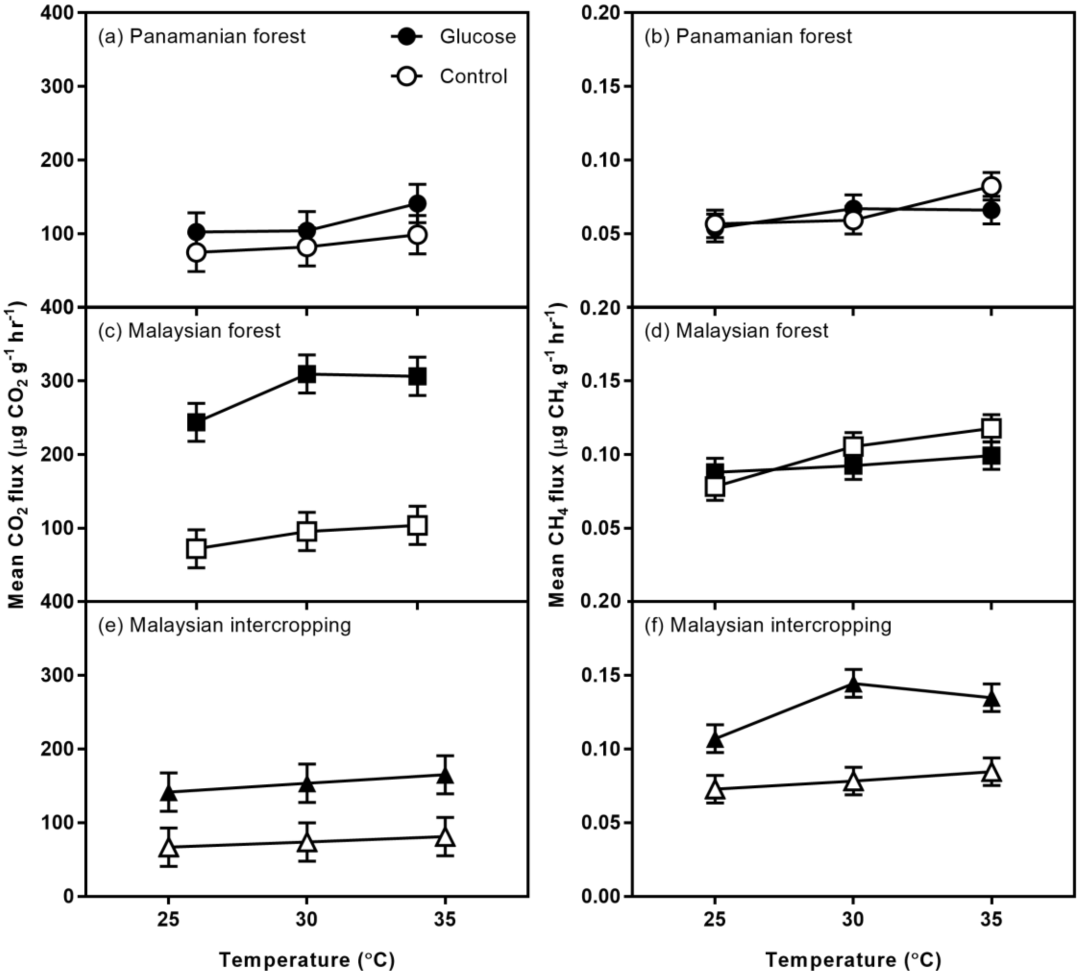

Figure 3: Mean CO$_2$ and CH$_4$ fluxes for (a-b) Panamanian forest, (c-d) Malaysian forest, (e-f) Malaysian pineapple intercropping. Means ± one SE (n = 3).

Table 2: Q_{10} for Panamanian and Malaysian forests, and Malaysian pineapple intercropping sites in the presence and absence of glucose. Mean ± one SE (n = 3).

		CO_2		CH_4	
Site	**Glucose**	**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