Evaluation of vegetation communities, water table, and peat composition as drivers of greenhouse gas emissions in lowland tropical peatlands

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Abstract

Tropical peatlands are globally important source of greenhouse gases to the atmosphere, but data on carbon fluxes from these ecosystems is limited due to the logistical challenges of measuring gas fluxes in these ecosystems. Proposals to overcome the difficulties of measuring gas carbon fluxes in the tropics include remote sensing (top-down) approaches. However, these require information on the effect of vegetation communities on carbon dioxide (CO_2) and methane (CH_4) fluxes from the peat surface (bottom-up). Such information will help reducing the uncertainty in current carbon budgets and resolve inconsistencies between the top-down and bottom-up estimates of gas fluxes from tropical peatlands. We investigated temporal and spatial variability of CO_2 and CH_4 fluxes from tropical peatlands inhabited by two contrasting vegetation communities (*i.e.*, mixed forest and palm swamp) in Panama. In addition, we explored the influence of peat chemistry and nutrient status (*i.e.*, factorial nitrogen (N) and phosphorus (P) addition) on greenhouse gas fluxes from the peat surface. We found that: i) CO_2 and CH_4 fluxes were not significantly different between the two vegetation communities, but did vary temporally across an annual cycle; ii) precipitation rates and peat temperature were poor predictors of CO_2 and CH_4 fluxes; iii) nitrogen addition increased CH_4 fluxes at the mixed forests when the water table was above the peat surface, but neither nitrogen nor phosphorus affected gas fluxes elsewhere; iv) gas fluxes varied significantly with the water table level, with CO_2 flux being 80% greater at low water table, and CH_4 fluxes being 81% higher with the water table above the surface. Taken together, our data suggested that water table is the most important control of greenhouse gas emissions from the peat surface in forested lowland tropical peatlands, and that neither the presence of distinct vegetation communities nor the addition of nutrients outweigh such control.

Keywords: Campnosperma, methane, nitrogen, pyrolysis, phosphorus, Raphia

1. Introduction

Tropical peatlands represent an important component in the global carbon cycle (Dommain et al., 2014; Sjögersten et al., 2014). They act simultaneously as carbon (C) sinks and sources; holding belowground ≈ 119 Gt C (Leifeld and Menichetti, 2018), and emitting annually 1.23 Gt C-CO_2 and 0.068 Gt C-CH_4 (Sjögersten et al., 2014). Land use change (*e.g.*, drainage, land clearing), and climate change (*e.g.* prolonged droughts) threaten C sequestration in tropical peatlands by creating conditions that promote rapid decomposition of peat (Houghton, 2012; Pearson et al., 2017; Turetsky et al., 2014). This can turn tropical peatlands into net carbon emitters to the atmosphere (Couwenberg et al., 2010; Hoyos-Santillan et al., 2016a; Page et al., 2011). Unfortunately, due to the logistical difficulties and demanding conditions that prevail in these ecosystems, there are a limited number of studies that have recorded *in situ* flux measurements. Consequently, the current estimates of greenhouse gas emission from peatlands in tropical regions are highly uncertain (Kirschke et al., 2013; Lawson et al., 2015; Tian et al., 2016). In order to reduce the uncertainties, further quantitative research on carbon exchange in tropical peatlands has to be conducted (Couwenberg et al., 2010). In addition, different approaches have been explored to develop proxies that, in conjunction with remote sensing techniques, allow to evaluate greenhouse gas emission from large areas of tropical peatlands without having to conduct massive field campaigns on a regular basis (Couwenberg and Fritz, 2012).

Vegetation and water table have been previously suggested as proxies to estimate greenhouse gas emissions from peatlands located in temperate regions (Couwenberg et al., 2011; Dias et al., 2010); however, limited information exist with respect to their application in tropical peatlands (Couwenberg et al., 2010). Vegetation exerts direct influence on greenhouse gas

emission through different mechanisms, for example: mediating gas transport to the atmosphere through aerenchymatous structures and lenticels (Pangala et al., 2013, 2017); allocating methanogens in woody tissue (Yip et al., 2018); modifying the redox conditions in the rhizosphere by transferring oxygen into the peat matrix (Hoyos-Santillan et al., 2016a); and releasing root exudates (Girkin et al., 2018). Vegetation also influences greenhouse gas emission by controlling: water table level and peat hydraulic conductivity (Baird et al., 2017; Couwenberg et al., 2011); the composition of litter and thus the peat forming material (Hoyos-Santillan et al., 2015); the litter decomposition through the Home Field Advantage effect (Hoyos-Santillan et al., 2018); and the functional structure of the microbial communities (Troxler et al., 2012). Some of these factors vary on a diurnal (Hoyos-Santillan et al., 2016a) and seasonal basis (Teh et al., 2017), further regulating greenhouse gas emission in peatlands. Likewise, water table plays an important role in defining the vegetation communities inhabiting a particular ecosystem. High water table limits the growth of certain species but favors the development of others (Järveoja et al., 2016). In tropical peatlands, in spite of fluctuations of the water table level, vegetation communities remain stable in the short term. However, in the long term, water table participates in the formation of domed structures (Phillips et al., 1997), in which the availability of nutrients varies from the center of the dome towards the outer borders of the peat deposit, influencing the spatial distribution of vegetation communities (*e.g.*, concentric arrangements) (Sjögersten et al., 2011). Therefore, it is plausible that the spatial distribution of different vegetation communities, and their associated characteristics, could be used as proxy to estimate the magnitude of carbon emissions in these ecosystems.

Besides vegetation, nutrients availability also exert a direct influence on biogeochemical processes in tropical peatlands (Hoyos-Santillan et al., 2018; Sjögersten et al., 2011). This influence is particularly relevant in ecosystems subjected, directly or indirectly, to the

addition of fertilizers for agriculture practices (Oktarita et al., 2017). For example, the addition of nitrogen has been observed to exert contrasting effects on greenhouse gas emissions (*e.g*., CO_2, nitrous oxide (N_2O)), increasing or decreasing their fluxes depending on the type of nitrogen component applied (*e.g*. urea, nitrate, ammonium) (Khalil et al., 2007), as well as the type of peat on which it is utilized (Comeau et al., 2016). In tropical peatlands, nutrients are also related to the conformation and distribution of vegetation communities in peat domes (Sjögersten et al., 2011). Thus, it is likely that the availability of nutrients affects greenhouse gas emissions by shaping the spatial distribution of vegetation species and simultaneously influencing heterotrophic respiration in the peat.

Neotropical peatlands are often forested by palms or evergreen broadleaved trees, forming distinct vegetation communities (Draper et al., 2014; Sjögersten et al., 2011). For instance, peat swamp forests in the Caribbean coast of Panama and Costa Rica typically support monodominant stands of the canopy forming evergreen palm *Raphia taedigera* (Mart.) (Hoyos-Santillan et al., 2016a; Myers, 1981; Phillips et al., 1997), or mixed forests composed of palms and evergreen broadleaved hardwood trees (*e.g*., *Campnosperma panamensis* (Standl.)) (Phillips et al., 1997; Urquhart, 1999). These forests emit both CO_2 and CH_4 fluxes, with seasonal and spatial variability in emissions related to both substrate availability (Girkin et al., 2018b) and CH_4 oxidation processes (Wright et al., 2011, 2013).

In addition, CO_2 and CH_4 are produced in the subsurface layers of peat through the entire stratigraphic profile (Hoyos-Santillan et al., 2016b; Wright et al., 2011). In domed peatlands, the depth of the peat layer varies among peatlands with distinct vegetation communities. For example, in Panama, the deepest peat deposits have been located at the top of the dome of the Changuinola peatland (inhabited by mixed forest and sawgrass) and at the Damani-Guariviara peatland (inhabited by mixed forest), reaching depths of 9.5 and 5.9 m, respectively (Hoyos-Santillan et al., 2016b; Phillips et al., 1997).

To test the viability of using vegetation communities as proxy for greenhouse gas emission, we monitored CO_2 and CH_4 surface emissions from two contrasting forest types, palm swamp and mixed forest (Sjögersten et al., 2011). Three peatlands for each type of forest were selected as study sites. The monitoring campaigns were distributed over one year, including a dry and a wet season. This approach was used to test the following hypotheses: (i) different vegetation communities present distinct magnitudes in their surface greenhouse gas fluxes; (ii) greenhouse gas emissions vary throughout the year due to seasonal fluctuation of the water table position; and iii) molecular composition of peat (*e.g.*, lignin, phenolic compounds, and fatty acids content) influences greenhouse gas emissions from the peat's surface. In addition, we conducted a N and P addition experiment in two sites, each one covered with one of the two contrasting vegetation communities. This experiment tested the hypothesis that (iv) addition of nutrients increases CO_2, CH_4, and N_2O emission in tropical peatlands.

2. Materials and methods

2.1 Site description

The study was conducted in the north-west Caribbean coast of Panama where several large peatlands are located within the Bocas del Toro province (Phillips et al., 1997). Rainfall averages 3,092 ± 181 mm yr^{-1}, with a mean annual air temperature of 25.9 ± 0.3 °C (2003 to 2011; Smithsonian Tropical Research Institute Physical Monitoring Program). There is no pronounced seasonality (Wright et al., 2011), although there are two periods of reduced rainfall from February to April and August to September.

147 Seven phasic communities have been identified in these peatlands (Phillips et al., 1997). We
148 studied two of these: palm swamp dominated by *Raphia taedigera* (Mart.), a canopy forming
149 palm in the Arecaceae family, and mixed forest dominated by *Campnosperma panamensis*
150 (Standl), an evergreen broadleaved hardwood tree in the Anacardiaceae family (Table 1; Fig.
151 S1). Three sites for each of these two types of vegetation communities were selected for this
152 study. The selection was based on their contrasting characteristics, considering that those
153 differences could potentially impact on greenhouse gas emissions from peat. For example, the
154 roots of *R. taedigera* palm are composed by hollow aerenchymatous tissue, including the
155 development of dense pneumatophores structures (Hoyos-Santillan et al., 2016a). These
156 structures are distributed throughout the upper peat layer, constituting a shallow (≈ 1.1 m
157 depth), but fibrous root system (Wright et al., 2011). This tissue participates in the reduction
158 of CH_4 emissions from peat, due to axial oxygen loss through *R. taedigera* root system
159 (Hoyos-Santillan et al., 2016a). By contrast, *C. panamensis* does not develop aerenchymatous
160 tissue but has woody lignified structural roots (≈ 1 m depth) with abundant surface knee roots
161 (Wright et al., 2011). This root system is not as dense as that of *R. taedigera* (Wright et al.,
162 2011), but does have lenticels to exchange gases with the atmosphere.

163 Palm sites had large amounts of palm leaf litter at the surface (Wright et al., 2011). The
164 mixed forest sites had large amounts of *C. panamensis* leaf litter at the surface but leaf litter
165 from other species was also present. Microtopography in these sites is characterized by an
166 uneven terrain, forming shallow ponds and raised areas (close to the trees associated with
167 root structures) (Hoyos-Santillan et al., 2016b). During the dry season, shallow ponds are no
168 longer present, due to the lowering of the water table, but the uneven microtopography
169 remains.

170 Peatlands selected for this study are freshwater (< 200 μS cm^{-1}) and their depth varies
171 between 1 to 6 m (Table 1). The water table in the peatlands fluctuates from + 0.15 to - 0.4 m

relative to the peat surface (Wright et al., 2011). The Changuinola peat deposit, where San San Pond Sak 1 and 2 sites are located, is an 80 km^2 ombrotrophic domed peatland (Cohen et al., 1989). The vegetation communities that formed the peat of the Changuinola peat deposit and the Damani-Guariviara peatland have shifted over time, thus the peat composition varies in botanical origin and its degree of humification through the stratigraphic profile (Hoyos-Santillan et al., 2015; Phillips et al., 1997). The texture of the peat on the top layers of all sites is coarse, mainly dominated by roots, whereas deeper layers have a finer composition without recognizable litter, indicating a higher degree of decomposition (Hoyos-Santillan et al., 2016b; Wright et al., 2011). In all the studied peatlands, the underlying mineral soil reflected an estuarine-marine origin, formed by sand and macrofossils (*e.g.*, gastropod shells, bivalves, and crustaceans) (Hoyos-Santillan, 2014).

2.2. Experimental programme and methodology

2.2.1 Vegetation survey

To characterise the two types of forest, vegetation inventories were conducted in 0.1 ha plots (20 × 50 m); all stems > 0.1 m in diameter at breast height (DBH) were mapped, measured, marked, and tagged. The basal area of the tree species found in the plots was calculated from the DBH data. However, given the multi-stem colonial growth of *R. taedigera*, it is plausible that basal area for this species was overestimated. The basal area for the San San Pond Sak sites corresponds to those published by Sjögersten *et al.* (2011) (Table S1).

2.2.2 Physicochemical parameters

A sampling well was installed at each plot to measure the level of the water table, *in situ* dissolved O_2, and temperature of the pore-water. These measurements were conducted at each site on each sampling and monitoring event (Table S2). Each well consisted of a 50 mm diameter PVC pipe with 10 mm diameter perforations at 50 mm intervals. The location of each sampling well corresponds to those presented in Table 1. Dissolved O_2 (DO; mg L^{-1}) and temperature (°C) were measured at the top 0.5 m of the peat profile at the sampling wells using a portable multiparametric probe (YSI 556 MPS, USA). Water table level was measured with a measuring tape at the sampling well of each site, in relation to the peat's surface. In addition, in order to account for the heterogeneity of the microtopography, water table position was assigned a categorical classification. The classification considered the position of the water table with respect to the peat's surface in the sites were the static chambers for measuring gases, were installed. The criteria used to assign the categories was: below peat surface (< 5 cm), at the surface (± 5 cm) or above the peat surface (> 5 cm). In the case of shallow ponds, the above the surface category was applied. Three samples of peat from the top 0.1 m layer of each site were used to conduct the physicochemical characterization. Peat pH and conductivity were determined in a 1:2.5 peat fresh weight (fw)-deionized water solution. Total C, nitrogen (N), and sulphur (S) were measured from 0.5 g homogenised peat samples by using a total element analyser (Thermo Flash EA 1112, CE Instruments, Wigan, UK). Peat ash was dissolved in 6 M HNO_3 to estimate the peat phosphorus (P) concentration by molybdate colorimetry (Andersen, 1976). For detailed methods see Hoyos-Santillan (2014).

2.2.3 Monitoring temporal variations on greenhouse gas fluxes

We measured greenhouse gas fluxes at three palm swamp forests dominated by *R. taedigera* and three mixed forest dominated by *Campnosperma panamensis* (Table 1, Fig. S1). Fluxes were measured on six occasions at each plot; three occasions during dry and three during wet season, respectively (December 2010 – September 2011, specific sampling dates are presented in Table S2). During each monitoring event, we measured greenhouse gas fluxes at three randomly chosen locations by triplicate within each plot. However, if shallow ponds were present within the plot due to microtopography and hydrology heterogeneity, three locations were selected to measure on top of the shallow ponds and three were selected in non-flooded areas. Thus, up to eighteen chambers were installed for the collection of gases at each plot during a single monitoring event. All fluxes were measured during daylight, between 10:00 and 16:00 h.

We used the static chamber technique to measure the greenhouse gas fluxes (Sjögersten et al., 2011). The chambers were made of opaque material, covering a 0.075 m^2 area, with a 0.1 m height, and 7 L volume. Each chamber had a sampling port equipped with a Suba-Seal® rubber septa. Although the forest floor was mostly unvegetated, trailing understory vegetation and fallen branches were removed, before the installation of the chamber. Peat disturbance was avoided as much as possible during the installation of the chambers, but slight pressure was applied to ensure an air-tight seal. Chambers were left to stabilize for approximately thirty minutes. This time period was used to install all chambers within the site and measure physicochemical parameters at the sampling well. Once installed and stabilized, prior to the collection of gas samples, the chamber headspace was homogenised by repeatedly pumping the air within the chamber with a 20 mL syringe equipped with a hypodermic needle. Afterwards, gas samples were collected from each chamber after 0, 2, 10 and 20 min and stored in Exetainers (Labco, Lampeter, UK). All samples were shipped to the University of Nottingham (Nottingham, UK) for analysis via gas chromatography. Vials were discarded for

chromatographic analyses if overpressure was absent (< 5 %). CO_2 and CH_4 concentrations were determined using a single injection system with a 1 mL sample loop that passed the gas sample using N_2 as carrier through a non-polar methyl silicone capillary column (CBP1-W12-100, 0.53 mm I.D., 12 m, 5 mm; Shimadzu UK LTD, Milton Keynes, UK) and porous polymer packed column (HayeSep Q 80/100). Thermal conductivity (TCD), flame ionization (FID) and electron capture detector (ECD) were used to measure CO_2, CH_4, and N_2O, respectively. Flux calculations were based on the linear accumulation of gases within the closed chamber; gas samples that did not follow a linear accumulation trend were discarded for the calculation of gas fluxes. The fluxes presented in this study do not separate heterotrophic (mainly from peat and labile organic matter) from autotrophic (mostly derived from roots) respiration (Lawson et al., 2015), and do not consider the greenhouse gas transport mediated through vegetation.

2.2.4 Nutrient addition experiment

The potential role of nutrient limitation on greenhouse gas emission was explored by a fertilization experiment. The experiment was conducted on two of the six sites selected for this study; specifically, at San San Pond Sak 1 (palm swamp) and San San Pond Sak 2 (mixed forest) in the Changuinola peat deposit (Table 1, Fig. S1). These sites were selected due to the existing information from this peatland in relation to nutrient availability across distinct vegetation communities (Sjögersten et al., 2011). The nutrient treatments were: N, P, N+P, and control (Ctrl). The experiment consisted of ten blocks distributed along 150 m transects running from south-east to north-west at the palm swamp and the mixed forest site (20 blocks in total) (Fig. S1). Each block was 10 × 10 m with the nutrient enrichment treatments applied at each corner, blocks were 5 m apart. Adjacent corners had the same nutrient treatment. Thus

all twenty blocks (10 per vegetation community) had Ctrl, N, P, and N+P treatments (Fig. S2). For further details on the experimental set up please refer to Hoyos-Santillan et al., (2018).

Nutrient enrichment was applied at the beginning of the experiment (October 2011) by filling 25 cm sections of dialysis tubing (Spectra/Por® membrane: 40mm diameter, 6000 to 8000 molecular weight cut off) with 0.86 mol of either N (Urea: $CO(NH_2)_2$ or P (calcium phosphate monobasic monohydrate: $Ca(H_2PO_4)_2 \bullet H_2O$) fertilizer. This allowed a slow release of nutrients through the membrane (Feller, 1995). After five months (March 2012), soil samples were collected to evaluate the impact of the nutrient treatments on surface peat properties (*i.e.* extractable and microbial nutrients) (Table S3). To do this, 10 × 10 × 10 cm samples of peat were carefully cut from the surface peat. Soil samples were stored in plastic bags at 4 °C for one week prior to nutrient analyses. Dissolved organic C (DOC) and dissolved N fractions (TDN = dissolved organic nitrogen (DON) + inorganic fraction (nitrate-nitrite and ammonium)) were extracted from surface peat (10 cm depth) and determined after a five-fold dilution with a TOC-TN analyser (Shimadzu, Columbia, MD) (Sjögersten et al., 2011). Readily-exchangeable P was extracted with anion exchange membranes (AEM) (Myers, Thien & Pierzynski 1999; Turner and Romero 2009) and determined by automated molybdate colorimetry using a flow injection analyser (Lachat Quikchem 8500, Hach Ltd, Loveland, CO). To estimate if the nutrient treatment affected microbial activity in the peat, extractable and microbial biomass C, N, and P were determined. Microbial C and N were estimated by $CHCl_3$ fumigation (Brookes et al., 1982; Vance et al., 1987), whereas microbial P was estimated by hexanol fumigation by resin strips (Myers et al., 1999; Turner and Romero, 2009). For further details see Hoyos-Santillan *et al.* (2018). For this experiment, surface greenhouse gas fluxes were measured before (October 2011) and five months after the addition of the nutrients (March 2012). Measurements were conducted at each of the

twenty blocks on each treatment location (4 treatments × 10 blocks × 2 vegetation communities).

2.2.5 Thermochemolysis

Tetramethylammonium-pyrolysis-gas chromatography-mass spectrometry (TMAH-Py-GC/MS) was used to characterize the organic composition of peat. Treating the peat samples with tetramethylammonium prior to Py-GC/MS analysis (i.e. TMAH-Py-GC/MS or thermochemolysis) prevents thermal degradation of lignin-derived monomers (monolignols) found in peat, as well as large fatty acids derived from plants epicuticular waxes or microorganisms (Steward et al., 2009). Individual compound concentrations were estimated by integrating the areas obtained in the pyrogram and calculating its corresponding concentration using the 5-α-cholestane as an internal standard; concentrations were expressed in relation to the total C content in the peat sample as μg compound mgC^{-1}. TMAH-Py-GC/MS products were assigned a chemical class based on their molecular similarity to its probable source molecule (Hoyos-Santillan et al., 2015; Schellekens, 2013). For this study, lignin, fatty acids and phenolic compounds were grouped. The short and long chain methylated fatty acids (Short < C20 and Long > C20) were further grouped into separate categories to be used as independent covariates. Data corresponding to the TMAH-Py-GC/MS analyses as well as further details on the methodology can be consulted in Hoyos-Santillan *et al.* 2016b.

2.3 Statistical analyses

315 Linear mixed models were used to analyse gas fluxes and were fitted by using Residual
316 Maximum Likelihood (REML). Gas fluxes were transformed (log_{10}) to fulfil the homogeneity
317 of variance requirements of the linear models. Level of significance of the differences
318 between the fixed effects was estimated by Wald tests using an F distribution ($P < 0.05$). For
319 the analysis of the seasonal variation of greenhouse gas fluxes, the vegetation community,
320 water table level, and season were used as fixed factors, while the specific site was included
321 as random factor. Water table level for the analysis was categorized as: below peat surface (<
322 5 cm), at the surface (± 5 cm) or above the peat surface (> 5 cm). The fluxes included in these
323 analyses comprise the six monitoring events at each site. For the analysis of variation of
324 greenhouse gas fluxes in relation to nutrient addition, the vegetation community and
325 treatment was used as a fixed factor, whereas the block was included as random factor.
326 Relationships between gas fluxes (log_{10} transformed) and physicochemical characteristics of
327 surface peat (top 50 cm of peat layer) (*e.g.*, peat depth, rainfall, dissolved O_2, lignin, fatty
328 acids (short and long), phenolic compounds) were explored using regression analyses. The %
329 of variance accounted (adjusted R^2) is presented in the figures. Results through text and
330 tables are presented as mean ± SE. All statistical analyses were performed using GenStat
331 (14th edition, VSN International, 2011).

3. Results

3.1 Vegetation survey and nutrients

Vegetation survey data indicated that at the Chiriqui, Cricamola and San San Pond Sak 1 sites, *R. taedigera* was the dominant species; whereas at the San San Pond Sak 2, Almirante and Damani-Guariviara sites, *C. panamensis* dominates (Table 1; Table S1). The deepest core was collected at the Damani-Guariviara site, followed by the San San Pond Sak 2 site, both dominated by *C. panamensis*; whilst the shallowest core was recorded at the Chiriqui site dominated by *R. taedigera*. The total depth of the peat deposit was independent of the vegetation community that currently dominates the area ($F_{1,4} = 0.94$, $P > 0.05$). Similarly, total nutrients at the top layer of peat did not varied significantly with respect to the vegetation community (TC: $F_{1,4}= 0.05$, $P > 0.05$; TN: $F_{1,4} = 0.2$, $P > 0.05$; TS: $F_{1,4} = 3.2$, $P > 0.05$; TP: $F_{1,4} = 3.4$, $P > 0.05$) (Table 2).

3.2.1 Spatial and temporal variation of greenhouse gas fluxes

No significant difference of the CO_2 and CH_4 fluxes between the two vegetation communities was observed, *i.e.*, palm swamp and mixed forest (Fig. 1; Table 3). However, the water table position with respect to the peat surface did influence both CO_2 and CH_4 emission (Fig. 2 and 3; Table 3).

In palm swamps, CH_4 fluxes presented a mean value of 3.99 ± 0.6 mg m^{-2} h^{-1}, with higher values being observed when the water table was located above the peat surface (> 5 cm; 6.33 ± 1.30 mg m^{-2} h^{-1}) in comparison with the water table being located below the surface (< 5 cm; 3.5 ± 0.64 mg m^{-2} h^{-1}). For mixed forest, the mean CH_4 flux was 3.19 ± 0.59 mg m^{-2} h^{-1}. Parallel to palm swamp, higher CH_4 flux from mixed forest occurred when the water table

was above the peat surface (4.25 ± 1.07 mg m^{-2} h^{-1}), in comparison with the 3.05 ± 1.2 mg m^{-2} h^{-1} observed when the water table was below the peat surface. The highest CH_4 flux registered for mixed forest and palm swamp were 48.89 mg m^{-2} h^{-1} (water table: - 5 cm) and 38.78 mg m^{-2} h^{-1} (water table: 8 cm), respectively. In the case of CO_2, higher fluxes were observed when water table was located below the peat surface for both palm swamp (383 ± 25 mg m^{-2} h^{-1}) and mixed forest (376 ± 25 mg m^{-2} h^{-1}) (Fig. 3). The highest CO_2 flux for mixed forest and palm swamp were 913.18 mg m^{-2} h^{-1} (water table: - 30 cm) and 719.94 mg m^{-2} h^{-1} (water table: - 20 cm), respectively. Both CO_2 and CH_4 fluxes varied significantly through the year (Fig. 1, Table 3). The CO_2 flux followed a seasonal pattern, increasing during periods of low rainfall and water table draw down (Fig. 1a,b). By contrast, the CH_4 flux did not follow a seasonal trend associated to precipitation (Fig. 1c,d).

3.2.2 Greenhouse gas flux and peat physicochemical characteristics

Among the physicochemical variables that were explored by linear regression (*e.g.*, water table level, C:N ratio, methylated fatty acids, lignin content), only water table had a significant inverse linear relationship with CO_2 flux (Fig. 4; Table S4). However, it is important to consider that, the amount of variance accounted by the model predicting CO_2 flux from water table levels was low (*i.e.*, $R^2 = 0.15$). Long chain fatty acids (> C20), which represent a relatively labile substrate in peat, had a significant inverse linear relationship with CH_4 flux ($R^2 = 0.15$; Table S4). A qualitative difference between the composition of surface peat chemistry between the two phasic communities (*i.e.*, mixed forest and palm swamp) has been previously reported (Hoyos-Santillan et al., 2016b). This difference is mainly related to the relative abundance of distinct lignin moieties (*e.g.*, *p*-coumaryl, coniferyl, and sinapyl), which are related to the recalcitrance of organic matter. However, although lignin and

phenolic compounds abundance is related to organic matter quality, they did not present a significant linear regression model for CO_2 or CH_4 (Table S4).

3.3 Effect of nutrient addition on greenhouse gas fluxes

Five months after the addition of nutrients *in situ* at the San San Pond Sak peatland (San San Pond Sak 1 – palm swamp and San San Pond Sak 2 - mixed forest; Fig. S1), N and P did not affect the content of dissolved organic carbon at the top peat layer of the study sites (DOC-$N_{addition}$: $F_{1,29} = 1.53$, $P > 0.05$; DOC-$P_{addition}$: $F_{1,29} = 0.02$, $P > 0.05$) (Hoyos-Santillan et al., 2018). However, the addition of nitrogen did significantly increase the content of total dissolved nitrogen in the surface peat (TDN-$N_{addition}$: $F_{1,28} = 8.71$, $P < 0.01$) and the addition of P increased the content of readily-exchangeable P in the upper layer of peat (REP-$P_{addition}$: $F_{1,56} = 7.67$, $P < 0.01$) (Table S5) (Hoyos-Santillan et al., 2018).

During the greenhouse gas monitoring event at the fertilized sites, water table was 10 cm above the peat surface at the mixed forest and 25 cm below the peat surface at the palm swamp. Fluxes of CO_2, CH_4, and N_2O were significantly different between the two vegetation communities (CO_2-Vegetation community: $F_{1,18} = 12.79$, $P < 0.01$; CH_4-Vegetation community: $F_{1,14} = 53.82$, $P < 0.001$); N_2O-Vegetation community: $F_{1,13} = 138$, $P < 0.001$). Nutrient addition only increased CH_4 fluxes when N alone was added at the mixed forest (CH_4-Treatment: $F_{3,24} = 18.79$, $P < 0.001$) (Fig. 5c). Addition of N, P, and NP did not have a significant effect on the fluxes of CH_4 at the palm swamp, nor on the CO_2 and N_2O fluxes from both vegetation communities (Fig. 5).

4. Discussion

403 4.1 Variation in CO_2 and CH_4 fluxes due to vegetation communities

404 In our first hypothesis, we set out to test how vegetation communities could potentially
405 influence the magnitude of CO_2 and CH_4 fluxes in coastal tropical peatlands. Our results
406 suggest that, throughout a year, there was no significant difference in the magnitude of the
407 CO_2 and CH_4 fluxes due to the vegetation community (Fig. 1; Table 3). Therefore, the overall
408 CO_2 and CH_4 fluxes, from the peat surface, do not vary between the mixed forest and palm
409 swamp in spite of the physiological differences between the dominant species inhabiting the
410 sites *(i.e., C. panamensis* and *R. taedigera*) (Table S1), particularly the contrasting structure
411 of their root system. It is important to mention that our approach did not measure CH_4
412 transport through the vegetation structures (*e.g.* lenticels, pneumatophores, stems, leaves)
413 which could be potentially different among the distinct tree species (Welch et al., 2019).
414 Indeed, it has been quantified that large quantities of CH_4 are emitted through trees in tropical
415 ecosystems, contributing with up to 58 % of the total CH_4 fluxes from tropical ecosystems
416 (Pangala et al., 2017). Furthermore, it has been reported that roots respiration contributes
417 with up to 49 % of the overall CO_2 flux from the peat surface (Girkin et al., 2018a).

418 Despite the fact that it has been observed that belowground peat is also actively producing
419 CO_2 and CH_4 (Wright et al., 2011), the mean peat depth, varying from 96 ± 7 to 483 ± 98 cm
420 (Table 1), did not provide a reliable predictor for the overall CO_2 and CH_4 gas fluxes from the
421 peat surface. This may be due to the fact that the layers contributing the most to the peat
422 surface CO_2 and CH_4 fluxes correspond to those located in the top 1 m, under water logged
423 conditions (Hoyos-Santillan et al., 2016b; Wright et al., 2011). Consequently, even though
424 CO_2 and CH_4 are produced below the 1 m peat layer, deeper layers contribute to lesser extent
425 to the overall production and do not significantly affect the vertical cumulative flux of these
426 gases. In addition, gas transport mediated by vegetation, including radial oxygen loss through
427 the roots (Hoyos-Santillan et al., 2016a), as well as the release of root exudates (Girkin et al.,

2018), are mainly constrained to the upper peat layers in the rhizosphere influence zone, were most of peat's CO_2 and CH_4 are produced.

The magnitude of the CO_2 and CH_4 fluxes from the peat surface measured in this study are consistent with those previously reported for peatlands in South East Asia, South America, Central America, Hawaii and the Congo River Basin (Sjögersten et al., 2014). Thus, our fluxes fall within a relatively well constrained range of magnitudes comprising several types of vegetation and different geographical locations. For example, our maximum recorded CO_2 fluxes (*i.e.*, 913.18 and 719.94 mg m^{-2} h^{-1}) are comparable to those previously reported for Indonesia (950 mg m^{-2} h^{-1}) (Hirano et al., 2009), Malaysia (905 mg m^{-2} h^{-1}) (Melling et al., 2005), and Brazil (583 mg m^{-2} h^{-1}) (Belger et al., 2011). Likewise, our maximum registered CH_4 fluxes (48.89 and 38.78 mg m^{-2} h^{-1}) are in the same order of magnitude than the maximum reported for Hawaii (14.17 mg m^{-2} h^{-1}) (Grand and Gaidos, 2010), Costa Rica (40.4 mg m^{-2} h^{-1}) (Nahlik and Mitsch, 2011), Venezuela (95.3 mg m^{-2} h^{-1}) (Smith et al., 2000), and Brazil (47.3 mg m^{-2} h^{-1}) (Devol et al., 1990).

4.2 Influence of water table on CO_2 and CH_4 fluxes

With respect to our second hypothesis, predicting higher CO_2 fluxes during the dry season in comparison with the wet season and the opposite for CH_4 fluxes, CO_2 fluxes did suggest an apparent seasonal trend, increasing as monthly precipitation rates decreased (Fig. 1a,b). However, CH_4 fluxes did not show a clear seasonal pattern (Fig. 1c,d). The seasonal trend observed on the CO_2 fluxes has been previously described in other tropical peatlands, with high fluxes being observed during the dry season and relatively lower fluxes occurring during the wet season (Jauhiainen et al., 2005; Wright et al., 2013). This trend is related to the decrease of the water table level during low precipitation periods, exposing recently produced

organic matter (*e.g.* litter and root exudates) and peat to oxic conditions (Baird et al., 2017), under which rapid aerobic decomposition can occur (Hoyos-Santillan et al., 2015). Indeed, water table does directly respond to precipitation, raising several centimeters above the peat surface during heavy rainfall periods (> 30 cm) (Chimner and Ewel, 2004), and dropping below the surface as the precipitation is no longer sufficient to maintain a steady water table level close to or above the surface (Jauhiainen et al., 2005). We did observe higher CO_2 fluxes when the water table was located below the surface (Fig. 3a; Table 3). The CO_2 fluxes increased 80 and 51 % at the mixed forest and palm swamp, respectively, as the level of the water table decreased with respect to the peat surface. Such increases in CO_2 fluxes at lower water tables is plausibly linked to increased activity of the bacteria community or a shift in abundance of the microbial community, *e.g.* towards gram positive bacteria, which are more abundant in surface peat (Dhandapani et al., 2018; Jackson et al., 2009).

CH_4 fluxes did not present a clear seasonal trend associated with precipitation rates (Fig. 1c,d), this has been reported in other tropical peatlands (Wright et al., 2013), in association with a highly variable fluxes as the ones observed in this study. However, we did observe higher CH_4 fluxes when the water table was above the surface in comparison to those fluxes when the water table was located below the surface (Fig. 3b; Table 3). Methane fluxes were 39 and 81 % higher at the mixed forest and palm swamp, respectively, when the water table was located above the peat surface compared to when the water table was below the peat surface. This is due to the anoxic conditions being promoted by high water table levels, functioning as a barrier for oxygen transfer from the atmosphere to the peat matrix, facilitating methanogenesis (Sepulveda-Jauregui et al., 2018) (Fig. 3b. Table 3). Thus, our results are consistent with previous research indicating that the level of the water table with respect to the peat surface is among the main drivers controlling greenhouse gases fluxes (Cobb et al., 2017; Couwenberg et al., 2011; Hirano et al., 2009; Jauhiainen et al., 2005).

It is important to consider that, the water table level is directly related to the type of vegetation that is currently producing or produced the peat, the stratigraphic structure defining the hydraulic properties of peat (Couwenberg and Joosten, 1999; Joosten and Clarke, 2002), and the regional precipitation rates. Our results suggest that, the vegetation at the mixed forest and the palm swamp exert an overall equivalent effect on the water table and peat properties, creating similar conditions for greenhouse gases emissions in both vegetation communities. Nevertheless, microtopography can promote strong fluctuations of the water table levels during the same day at the same area (Lampela et al., 2014), potentially affecting CO_2 and CH_4 fluxes in relatively short periods of time. It is necessary that new and larger data sets of greenhouse gas fluxes are produced, considering the water table fluctuations, in order to reduce the uncertainty of the current greenhouse gas budgets from tropical peatlands. Furthermore, since greenhouse gas emissions transported through vegetation were not measured in this study, it is important that future studies explore the contribution of such fluxes to the overall emissions in different ecosystems, as well as exploring the interaction between the water table level and the tree mediated transport (*e.g.*, effect of water table on pneumatophores and lenticels functioning) (Welch et al., 2019).

4.3 Peat composition effect on CO_2 and CH_4 fluxes

In our evaluation of our third hypotheses, testing how peat composition could potentially affect CO_2 and CH_4 fluxes (*i.e.* C:N ratio; peat content of lignin, short and long fatty acids, and phenolic compounds), only the content of long fatty acids moderately influenced CH_4 fluxes (Table S4). This is related to the origin of the main substrates contributing to produce CO_2 and CH_4 in peat. For example, readily decomposable compounds such as root exudates (*i.e.*, young carbon) (Couwenberg and Fritz, 2012; N.T. Girkin et al., 2018; Segers, 1998) and

compounds derived from recently fallen litter (Hoyos-Santillan et al., 2016b) are the most important carbon sources for heterotrophic microbial communities involved in methanogenic pathways. Regarding the abundance of lignin moieties in the surface peat, sites dominated by *R. taedigera* have been reported to have higher content of *p*-coumaryl alcohol than sites dominated by *C. panamensis*, and sites dominated by *C. panamensis* have a higher content of coniferyl and sinapyl alcohols (Hoyos-Santillan et al., 2016b). This is due to the fact that monocotyledoneous angiosperms (*e.g.*, *R. taedige*ra palms), develop hydroxyl phenol-guaiacyl-syringyl lignin (Ek et al., 2009), whilst dicotyledonous trees (*e.g.*, *C. panamensis* hardwood tree) develop syringyl-guaiacyl lignin, rich in coniferyl alcohol (Ek et al., 2009). These differences contribute to define the recalcitrance of peat; for example, hardwood lignin is more resistant to decomposition (Vancampenhout et al., 2008) than phenol-guaicyl-syringyl lignin. However, lignin content was not a good predictor for CO_2 or CH_4 gas fluxes.

Rapid decomposition of old peat mainly occurs if water table draws down (*e.g.*, peat drainage), for a period of time long enough for oxic conditions to be stablished (Hooijer et al., 2012). However, under waterlogged conditions, the less recalcitrant organic matter remains as the main substrate for CO_2 and CH_4 production (Hoyos-Santillan et al., 2016b). Consequently, in order to maintain the stability of old peat, (> 5000 years old in the study area), all factors necessary to maintain a high water table, such as the input of autochthonous vegetation litter, constant input of water, and the stability of the peat structure at top layers must be preserved.

4.4 Nutrient addition impact on CO_2, CH_4, and N_2O fluxes

Regarding our fourth hypothesis, predicting that the addition of N and P to the peat would increase CO_2 CH_4, and N_2O fluxes, our data showed that only the individual addition of

525 nitrogen increased CH_4 fluxes in the mixed forest (Fig. 5c). The increase in CH_4 fluxes as
526 response to N addition has been previously reported for several ecosystems (Banger et al.,
527 2012; Liu and Greaver, 2009), and has been related to alterations on the methanogenesis and
528 methanotrophy rates. Indeed, the balance between these two processes, occurring
529 simultaneously in soil, determines the net CH_4 emission (Aerts and Toet, 1997; Schnell and
530 King, 1994). The mechanisms that have been associated to an increase in CH_4 emissions due
531 to N addition are related to the inhibition of methanotrophy and the enhancement of
532 methanogenesis (Banger et al., 2012). For example, in our experiment, it is plausible that the
533 following mechanisms, inhibiting CH_4 oxidation in peat, were responsible for the net increase
534 of CH_4 emission following N addition at the mixed forest: i) competitive inhibition of
535 methane monooxygenase (MOO) by ammonium (NH_4^+) (Bédard and Knowles, 1989), and ii)
536 toxicity of nitrite (NO_2^-), which is the end product of methanotrophic ammonia oxidation, to
537 methanotrophs (Schnell and King, 1994). The addition of P or NP did not significantly
538 influence CO_2, CH_4, or N_2O fluxes. Consistently with the seasonal monitoring experiment,
539 the water table played a major role as driver of greenhouse gas fluxes. The CO_2 fluxes were
540 significantly higher when the water table was located below the water surface at the palm
541 swamp, whereas higher CH_4 fluxes were observed when the water table was above peat
542 surface at the mixed forest (Fig. 3). Since the water table has such a strong effect on the
543 magnitude of the fluxes, it is possible that the controls posed by the water table had cancelled
544 out, to some extent, the effect related to the vegetation community or nutrient addition. The
545 higher fluxes of N_2O observed with low water table are explained by the dependency of N_2O
546 production with the oxic-anoxic conditions in the peat. As the water table drops, ammonia is
547 oxidized through nitrification producing NO_2^- and NO_3^-; NO_2^- is then reduced under
548 microaerophilic conditions in areas of the peat matrix with 70 – 80 % of moisture saturation
549 releasing as one of the byproducts N_2O (Butterbach-Bahl et al., 2013). Thus, the fluctuation

of the water table may work as a two stage system that, during the low level conditions, produces the substrates that are precursors for N_2O once the water table rises. The average N_2O fluxes at the mixed forest and the palm swamp (mixed forest: 0.018 ± 0.005 mg m^{-2} h^{-1}; palm swamp: 0.206 ± 0.012 mg m^{-2} h^{-1}) are in the same order of magnitude of those reported for pristine and anthropogenically impacted palm swamps in the region (pristine: 0.06 ± 0.008 mg m^{-2} h^{-1}; anthropogenically impacted: 0.09 ± 0.015 mg m^{-2} h^{-1}) (Hoyos-Santillan et al., 2016a).

Alternatively, it is plausible that the addition of nutrients did not influence the greenhouse gas fluxes because the system was not limited by N or P, but was limited by the availability of easily degradable organic matter that could be used for the heterotrophic processes involved in the different gas production pathways. Indeed, nutrient addition does not affect litter decomposition in this ecosystems either (Hoyos-Santillan et al., 2018).

4.5 Implications for the estimation of CO_2 and CH_4 fluxes on a regional scale

The type of vegetation currently inhabiting the studied peatlands, the mean peat depth, the peat composition and the nutrient availability did not represent good predictors of the overall fluxes of CO_2 and CH_4 from the peat surface. As consequence, our results suggest that discrimination among vegetation communities does not represent a relevant aspect when developing projections of CO_2 or CH_4 emissions from the surface of tropical forested peatlands. This is important when developing projections of carbon budgets by using remote sensing approaches (top-down), for it would be possible to include all types of forested peatlands into one category rather than developing thorough vegetation surveys. It is important to consider that our estimations do not consider the emissions transported through vegetation. Evaluating such contribution would require further studies on the specific

capacity of gas conduction by different plant species. However, in line with literature, the water table level was one of the main drivers controlling greenhouse gas emissions in the studied ecosystems (Couwenberg et al., 2011; Couwenberg and Fritz, 2012). Therefore, CO_2 and CH_4 fluxes in coastal tropical peatlands could potentially be estimated, within a relatively narrow range, if the fluctuation of the water table is measured in a regular basis through satellite or airborne imagery (Bechtold et al., 2018; Kalacska et al., 2018). For example, it has been possible to evaluate the dynamics of water table in temperate peatlands by using the Advance Synthetic Aperture Radar data from ENVISAT and Sentinel satellites (Asmub et al., 2018; Bechtold et al., 2018; Dabrowska-Zielinska et al., 2016). Thus, by reducing uncertainty on the measurements of greenhouse gas fluxes at the peat's surface, and relating them with variables such as the level of the water table, it would be possible to develop better top-down projections, with seasonal resolution, of the carbon fluxes from tropical peatlands. Furthermore, since the CO_2 and CH_4 fluxes were independent from the peat depth, it is not required to measure it in order to develop estimations of the overall greenhouse gas fluxes.

Based on our average fluxes, including the distinct positions of the water table (CO_2-above surface: 230.97 ± 20.56 mg m^{-2} h^{-1}, CH_4-above surface: 5.43 ± 1.75 mg m^{-2} h^{-1}; CO_2-below surface: 381.44 ± 36.85 mg m^{-2} h^{-1}, CH_4-below surface: 3.25 ± 0.46 mg m^{-2} h^{-1}), we estimated that the contribution of CH_4 to the overall emissions from the peat surface, accounts for ≈ 20 % of the total emissions when the water table is below the surface (expressed as CO_2 equivalents (CO_{2eq}; global warming potential value relative to CO_2: CH_4 = 28). This contribution increases, with respect to CO_2, as the fraction of the flooded peatland area increases, potentially reaching 40 % in terms of CO_{2eq}, considering the scenario where water table for the entire peatland is above the surface (Fig. 6). Nevertheless, CO_2 remains the most important contributor to greenhouse gas emissions in these ecosystems under both the non-

598 flooded or completely flooded scenarios, as previously observed in other tropical peatlands
599 (Hergoualc'h and Verchot, 2014; Hirano et al., 2009).

600

601 **5. Conclusions**

602

603 We conclude that the magnitude of the fluxes of CO_2 and CH_4 at the peat surface in forested
604 lowland tropical peatlands is independent of the vegetation communities. However, water
605 table level functions as a strong factor controlling CO_2 and CH_4 fluxes from forested tropical
606 peatlands, with CO_2 and CH_4 fluxes increasing when the water table was below or above the
607 peat surface, respectively. Therefore, the distribution of vegetation communities alone should
608 not be used as a proxy to estimate the magnitude of greenhouse gas emissions. Finally,
609 additional relevance must be given to the development of remote sensing alternatives
610 allowing to monitor the water table in tropical peatlands on a regular basis. This will provide
611 valuable information that will help to predict large fluctuations on the magnitudes of CO_2,
612 CH_4, and N_2O fluxes in these ecosystems.

613

614 **Acknowledgments**

615 J.H.S. thanks The National *Council* on Science and Technology (*CONACyT-Mexico*) for his
616 PhD scholarship (211962). The authors also thank the Light Hawk program for its support in
617 the aerial surveys. We thank Erick Brown for field assistance, and Gabriel Jácome, Plinio
618 Góndola, Dayana Agudo, Tania Romero, Luis A. Ramos, Dianne de la Cruz, Vanessa Pardo,
619 John Corrie and Darren Hepworth for logistical and laboratory support. The authors declare
620 that there are no conflicts of interest.

Data accessibility

Data to support this article is publicly available at Dryad Digital Repository

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889

890 **Figures and tables captions**

891

892 **Fig. 1** Greenhouse gas fluxes across an annual cycle: CO_2 (a,b) and CH_4 (c,d) fluxes at the
893 mixed (a,c) forest and palm swamp (b,d). Dash line represents cumulative monthly
894 precipitation. Relevant statistics are presented in Table 3.

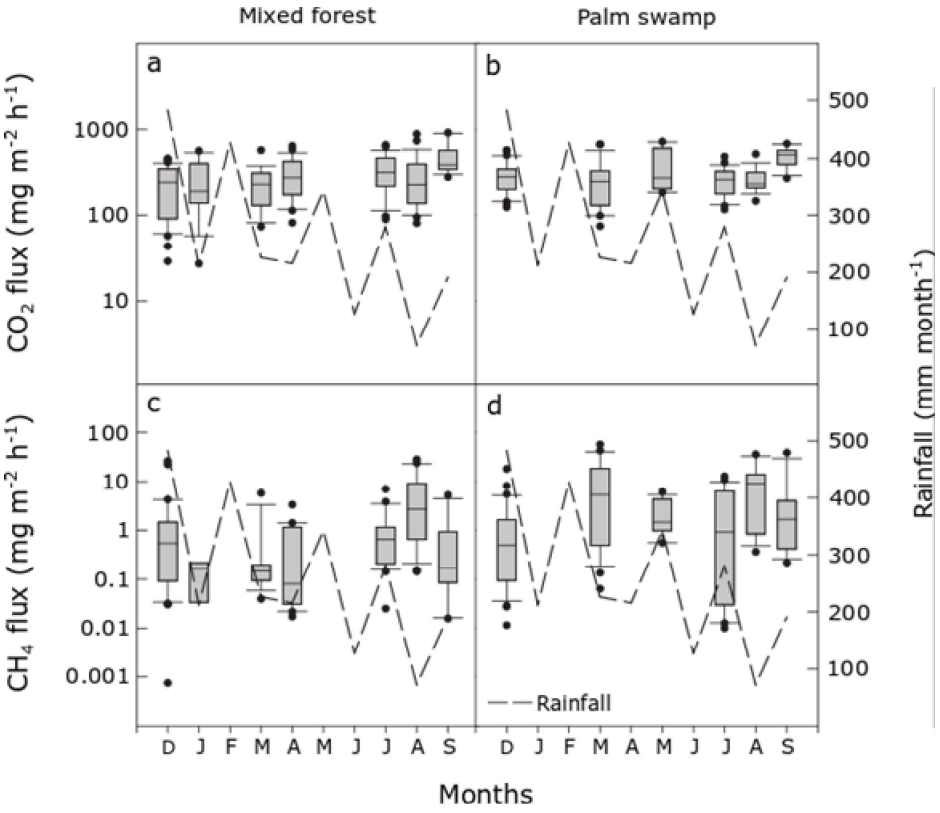

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Fig. 2 Water table level at all sites during the annual monitoring period. Open and closed circles correspond to mixed forest (○) and swamp sites (●), respectively.

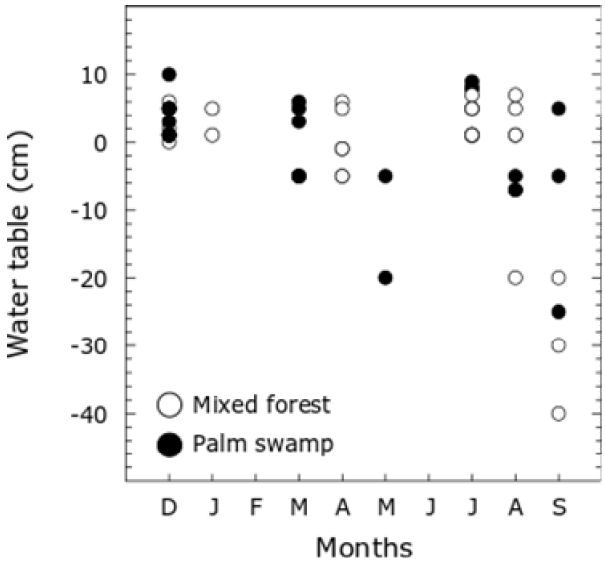


Fig. 3 Effect of water table position (above, at, and below the surface) on CO_2 (a) and CH_4 (b) fluxes at the mixed forest (grey boxes) and palm swamp (white boxes) sites. Relevant statistics are presented in Table 3.

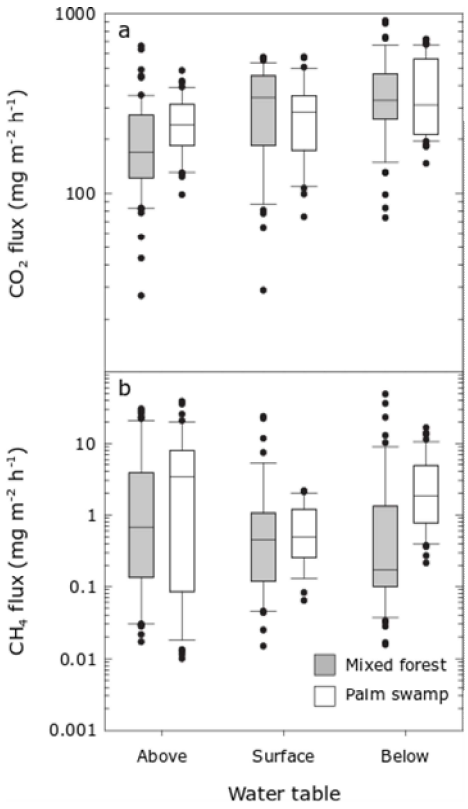


Fig. 4 Regression analyses between greenhouse fluxes (CO_2 (a,b,c) and CH_4 (d,e,f)) and *in situ* parameters (water table level, dissolved oxygen in top 0.5 m, and peat's surface temperature). Symbols represent mean ± SE. Variance accounted by the model is reported as the adjusted R^2 within the figures; a summary of the statistical information regarding the regressions analyses is presented in Table S4.

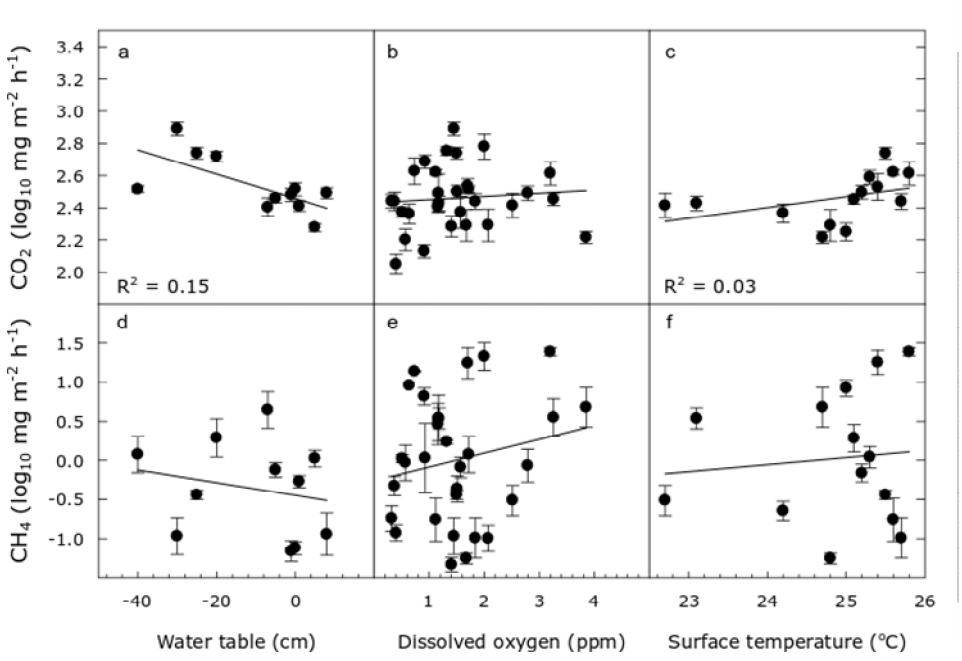
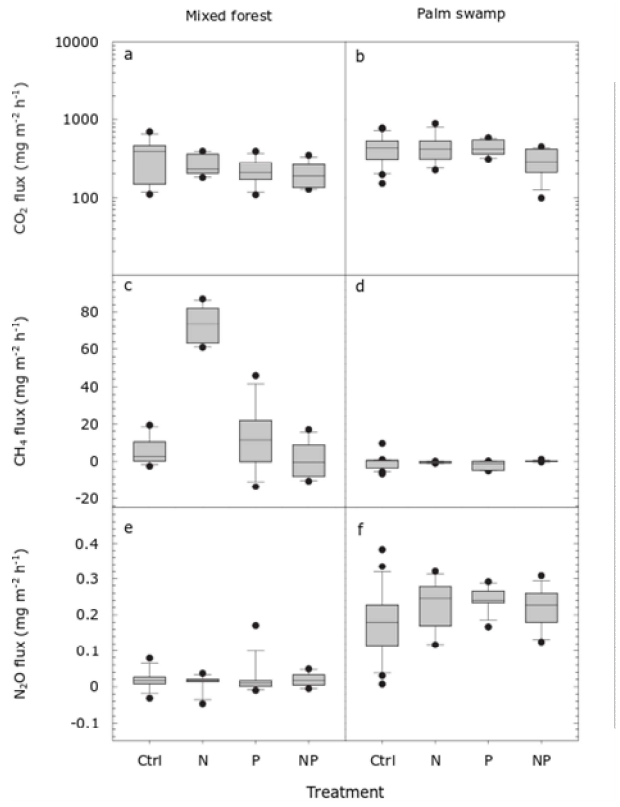
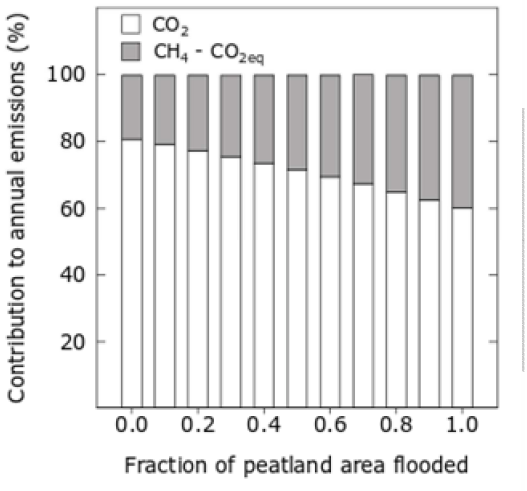


Fig. 5 Effect of control (Ctrl), nitrogen (N), phosphorus (P), and nitrogen+phosphorus (NP) treatment on CO_2 (a,b), CH_4 (c,d), and N_2O (e,f) fluxes at the mixed forest (a,c,e) and palm swamp (b,d,f). Statistical analyses are presented in the text.



912

913 **Fig. 6** Relative contribution of CO_2 (white bars) and CH_4 (grey bars) to the overall annual
914 emissions as function of the percentage of flooded area. CH_4 contribution is presented as CO_2
915 equivalents (CO_{2eq}; CO_2:CH_4 GWP = 28). Calculations are based on the mean greenhouse
916 gas fluxes under the distinct flooding scenarios (water table above and below the peat's
917 surface).



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920 **Table 1.** Location and characteristics of study sites.

Table 1. Location and characteristics of study sites

Site		Coordinates	Distance to coast (m)	Phasic community	% basal area (m^2 ha^{-1})	Peat depth (cm)[c]	^{14}C (yr B.P.)
1	Chiriquí Grande	8°58'28.22"N, 82°07'52.85"W	140	Palm swamp	88.3	96 ± 7	-
2	Cricamola River	8°57'17.70"N, 81°54'41.35"W	1400	Palm swamp	70.9	316 ± 37	-
3	San San Pond Sak 1[a]	9°25'29.20"N, 82°24'05.60"W	500	Palm swamp	98.9	187 ± 5	-
4	San San Pond Sak 2[b]	9°25'15.00"N, 82°24'14.64"W	1000	Mixed forest	38.7	362 ± 19	3,040 ± 80[d]
5	Damani-Guariviara	8°57'02.34"N, 81°49'32.40"W	518	Mixed forest	31.6	483 ± 98	5,100 ± 40[e]
6	Almirante Bay	9°18'17.46"N, 82°21'07.14"W	200	Mixed forest	29.5	165 ± 15	-

[a,b] San San Pond Sak sites 1 and 2 correspond to sites 1 and 2, respectively, from Sjögersten et al. (2011). Nutrient addition experiment was conducted in these sites
[c] Peat definition: 30 % of dry weight organic matter (Joosten and Clarke 2002). Depths correspond to the mean values recorded when peat cores were collected and do not reflect the overall depth in the sites (mean ± SE, n = 3)
[d] Data from Phillips and Bustin (1996); the maximum age of the deposit is estimated between 4,000 to 4,500 yr
[e] Accelerator mass spectrometer (AMS) dating Beta-300182; Cal BP ± 2 σ = 5,920 to 5,740 (Hoyos-Santillan 2014). Peat sample from 6 m depth

921 **Table 2.** Physicochemical characteristics of peat from the top 10 cm layer.

Table 2. Physicochemical characteristics of peat from the top 10 cm layer 922

Site	pH	Conductivity	Bulk Density	Loss on ignition	Total elements			
					C	N	S	P
		µS cm^{-1}	g cm^{-3}	%	mgC g^{-1}	mgN g^{-1}	mgS g^{-1}	µgP g
Chiriqui Grande	4.79 ± 0.08	142 ± 26	0.06 ± na	88.5 ± 2.8	356 ± 120	12.7 ± 5.3	3.9 ± 1.6	476 ± na
Cricamola River	5.52 ± 0.75	108 ± 15	0.13 ± na	71.9 ± 9.4	458 ± 250	22.9 ± 18.2	4.7 ± 1.6	216 ± na
San San Pond Sak 1[a]	5.05 ± 0.23	64 ± 50	0.11 ± na	91.7 ± 2.3	502 ± 200	12.1 ± 5.5	1.3 ± 0.7	267 ± na
San San Pond Sak 2[b]	5.34 ± 0.53	62 ± 25	0.11 ± na	94.2 ± 0.4	506 ± 250	20.3 ± 12.3	25.2 ± 12	205 ± na
Damani-Guariviara	5.38 ± 0.55	55 ± 18	0.11 ± na	92.9 ± 2.1	536 ± 190	15.8 ± 1.5	57.7 ± 13	50 ± na
Almirante Bay	5.59 ± 0.09	57 ± 10	0.09 ± na	94.6 ± 0.6	470 ± 40	20.9 ± 2.9	2.1 ± 0.1	212 ± na

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[a,b] San San Pond Sak sites 1 and 2 correspond to Sites 1 and 2 respectively from Sjögersten *et al*. (2011) 926

Values are mean ± SE of three peat samples, with the exception of bulk density and P, which were measured from a single sample
Bulk density and total elements are presented in a dry weight basis. na, not available 927

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929 **Table 3.** Summary of REML outputs: CO_2 and CH_4 fluxes (log_{10} mg m^{-2} h^{-1}).

Table 3. Summary of REML outputs: CO_2 and CH_4 fluxes (log_{10} mg m^{-2} h^{-1})

	F	df	*P*
CO_2			
Vegetation community (VC)[a]	0.54	1,4	> 0.05
Water table (WT)[b]	34.71	2,267	< 0.001
Time[c]	10.05	5,266	< 0.001
VC × WT	0.79	2,268	> 0.05
VC × Time	3.45	5,267	< 0.01
WT × Time	6.04	6,267	< 0.001
VC × WT × Time	7.51	2,265	< 0.001
CH_4			
Vegetation community (VC)	0.90	1,4	> 0.05
Water table (WT)	3.26	2,250	< 0.01
Time	15.54	5,250	< 0.001
VC × WT	0.48	2,251	> 0.05
VC × Time	23.44	5,250	< 0.001
WT × Time	3.87	6,251	< 0.001
VC × WT × Time	4.12	2,250	< 0.05

Notes: [a]Vegetation community: three *R. taedigera* palm swamps and three *C. panamensis* mixed forests; [b]Water table classification considered: below peat surface, at the surface or above the peat surface; [c]Time corresponds to the six sampling blocks distributed through the year (*i.e*. three during rain and three during dry season)

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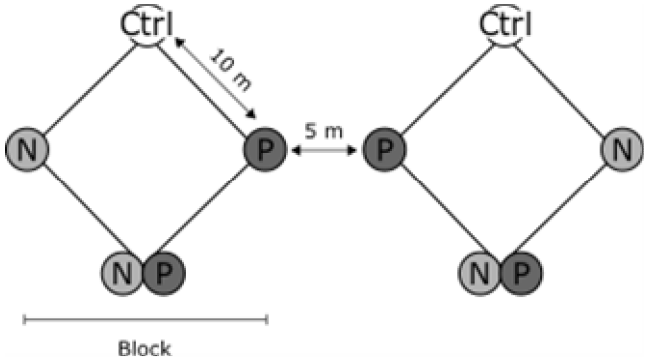
Figure S1. Location of palm swamp and mixed forests sites for annual monitoring of CO_2 and CH_4 fluxes from peat surface. The distribution of blocks for the fertilization experiment are presented for the San San Pond Sak 1 and San San Pond Sak 2 sites.

Figure S2. Schematic diagram outlining the experimental set up for the nutrient addition, (Ctrl) control, (N) nitrogen and (P) phosphorous. The diagram is taken from (Hoyos-Santillan et al., 2018). The same set up was used at the palm swamp and the mixed forest sites. Ten blocks were set up at each site with litterbags placed both at the peat surface and at 50 cm depth. Distribution of blocks in San San Pond Sak 1 and San San Pond Sak 2 is presented in Fig. S1.



943 **Table S1.** Vegetation survey: Contribution to the total basal area (%) of trees species from individuals with ≥ 10 cm diameter at breast height.

Table S1 Vegetation survey: Contribution to the total basal area (%)*of trees species from individuals with ≥ 10 cm diameter at breast height

Species	Chiriqui	Cricamola	San san pond sak 1[a]	San san pond sak 2[b]	Almirante	Damani-Guariviara
Alchornea latifolia Sw.			0.3	0.6	0.1	
Ardisia sp.				1.0	0.4	
Campnosperma panamensis Standl.			0.2	**38.7**	**75.6**	**77.4**
Cassipourea elliptica (Sw.) Poir.				25.0	6.0	
Chrysobalanus icaco L.						
Clusia cf. rosea Jacq.				1.1		0.8
Cyrilla racemiflora L.						
Drypetes standleyi G.L. Webster				1.0	0.5	
Elaeis oleifera	5.51					
Euterpe precatoria Mart.				10.0	1.4	0.6
Fabaceae						5.13
Ficus brevibracteata W.C. Burger			0.3			
Ficus costaricana (Liebm.) Miq.				0.3		
Ficus maxima Mill.			0.2			
Ficus sp.	2.8	3.0		0.3		
Inga sp		0.2				
Myrica mexicana Humb. & Bonpl. ex Willd.						0.6
Manicaria saccifera		22.7				5.6
Maquira guianensis	6.8					
Pterocarpus officinalis	3.71					
Raphia taedigera (Mart.) Mart.	**80.5**	**70.9**	**98.9**		12.5	
Symphonia globulifera L.f.	0.5			21.7	3.2	
Trophis		0.1				

[a,b] San San Pond Sak sites 1 and 2 data correspond to that from Sites 1 and 2, respectively, from Sjögersten *et al*. (2011)

*Species contributing the most to the proportion of the basal area are presented in bold font.

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946 **Table S2.** Sampling and monitoring dates for greenhouse gas fluxes (mm/dd/yy).

Table S2. Sampling and monitoring dates for greenhouse gas fluxes during wet and dry seasons (mm/dd/y)

Site	Block 1 (wet)	Block 2 (dry)	Block 3 (wet)	Block 4 (wet)	Block 5 (dry)	Block 6 (dry)
Chiriquí Grande	12/16/2010	03/24/2011	05/17/2011	07/06/2011	08/11/2011	09/15/2011
Cricamola River	12/10/2010	03/19/2011	05/28/2011	07/14/2011	08/10/2011	09/14/2011
San San Pond Sak 1[a]	12/07/2010	03/06/2011	05/16/2011	07/17/2011	08/12/2011	09/16/2011
San San Pond Sak 2[b]	12/21/2010	01/16/2011	04/27/2011	07/11/2011	08/14/2011	09/11/2011
Damani-Guariviara	12/08/2010	03/17/2011	04/07/2011	07/13/2011	08/09/2011	09/12/2011
Almirante Bay	12/05/2010	03/25/2011	04/06/2011	07/15/2011	08/13/2011	09/13/2011

[a,b] San San Pond Sak sites 1 and 2 correspond to Sites 1 and 2, respectively from Sjögersten *et al*., 2010
Gas samples were collected during daylight between 9 am and 4 pm
Wet and dry seasons were defined based on the historic data from the Smithsonian Tropical Research Institute Physical Monitoring Program

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952 **Table S3.** Extractable and microbial dissolved organic carbon (DOC), total dissolved nitrogen (TDN), and readily-exchangeable phosphorus

953 (REP) at the fertilized plots. Data is presented as mean ± SE.

Table S3. Extractable and microbial dissolved organic carbon (DOC), total dissolved nitrogen (TDN), and readily-exchangeable phosphorus (REP) at the fertilized plots.

Site	Community	Treatment	DOC (µgC g^{-1})		TDN (µgN g^{-1})		REP (µgP g^{-1})	
			Ext	Mic	Ext	Mic	Ext	Mic
PS1[a]	Palm swamp	C	240.7 ± 29.6	1254.7 ± 266	62.5 ± 5.9	170.2 ± 38.0	24.8 ± 3.0	239.4 ± 22.3
		N	151.9 ± 11.4	609.0 ± 156.7	43.7 ± 6.9	81.8 ± 22.6	14.5 ± 3.3	186.2 ± 42.8
		P	237.1 ± 10.4	714.1 ± 353	67.2 ± 19.7	102.6 ± 51.5	243.6 ± 65.6	149.7 ± 45.6
		NP	291. 5 ± 86.8	826.2 ± 303.7	78.3 ± 22.6	103.9 ± 32.2	212.1 ± 44.3	151.1 ± 70.1
PS2[b]	Mixed forest	C	176.0 ± 45.6	331.2 ± 54.9	46.1 ± 10.2	40.0 ± 6.0	7.8 ± 1.8	146.8 ± 46.0
		N	159.4 ± 65.3	296.8 ± 38.2	886.5 ± 333.4	144.7 ± 74.8	5.7 ± 1.3	79.4 ± 8.3
		P	234.1 ± 46.7	371.2 ± 120.6	50.9 ± 4.9	53.5 ± 19.7	73.9 ± 39	56.7 ± 14.6
		NP	170.6 ± 10.9	299.9 ± 57.9	199.6 ± 82.3	79.3 ± 23.2	90.4 ± 67.4	72.2 ± 20.9

[a,b] San San Pond Sak sites 1 and 2 correspond to Sites 1 and 2 respectively from Sjögersten *et al*. (2011)

DOC, TDN, and REP are presented on a dry weight basis

Ext: extractable; Mic: microbial

Data is presented as mean ± SE of five blocks for each vegetation community

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959 **Table S4.** Summary of linear regression models for CO_2 and CH_4 fluxes (log_{10} mg m^{-2} h^{-1}): physicochemical characteristics of peat and TMAH-

960 Py-GC/MS analyses.

Table S4. Summary of linear regression models for CO_2 and CH_4 fluxes (log_{10} mg m^{-2} h^{-1}): physicochemical characteristics of peat and TMAH-Py-GC/MS analyses

		Intercept	s.e.	t pr.	Slope	s.e.	t pr.	R^2
CO_2								
Physicochemistry and environmental factors								
Rainfall	(mm)	2.469	0.033	< 0.001	-0.0002	0.000	> 0.05	0.00
Water table	(cm)	2.395	0.014	< 0.001	-0.0107	0.001	< 0.001	0.16
Peat depth	(cm)	2.495	0.034	< 0.001	-0.0003	0.000	< 0.05	0.01
Dissolved O_2[a]	(ppm)	2.381	0.031	< 0.001	0.0264	0.018	> 0.05	0.00
Temperature[b]	(°C)	1.090	0.544	< 0.05	0.0545	0.021	< 0.05	0.03
C:N	-	2.413	0.078	< 0.001	0.0001	0.001	> 0.05	0.00
Peat composition	(μg mgC^{-1})							
Lignin		2.265	0.047	< 0.001	0.004	0.001	< 0.01	0.00
Fatty Acids								
	Short (< C20)	2.393	0.032	< 0.001	0.0029	0.003	> 0.05	0.00
	Long (> C20)	2.522	0.032	< 0.001	- 0.008	0.002	< 0.001	0.00
Phenolic		2.539	0.038	< 0.001	- 0.109	0.031	< 0.001	0.00
CH_4								
Physicochemistry and environmental factors								
Rainfall	(mm)	0.189	0.114	> 0.05	-0.0013	0.000	< 0.001	0.04
Water table	(cm)	-0.180	0.053	< 0.001	-0.0017	0.005	> 0.05	0.00
Peat depth	(cm)	0.230	0.122	> 0.05	-0.0014	0.000	< 0.001	0.00
Dissolved O_2	(ppm)	-0.335	0.115	< 0.01	0.0820	0.069	> 0.05	0.00
Temperature	(°C)	-1.630	1.990	> 0.05	0.0603	0.080	> 0.05	0.00

C:N	-	-0.382	0.096	< 0.001	0.0041	0.001	< 0.01	0.00
Peat composition	(μg mgC^{-1})							
Lignin		-0.318	0.171	> 0.05	0.004	0.004	> 0.05	0.00
Fatty Acids								
	Short (< C20)	-0.309	0.112	< 0.01	0.020	0.013	> 0.05	0.00
	Long (> C20)	0.534	0.108	< 0.001	-0.051	0.007	< 0.001	0.15
Phenolic		-0.366	0.140	< 0.05	0.186	0.115	> 0.05	0.00

Notes: [a,b]Dissolved oxygen, conductivity, and temperature in pore water at the top 50 cm layer of peat.
n.s. = not significant

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