# Hydrometeorological sensitivities of net ecosystem carbon dioxide and methane exchange of an Amazonian palm swamp peatland

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## Abstract

Tropical peatlands are a major, but understudied, biophysical feedback factor on the atmospheric greenhouse effect. The largest expanses of tropical peatlands are located in lowland areas of Southeast Asia and the Amazon basin. The Loreto Region of Amazonian Peru contains ~63,000 km$^2$ of peatlands. However, little is known about the biogeochemistry of these peatlands, and in particular, the cycling of carbon dioxide ($CO_2$) and methane ($CH_4$), and their responses to hydrometeorological forcings. To address these knowledge gaps, we established an eddy covariance (EC) flux tower in a natural palm (*Mauritia flexuosa* L.f.) swamp peatland near Iquitos, Peru. Here, we report ecosystem-scale $CO_2$ and $CH_4$ flux observations for this Amazonian palm swamp peatland over a two-year period in relation to hydrometeorological forcings. Seasonal and short-term variations in hydrometeorological forcing had a strong effect on $CO_2$ and $CH_4$ fluxes. High air temperature and vapor pressure deficit (VPD) exerted an important limitation on photosynthesis during the dry season, while latent heat flux appeared to be insensitive to these climate drivers. Evidence from light-response analyses and flux partitioning support that photosynthetic activity was downregulated during dry conditions, while ecosystem respiration (RE) was either inhibited or enhanced depending on water table position. The cumulative net ecosystem $CO_2$ exchange indicated that the peatland was a significant $CO_2$ sink ranging from −465 (−279 to −651) g C m$^{-2}$ y$^{-1}$ in 2018 to −462 (−277 to −647) g C m$^{-2}$ y$^{-1}$ in 2019. The forest was a $CH_4$ source of 22 (20 to 24) g C m$^{-2}$ y$^{-1}$, similar in magnitude to other tropical peatlands and larger than boreal and arctic peatlands. Thus, the annual carbon budget of this Amazonian palm swamp peatland appears to be a major carbon sink under current hydrometeorological conditions.

## 1. Introduction

Tropical peatlands are long-term carbon dioxide ($CO_2$) sinks, representing about 88.6 Pg of soil carbon or nearly 20% of global peat carbon (Leifeld and Menichetti, 2018; Page et al., 2011). However, they are also a methane ($CH_4$) source (Frankenberg et al., 2005; Pangala et al., 2017; Saunois et al., 2017), representing an important biophysical feedback on Earth's radiative forcing (Kirschke et al., 2013). Furthermore, when they are disturbed, and especially when drained for agriculture, they can become a major $CO_2$ source (Lilleskov et al., 2019). It is important, therefore, to understand the role that intact tropical peatlands play in terms of their net biogeochemical forcing on climate.

There is evidence for an increase in global $CH_4$ mixing ratios (i.e. 6.7 ppb/year from 2009 to 2013 and 7.5 ppb/year from 2014 to 2017) with a pronounced increase in equatorial zones (*Nisbet et al.*, 2016; 2019). Global top-down and $^{13}C$ isotope analyses suggest that this increasing trend has largely been driven by changes in natural biogenic sources in response to warmer and wetter tropical conditions (Nisbet et al., 2016; Saunois et al., 2017). However, large uncertainties persist in these source estimates because of a lack of $CH_4$ observations in the tropics (Knox et al., 2019; Saunois et al., 2020, 2017), and it is difficult to rule out other factors such as increased anthropogenic emissions or decreased $CH_4$ sink strength (Montzka et al., 2011; Schaefer et al., 2016).

The $CO_2$ budgets for Amazonian forests have been reported to range from large sinks (Grace et al., 1995; Hutyra et al., 2007; Kiew et al., 2018; Malhi et al., 1998) to large sources (Hutyra et al., 2007; Saleska et al., 2003) depending on forest type, disturbance history, climate, and methodological approaches related to eddy covariance (EC) data filtering and gap-filling. Some key patterns that have emerged indicate that the net uptake of $CO_2$ can either increase or decrease during the dry ("greening") season (Hutyra et al., 2007; Malhi et al., 1998; Restrepo-Coupe et al., 2013) and that some systems can switch to an annual source resulting from increased ecosystem respiration (RE) during the wet season (Saleska et al., 2003). The majority of these previous studies have examined the $CO_2$ budgets of evergreen forests growing on mineral soils. To our knowledge, there have been no EC-based studies that have examined the $CO_2$ or $CH_4$ budget of palm swamp peatlands, or any peatland, within the Amazonian basin. There is an important need, therefore, for increasing capacity for direct $CO_2$ and $CH_4$ flux observations to improve process understanding and to reduce the uncertainties of $CO_2$ and $CH_4$ budgets in Amazonian peatlands. Quantifying and understanding the energy balance characteristics of these systems is also needed to help diagnose and model how hydrometeorological forcings influence their carbon budgets.

The largest expanses of tropical peatlands are located in lowland areas of Southeast Asia, the Congo Basin, and the Amazon basin (Dargie et al., 2017; Gumbricht et al., 2017; Page et al., 2011). The Loreto Region of Amazonian Peru is comprised of about 63,000 $km^2$ of peatlands within the Pastaza-Marañon Foreland Basin (PMFB) (Draper et al., 2014). However, the extent of low elevation peatlands in Peru has only recently been documented, and little is known about their biogeochemistry and ecophysiology. To help address these knowledge gaps, we established an EC flux tower in a low disturbance palm swamp peatland in the Quistococha Forest Park (AmeriFlux Site PE-QFR, https://ameriflux.lbl.gov/sites/siteinfo/PE-QFR), near Iquitos, Peru in spring 2017 in collaboration with the Instituto de Investigaciones de la Amazonia Peruana (IIAP). The objectives of this current research were to: 1) Present the first measurements of energy fluxes and net ecosystem $CO_2$ and $CH_4$ exchange from an Amazonian palm swamp peatland; 2) Examine how the biophysical controls and magnitudes of these fluxes differ from other Amazonian forests; and

3) Assess if these ecosystems have a net radiative cooling effect on climate when considering the contemporary $CO_2$ and $CH_4$ balance and global warming potentials (GWP).

## 2. Methodology

### 2.1. Research site

The study site is located in the equatorial Amazon in a natural protected forest park named Quistococha, 10 km southwest of Iquitos city in the Loreto Region of Peru. The park is administrated by the Office of Tourism of the Regional Government (DIRCERTUR) and is an official scientific research area for IIAP. The EC flux tower (42 m) is located at 73° 19' 08.1" W; 3° 50' 03.9" S, and 104 m above sea level, within a natural low disturbance palm swamp peatland that is part of the park. The tower location and the flux footprint climatology (Kljun et al., 2015) are shown in Figure 1. We note that fetch is inadequate for northerly wind flow and these data have been filtered according to quality control assessments (described below). The flux footprint generally represents a pristine natural tropical peatland, but does include some potential influence where forest degradation is taking place (Figure 1). Bhomia et al., (2019) have quantified some areas of disturbance near the site as medium impact. Here, *Mauritia flexuosa* have been cut for their fruits and woody trees have been cleared, leading to differences in forest structure and composition compared to the pristine areas. Two disturbance areas have been well documented in the Bhomia et al., (2019) study. First, there is a disturbed area located approximately 1 km SSW of the tower and more than 400 m from the flux footprint 80% isopleth. Second, there is an area of disturbance located NE of the tower, which is adjacent to the lake and, consequently, has been filtered according to our flux footprint QA/QC procedures.

Palaeoecological studies indicate that peat began to form at this site about 2200 to 2300 years before present (BP), and the current vegetation community was established about 400 years BP

(Roucoux et al., 2013). The tree density and basal area for the study site is approximately 1846 ± 335 trees $ha^{-1}$ and 19.4 ± 2.8 $m^2$ $ha^{-1}$, respectively for stems with diameter at breast height (DBH) greater than 10 cm (Bhomia et al., 2019). The major palm type, ranked by stem density and basal area, is *Mauritia flexuosa* L.f. (21.3 m height on average), which represents about 65% of the total palm basal area at this site (Bhomia et al., 2019; Roucoux et al., 2013). The next most important tree species within Quistococha, ranked according to stem density, include *Tabebuia insignis*, *Hevea nitida*, *Mauritiella armata*, and *Fabaceae* sp. (Bhomia et al., 2019; Roucoux et al., 2013). The peatlands in the Quistocochia study area range from oligotrophic to minerotrophic because they are seasonally or intermittently inundated by floodwater from the major rivers (*Draper et al.* 2014; Lähteenoja et al., 2009a; Finn et al., 2020). Total aboveground and belowground biomass carbon stocks are estimated at 97.7 ± 15 Mg C $ha^{-1}$ and 24.9 ± 4.1 Mg C $ha^{-1}$, respectively (Bhomia et al., 2019). The vegetation at this site is broadly representative of the Pastaza-Marañon basin, where *M. flexuosa* is the dominant palm species, and is under significant anthropogenic pressure within the region for its valuable source of fruits, with destructive harvest reducing population density in unprotected forests (Hergoualc'h et al., 2017).

The peat layer thickness varies from 1.92–2.45 m (Bhomia et al., 2019; Lähteenoja et al., 2009b) with a total soil C pool of ~740 Mg C $ha^{-1}$. Overall, the average ecosystem carbon stock, including soil, litter, debris, and vegetation, for Quistococha is approximately 876.9 ± 108.5 Mg C $ha^{-1}$ (Bhomia et al., 2019). The historical average soil carbon accumulation for these peatlands, estimated from peat inventories and carbon dating, is approximately 74 ± 15 g C $m^{-2}$ $y^{-1}$ over the past 2300 years (Lähteenoja et al., 2009b).

The mean annual air temperature and precipitation for the Puerto Almendras Ordinary Weather Station (6 km from the EC tower site), Iquitos (2003–2017) were 27.2 ℃ and 2753.2 mm, respectively (Servicio Nacional de Meteorología e Hidrología del Perú, 2019). The site is characterized by a wet season (typically February to April) with minimum and maximum air temperatures of 22.9 ℃ and 31.8 ℃, respectively, and a dry season (typically August to September) with minimum and maximum air temperature of 22.5 ℃ and 32.7 ℃, respectively. Precipitation during the wet and dry seasons is typically 810 mm and 545 mm, respectively. The water table position is often located above the soil surface during the latter part of the wet season (i.e. 80 to 150 cm in May and June) and rarely drops below a level of 20 cm from the soil surface (Hergoualc'h et al., 2020; Kelly et al., 2017). Although the site is characterized by a dry season (reduced precipitation) we note that during this study that soil water availability was non-limiting.

### 2.2. Micrometeorological measurements

Eddy covariance flux measurements of energy, water vapor, $CO_2$ and $CH_4$ were established in January 2017. However, $CH_4$ flux measurements during 2017 and 2018 were made sporadically due to sensor failure related to a manufacturer defect. Furthermore, a lightning strike in early 2017 caused substantial damage to the instrumentation and major data loss. Consequently, we focus our analyses on the period January 1, 2018 to December 31, 2019 for **energy** and $CO_2$ fluxes and January 1, 2019 to December 31, 2019 for $CH_4$ fluxes.

The EC system consists of open-path analyzers for $CH_4$ (LI-7700, LI-COR Inc., Lincoln, NE, USA) and $CO_2$ (LI-7500, LI-COR Inc.) with turbulence measured using a 3D ultrasonic anemometer (CSAT3, Campbell Scientific Inc. Logan, UT, USA) mounted at 40 m above the ground (about 20 m above the mean canopy height). In February 2019, a new LI-7700 was installed at the site to improve the reliability of the $CH_4$ flux measurements. A datalogger (CR5000, Campbell Scientific Inc., Logan UT, USA) was used to record data from the EC sensors that were sampled at a rate of 10 Hz. Our group has tested and evaluated the long-term (3.5 years) performance of the LI-7700 analyzer in comparison to a closed-path system (TGA100A, Campbell Scientific Inc.) at a sub-boreal peatland site (Deventer et al., 2019), and found good agreement in half-hourly fluxes and excellent agreement on annual budgets. Here, we apply the same flux processing strategies performed by Deventer et al. (2019).

Raw 10 Hz data were processed and block-averaged to half-hourly fluxes using the EC approach (Baldocchi et al., 1988). We used custom software developed in MATLAB (The Mathworks Inc., Natick, MA, USA) for raw data processing and flux calculations (Deventer et al., 2019; Wood et al., 2017) and followed the recent ICOS (Integrated Carbon Observation System) guidelines for $CO_2$ and $H_2O$ flux calculations (Sabbatini et al., 2018) and $CH_4$ flux calculations (Nemitz et al., 2018). Raw data quality checks included completeness of the dataset, amplitude resolution, and dropouts. Further, the raw data (not including $CH_4$) were de-spiked and time lags between wind velocity and scalar measurements were compensated for by maximizing the covariance. Spectral corrections for high-pass (Moncrieff et al., 2006) and low-pass (Fratini et al., 2012) filtering and lateral sensor separation (Horst and Lenschow, 2009) were applied. Half-hour wind vectors and fluxes were rotated into the natural wind coordinate system using a two-dimensional rotation (Tanner and Thurtell, 1969; Morgenstern et al., 2004). The Webb-Pearman-Leuning (WPL) terms were applied to compensate for the effects of sensible ($H$) and latent heat ($LE$) fluxes on measured $CO_2$ and $CH_4$ density fluctuations (Webb et al., 1980). Spectroscopic corrections were also applied to the $CH_4$ open-path measurements (McDermitt et al., 2011). A correction associated with sensor-path heat exchange (i.e. 'sensor self-heating') of the $CO_2$/$H_2O$ open-path analyzer was computed following Burba et al., (2008). A single-level storage flux term was calculated and summed with the turbulent fluxes to estimate net ecosystem exchange of energy, $CO_2$ and $CH_4$ following Morgenstern et al., (2004) (Figure S1). We observed very similar diel patterns of storage to that described in Morgenstern et al., (2004) and a similar ratio of storage flux to eddy flux for $CO_2$.

Flux QA/QC was based on sensor diagnostics, wind direction, as well as low friction velocity ($u_*$). Periods of sensor malfunction were identified by sensor diagnostic values, as well as low signal strength of the open-path gas analyzers (RSSI<10 for LI-7700, and AGC>90 for the LI-7500). A wind direction filter (WD>320° or WD<70°) was applied to eliminate periods when the flux footprint was influenced by the nearby lake. Periods of low $u_*$ were removed by applying an annual threshold ($u_*$ = 0.082 m s$^{-1}$) that was determined using the REddyProc package, which implemented the moving point detection method (Papale et al., 2006). After applying these QA/QC procedures, the time series of half-hourly fluxes for net ecosystem $CO_2$ exchange ($CO_2$ NEE), *LE* and *H* were de-spiked following the methods of Papale et al. (2006), while the $CH_4$ flux (NEE $CH_4$) time series was filtered following Taylor et al., (2018) by removing any points outside of 2 standard deviations of the overall mean.

Following these QA/QC procedures, the data retention was approximately 28% and 44% for energy, 23% and 36% for $CO_2$, and 0% and 26% for $CH_4$ in 2018 and 2019, respectively. The 0% retention in 2018 for $CH_4$ was caused by sensor failure.

Gap-filling of $CO_2$ fluxes was performed to estimate annual budgets following the look-up table method based on the approach of Reichstein et al. (2005) and were implemented in the REddyProc package. The uncertainty in the annual totals resulting from data losses and gap-filling was determined using a Monte-Carlo strategy (Griffis et al., 2003). Here, we artificially increased the amount of missing observations by randomly removing 5%, 10%, 15%, and 20% of the valid data and repeated this process 500 times per year. The uncertainty in cumulative NEE increased from about 13% to 40% as we increased data loss from 5% to 20%, respectively. We also observed a slight increase in the cumulative carbon uptake as a function of the amount of missing data (Figure S2 and Table S1).

We provide $CO_2$ NEE budget estimates with and without the sensor self-heating corrections applied because there is considerable debate regarding its application (Deventer et al., 2020). The annual $CH_4$ NEE budget was estimated using two approaches: 1) by fitting a skewed Laplace distribution to the half-hourly observations for each month and then extrapolating these monthly mean fluxes to an annual budget; and 2) by using an artificial neural network (ANN) modeling approach to replace missing or invalid observations following Deventer et al., (2019).

The partitioning of $CO_2$ NEE into gross primary productivity (GPP) and ecosystem respiration (RE) was performed using the REddyProc package (Wutzler et al., 2018). Here we use the micrometeorological sign convention for NEE (i.e. a negative flux indicates a net ecosystem sink) where NEE = RE – GPP. The REddyProc package employs the Lasslop et al. (2010) approach, which utilizes a hyperbolic light-response curve to model RE from the daytime $CO_2$ NEE data (Falge et al., 2001). This algorithm accounts for vapor pressure deficit (VPD) limitation on photosynthesis following (Körner, 1995) and uses modeled RE to account for the temperature dependency of respiration (Lloyd and Taylor, 1994).

Supporting hydrometeorological measurements included net radiation (NR-lite, Kipp and Zonen, B.V., Delft, The Netherlands), solar radiation (LI-200R, LI-COR Inc.), photosynthetically active radiation (LI-190R, LI-COR, Inc.), air temperature and relative humidity (HMP45C, Campbell

Scientific Inc.), precipitation (TE-525L, Texas Electronics Dallas, TX, USA), soil volumetric water content (CS616, Campbell Scientific Inc.), measured at a soil depth of 10 cm and soil heat flux (HFP01-L, Hukseflux Inc., Delft, Netherlands) measured at a soil depth of 10 cm. Water table position was measured using a HOBO-U20 water level data logger (Onset Computer Corporation, Bourne, MA, USA), which was deployed 1 m below the soil surface within a plot 500 meters northwest of the tower.

## 3. Results and Discussion

### 3.1. Hydrometeorology and phenology

A distinguishing hydrometeorological feature between 2018 and 2019 was the duration and intensity of the dry season (Figure 2). In 2018, the dry season was characterized by monthly precipitation totals less than 140 mm over the period June through October. In 2019, the dry season was limited in duration to August through September. Total precipitation in 2018 was 3032.9 mm (10.2 mm/d and 4.4 mm/d for the wet and dry seasons, respectively) and 2943.9 mm in 2019 (10.1 mm/d and 3.5 mm/d for the wet and dry seasons, respectively), which exceeded the average for the most recent 15-year period (2003 to 2017) at Iquitos. This site is characterized by a stable thermal environment at seasonal to annual time scales. The mean annual air temperatures in 2018 and 2019 were 25.6 °C and 25.7 °C, respectively. The mean seasonal peak-to-trough amplitude of daily average air temperature was approximately 1.5 °C (Figure 2). During the wet and dry seasons, the mean air temperatures were remarkably similar at 26.0 °C and 26.1 °C and 25.6 °C and 26.2 °C for 2018 and 2019, respectively. The mean annual air temperature in both years was about 1.5 °C lower compared to the recent 15-year period for Iquitos.

Leaf area index (LAI) from the Moderate Resolution Imaging Spectroradiometer (MODIS, MCD15A2H Version 6) (DAAC, 2018; Myneni et al., 2015) showed seasonality that followed wet/dry season patterns (Figure 3 and Figure S3). The mean annual LAI (± 1 standard deviation) in 2018 and 2019 was 3.9 (± 0.8) and 4.90 (± 0.8), respectively, which is slightly lower than the 5-year mean LAI of 4.1 (± 0.5). Note that some of the short-term variability in LAI is likely caused by the effects of weather conditions on the MODIS LAI retrieval. LAI typically reached 4 to 5 at the end of the wet period (around day of year, DOY, 100), with a pronounced seasonal peak of about 5 during the dry period (~DOY 250). The mean LAI during the 2018 wet and dry seasons was 3.2 ± 0.6, 4.4 ± 0.9, respectively; while in 2019, mean wet and dry season LAI was 3.7 ± 0.8, 5.0 ± 0.4, respectively. The higher LAI observed during the dry season was statistically significant ($p < 0.01$) according to a two-sample t-test. Similar patterns, magnitudes, and seasonal amplitudes of LAI have been reported previously in the Amazon and are thought to be driven by net leaf abscission during the wet season followed by net leaf flushing during the dry season (Huete et al., 2006; Myneni et al., 2007; Saleska et al., 2016; Smith et al., 2019).

The mean annual net radiation ($R_n$) balance in 2018 (110.8 ± 202.8 W m$^{-2}$) was nearly identical to that in 2019 (111.2 ± 203.5 W m$^{-2}$) (Figure 4). The mean midday values of $R_n$ were approximately 450 ± 200 W m$^{-2}$ during the wet season and increased to about 500 ± 202 W m$^{-2}$ during the dry period because of clearer sky conditions. The mean daytime VPD at 41 m height, was 8.0 hPa (8.7 hPa for the wet period; 8.8 hPa for the dry period) and 7.3 hPa (6.8 hPa for the wet period; 10.5 hPa for the dry period) in 2018 and 2019, respectively. In both years, there were instances when VPD increased substantially during the dry period. For example, on DOY 242 (August 30, 2019) air temperature and VPD exceeded 31 °C and 17 hPa, respectively (Figure 4). Water table position was on average, above the surface in 2018 (+0.034 m) and 2019 (+0.034 m). However, the seasonal dynamics and range varied considerably between each year (Figure S4). In 2019, the water table position showed slightly more dynamic range (0.35 m) compared to 2018 (0.32 m). In 2018, water table position was relatively low during the early wet season and over the period DOY 170 (June 19) to DOY 290 (October 17). In 2019, the water table was generally at or above the surface, but was periodically below the surface from DOY 215 (August 3) to DOY 330 (November 26). Volumetric soil water content (θ, measurements initiated in 2019) remained above 0.77 in 2019 (Figure S4). During the dry season, θ showed a steady decline after DOY 150 (May 30) and reached a minimum value on DOY 240 (August 28).

The energy balance closure for this site (Figure S5) was reasonably good with turbulent heat fluxes ($H + LE$) accounting for more than 72% of the available energy ($R_n$-$S$). The energy balance closure at this site was in the range (i.e. 0.53 to 0.99) reported for a broad range of AmeriFlux sites (Wilson et al., 2002) and was similar to the energy balance closure (0.70 to 0.78) reported for broadleaf and wetland sites (Stoy et al., 2013). The dominant sink for the available energy was *LE* (Figure 5). On an annual basis, mean midday *LE* was approximately 255 W m$^{-2}$, and nearly identical in both years. The median Priestley-Taylor coefficient (α=1.12) indicated that evaporation was not significantly limited by water availability or canopy resistance. Mean midday *H* flux for the same period was approximately 60 W m$^{-2}$, yielding midday Bowen ratio (= $H/LE$) values that were typically 0.24. Mean midday *LE* peaked at about 300 W m$^{-2}$ during the dry season. The midday wet season *LE* was about 30 to 90 W m$^{-2}$ lower than during the dry season, indicating that *LE* was energy limited. This is supported by the fact that the mean equilibrium evaporation rate increased from 350 W m$^{-2}$ during the wet season to 400 W m$^{-2}$ during the dry season. As expected, *LE* was a strong linear function of $R_n$ ($LE = 0.54R_n$+23.7, $r^2 = 0.76$, RMSE = 54.3, df = 12,602, $p < 0.01$, all data combined for 2018 and 2019) and was relatively insensitive to changes in VPD or air temperature, $T_a$ (Figure 6 and Figure S6) or water table position. Overall, *LE* accounted for about 54% of $R_n$. These Bowen ratio values and evaporative fractions are considerably lower than the first ever measurements (Bowen ratio = 0.43 and evaporative fraction = 0.698) reported for a tropical rain forest by Shuttleworth et al., (1984). The cumulative evaporative flux accounted for about 1100 mm or 36% of the annual precipitation. These results imply that runoff and drainage are an important component of the water balance and, therefore, the carbon balance in these palm swamp peatlands (discussed in section 3.5).

Analyses of energy balance data from the Large Scale Biosphere-Atmosphere Experiment in the Amazon (LBA) also support these findings (da Rocha et al., 2009). Their research demonstrated that "wet" sites, experiencing greater than 1900 mm of annual precipitation, showed higher *LE* during the dry season when available energy increased due to reduced cloud cover. The LBA wet sites showed Bowen ratio values that were in the range of 0.32 to 0.36, indicating that the Quistococha palm swamp forest studied here was wetter with relatively more energy partitioned into *LE* (i.e. Bowen ratio of ~ 0.24). The diel *LE* patterns described here for the wet and dry seasons are consistent with those reported by Hutyra et al., (2007) for a primary growth evergreen forest, located in the Tapajós National Forest, Pará, Brazil. In their study, they concluded that *LE* increased during the dry season and observed a similar linear relation with $R_n$ for the wet and dry seasons (i.e. *LE* was a linear function of $R_n$ with a slope of 0.57 for wet seasons and 0.54 for dry seasons). In contrast, *LE* has been reported to peak during the wet season at other Amazonian sites (Malhi et al., 2002; Vourlitis et al., 2002). Malhi et al., (2002) found that *LE* was limited during the dry season by a reduction in canopy conductance in response to reduced soil water content. They showed that *LE* was a linear function of $R_n$ with a slope of 0.65 during the wet season and a slope of only 0.38 during the dry season. Given the relative high water table position at the

Quistococha site (Figure S4), and the lack of response of *LE* to changes in VPD (Figure 6 and Figure S6), we conclude that *LE* was not water limited during the dry period of 2018 or 2019. Our results support a broader analysis of energy balance in the tropics that found $R_n$ explained 87% of the variance in monthly *LE* across sites with an evaporative fraction ($LE/R_n$) of 0.72 (Fisher et al., 2009).

### 3.3. Net ecosystem $CO_2$ exchange

Half-hourly $CO_2$ NEE ranged from about −60 to +30 μmol m$^{-2}$ s$^{-1}$ over the two-year period. The annual mean midday $CO_2$ NEE was about −20 ± 8 μmol m$^{-2}$ s$^{-1}$ in both years (Figure 7). In each year, net $CO_2$ uptake was diminished immediately after the wet season and through the duration of the dry season (Figure 7) despite higher LAI and greater available energy in the dry season. This seasonal effect was related to a reduction in GPP (described below) and was more pronounced in 2018 because of a more intense dry down that extended from June through October (Figure 2). The water table position dropped during this period, but remained above the surface (Figure S4). Similar results have been reported by Kiew et al., (2018) for a peat swamp forest in Sarawak, Malaysia. They concluded that enhanced RE during the dry season was the dominant control on NEE. In contrast, Hutyra et al., (2007) found that phenology and available light were the dominant controls *via* canopy photosynthesis in an evergreen tropical rain forest in Tapajós. Here, we observed a decline in GPP during dry periods and a more variable response in RE (described below).

In 2018, $CO_2$ NEE reached –26.0 μmol m$^{-2}$ s$^{-1}$ at midday during the wet season, but was substantially lower at −18.2 μmol m$^{-2}$ s$^{-1}$ during the dry season. Similar patterns were observed in 2019, with midday $CO_2$ NEE reaching −20.6 μmol m$^{-2}$ s$^{-1}$ during the wet season. The dry season midday fluxes were also diminished (−16.0 μmol $m^{-2}$ $s^{-1}$). The magnitude of peak daytime $CO_2$ NEE at Quistococha was in very good agreement with that observed for a lowland *terra firme* (mineral soil wetland) tropical rain forest at the Reserva Biológica do Cuieiras, Amazonia, Brazil (Malhi et al., 1998). They observed a mean net uptake of $CO_2$ at midday of about −15 to −20 μmol $m^{-2}$ $s^{-1}$. Very similar daytime patterns were also reported by Carswell et al., (2002) for a *terra firme* forest near Belém, Pará, Brazil (eastern Amazonia).

We combined data from 2018 and 2019 to examine the light response of $CO_2$ NEE. The photosynthetic and respiratory parameters were obtained using a non-linear least squares optimization of the light-response function following Landsberg and Gower, (1997) and Griffis et al., (2003). These light response analyses indicated a mean apparent canopy photosynthetic capacity ($A_{max}$), apparent quantum yield (α), and day respiration ($R_d$) of 43.0 μmol $m^{-2}$ $s^{-1}$, 0.09, and 11.9 μmol $m^{-2}$ $s^{-1}$, respectively (Figure 8 and Table 1). These values are consistent with other tropical rain forests (Malhi et al., 1998) and are similar to that reported for deciduous aspen boreal forests during peak summer growth (Griffis et al., 2003). There was evidence that high values of PAR, air temperature, and VPD limited the uptake of $CO_2$ in this palm swamp forest (Figure 8 and Figure S7). Light-response analyses conducted by Malhi et al., (1998) also found evidence of reduced apparent photosynthetic capacity at elevated VPD (see their Figure 6b). High air temperature and VPD can reduce stomatal conductance, despite having ample soil water because stomatal conductance is largely determined by leaf water status (Buckley, 2019, 2017). If the evaporative demand exceeds what the plant vascular system can supply, the leaf can lose turgor, despite adequate available soil water. Similar patterns have been observed for other wetlands and peatlands (Blanken and Rouse, 1996; Otieno et al., 2012) and more broadly across eddy covariance flux sites (Novick et al., 2016).

Additional light-response analyses were conducted for conditions when the air temperature was above or below a threshold of 25 °C. These analyses indicated a substantial reduction in $A_{max}$ at high temperatures. The light-response parameters for low vs high temperature conditions were $A_{max}$ = 57.8 μmol m$^{-2}$ s$^{-1}$, α = 0.07, and $R_d$ = 11.6 μmol m$^{-2}$ s$^{-1}$ ($R^2$ = 0.35, *df* = 1176) vs $A_{max}$ = 40.6 μmol m$^{-2}$ s$^{-1}$, α = 0.09, and $R_d$ = 10.7 μmol m$^{-2}$ s$^{-1}$ ($R^2$ = 0.39, *df* = 4703), respectively (Table 1).

Light response analyses for the wet and dry seasons indicated substantially higher photosynthetic capacity ($A_{max}$) during the wet season (Table 1), despite the differences observed in LAI. During the 2018 wet season, the $A_{max}$ was 58.0 μmol m$^{-2}$ s$^{-1}$ versus 37.7 μmol m$^{-2}$ s$^{-1}$ during the dry season (Figure 9). A less pronounced pattern was observed in 2019, with a wet season $A_{max}$ of 45.5 μmol m$^{-2}$ s$^{-1}$ and a dry season $A_{max}$ of 40.0 μmol m$^{-2}$ s$^{-1}$. Our analyses indicated that higher PAR and VPD and lower water table position during the dry seasons limited photosynthesis. For example, in 2018 mean PAR, VPD, and WT values were +20 μmol m$^{-2}$ s$^{-1}$, +1.0 hPa, and -1.2 cm, relative to the wet season values. These analyses also suggest that the higher available energy during the dry season enhanced surface evaporation relative to plant transpiration.

We found that mean annual midday GPP was about 26.0 ± 8.1 μmol m$^{-2}$ s$^{-1}$ and midday RE was approximately 8.1 ± 7.9 μmol m$^{-2}$ s$^{-1}$ (Figure 10 and Figure 11). The partitioned GPP values showed evidence for light-inhibition at PAR values greater 1000 μmol m$^{-2}$ s$^{-1}$ and limitation imposed by high air temperature and VPD (Figure S7). There was also some evidence for declining GPP associated with the interplay between low water table position and high VPD (Figure S7). During the 2018 dry season, GPP was substantially reduced (i.e. by 8 μmol m$^{-2}$ s$^{-1}$) compared to the wet season, while midday partitioned RE decreased by about 2 μmol m$^{-2}$ s$^{-1}$. These results are somewhat surprising given the relatively high water table position and soil water content observed over the entire year. Such sensitivity to drier conditions (Figure S7) suggests that a substantial decline in the carbon sink strength could occur as air temperature continues to warm (Gloor et al., 2018) in the tropics or if the frequency of El Niño events or warm tropical North Atlantic Sea Surface Temperature (NTA-SST) anomalies increase (discussed further in Section 3.5). This hydrometeorological sensitivity highlights the need for longer-term measurements in these systems to assess the potential for acclimation and longer-term feedback responses.

The patterns we observed at this equatorial Amazonian site differed from LBA sites (Restrepo-Coupe et al., 2013; Saleska et al., 2003). For instance, Restrepo-Coupe et al., (2013) found that the dry season caused an increase in LAI and a progressive increase in canopy photosynthetic capacity at their equatorial flux site. Saleska et al., (2003) concluded that variations of RE was the dominant control on seasonal $CO_2$ NEE dynamics. They observed significant increases in RE during the wet season that contributed to a net carbon source in some years. Our results imply that RE is suppressed by flooding and likely redox limited. Recent work at a flood plain Amazonian forest near Cantão State Park, Brazil demonstrated that ecosystem productivity was limited by excessive soil water content during the flooded season, while GPP was enhanced by higher soil water content values during the dry/non-flooded period (Fonseca et al., 2019). Koren et al., (2018) reported a significant reduction in SIF, a proxy for GPP, for the western (2 to 5%) and eastern (10 to 15%) Amazon Basin, associated with high air temperatures and reduced soil water content.

Mean nighttime $CO_2$ NEE (i.e. measured RE) was 6.9 ± 10.5 $\mu$mol m$^{-2}$ s$^{-1}$ and 6.5 ± 10.5 $\mu$mol m$^{-2}$ s$^{-1}$ in 2018 and 2019, respectively (Figure S8). The mean nighttime RE was higher during the dry season (7.6 ± 11.0 $\mu$mol m$^{-2}$ s$^{-1}$, 8.2 ±11.3 $\mu$mol m$^{-2}$ s$^{-1}$) compared to the wet season (5.9 ± 9.8 $\mu$mol m$^{-2}$ s$^{-1}$, 5.7 ± 9.8 $\mu$mol m$^{-2}$ s$^{-1}$) in both 2018 and 2019, respectively. Carswell et al., (2002) found that mean nighttime RE increased from about 7.1 µmol $m^{-2}$ $s^{-1}$ in the wet season to 8.2 µmol $m^{-2}$ $s^{-1}$ in the dry season for the Belém, Pará, Brazil site. Hutyra et al., (2007) showed that the mean nighttime RE was typically 9.2 µmol $m^{-2}$ $s^{-1}$ during the wet season and decreased to 7.7 µmol $m^{-2}$ $s^{-1}$ during the dry season for the Tapajós site. Thus, our nighttime values are comparable in terms of magnitude, and similar in seasonal pattern to the *terra firme* ecosystem. Nighttime RE did not show any significant relation with respect to soil temperature, air temperature or soil water content, but were proportional to GPP (Figure S7). A similar conclusion was reported by Carswell et al., (2002) and Hutyra et al., (2007). This supports that the reduced net uptake of $CO_2$ during the dry season, or high temperature periods, was largely driven by a reduction in photosynthetic activity and a modest increase in RE.

### 3.4. Net ecosystem $CH_4$ exchange

The 2019 half-hourly $CH_4$ NEE values followed a skewed Laplace distribution, yielding a mean flux of 59.3 ± 89.3 nmol $m^{-2}$ $s^{-1}$. We did not observe a pronounced diel pattern in $CH_4$ NEE, however, emissions during the wet season were consistently higher (mean = 59.5 ± 89.0 nmol $m^{-2}$ $s^{-1}$) than during the dry season (mean = 46.9 ± 63.6 nmol $m^{-2}$ $s^{-1}$) with a slight increase during midday for the wet period (Figure 12 and Figure S9-S10). Recent work by Deshmukh et al., (2020) observed a significant diel cycle in $CH_4$ emissions for a natural forested tropical peatland in Sumatra, Indonesia that was correlated with photosynthetic flux and canopy conductance. Tang et al. (2018) also reported a significant diel pattern in $CH_4$ emissions for a two-month study conducted in a tropical peat forest in Sarawak, Malaysian Borneo, highlighting the potential importance of plant-mediated transport of $CH_4$.

Higher variability of NEE $CH_4$ at night was likely associated with lower friction velocities and may indicate short-term variability in the total flux caused by changes in $CH_4$ storage or the influence of ebullition events during these more stable atmospheric conditions (i.e. weaker boundary-layer mixing). Weak positive relationships were observed between $CH_4$ NEE and soil temperature, air temperature, and water table position at the weekly timescale (Figure 13), but were not statistically significant. This is likely related to the very small variations in soil temperature and water table position. Further, we found a weak positive relation (slope = 5.6 nmol $m^{-2}$ $s^{-1}$ $kPa^{-1}$) between $CH_4$ NEE and atmospheric pressure, but it was not statistically significant. Based on an analysis of the statistical distributions for high (>25 ℃) vs low (<25 ℃) temperatures, we found $CH_4$ fluxes to be very similar, 42.0 ± 66.7 nmol $m^{-2}$ $s^{-1}$ vs 42.3 ± 86.9 nmol $m^{-2}$ $s^{-1}$, respectively (Figure S11-S12). However, there was some evidence of increasing $CH_4$ emissions with increasing *LE* (Figure S13) and increasing $CO_2$ NEE magnitude (i.e increasing photosynthetic activity, Figure 13), suggesting that plant-mediated transport might be important. Indeed, Pangala et al., (2017) have shown that $CH_4$ emissions from central Amazonian tree stems were up to 200-fold greater than emissions from tropical peat swamp soils and the dominant diffusive flux component observed in the Amazonia. Tree bole $CH_4$ flux measurements have helped reconcile the large disparity observed between top-down and bottom-up $CH_4$ budget estimates for the Amazon Basin (Pangala *et al*., 2017).

Methane emissions have also been reported for a tropical peat swamp forest located in Sarawak, Malaysia based on the EC approach (Wong et al., 2018). They found that mean $CH_4$ emissions were 24.0 nmol $m^{-2}$ $s^{-1}$, substantially lower compared to the Quistococha palm swamp forest. Their research showed little dependence of $CH_4$ emissions on water table position, soil water content, or soil temperature, presumably because of the low variability of these potential environmental drivers. Our EC $CH_4$ fluxes are higher than soil chamber fluxes (5.2 to 43.3 nmol $m^{-2}$ $s^{-1}$) measured within the Quistococha Regional Park during the dry season of December 2011 and December 2012 (Finn et al., 2020) and are in relatively good agreement with *in situ* observations (mean annual flux densities ranging from 38.3 to 84.3 nmol $m^{-2}$ $s^{-1}$) in the same park over the period April 2015 to March 2018 (Hergoualc'h et al., 2020). Further, laboratory incubations using soil samples extracted from within the Quistococha Regional Park, indicate a $CH_4$ emission potential on the order of 80 nmol $m^{-2}$ $s^{-1}$ (van Lent et al., 2019), which also supports our observations.

### 3.5. Carbon budget and net radiative forcing

Cumulative $CO_2$ NEE in 2018 and 2019 indicated an overall carbon sink of about −465 (−279 to −651) g C $m^{-2}$ $y^{-1}$ and −462 (−277 to −647) g C $m^{-2}$ $y^{-1}$, respectively (Figure 14). The uncertainty estimates (40% relative uncertainty) in parentheses were derived from the Monte Carlo and gap filling analyses. Overall, we cannot conclude that the cumulative seasonal pattern of $CO_2$ NEE, or its annual total, differed significantly between years. However, we note an important divergence between each year over the period DOY 250 (September 7) to DOY 325 (November 21) that relates to a decline in water table position in 2019 relative to 2018 (Figure S4). Here, midday RE was enhanced by up to 4 μmol $m^{-2}$ $s^{-1}$ relative to the same period in 2018. These results further highlight the sensitivity of this palm swamp forest carbon balance to hydrometeorological conditions.

The cumulative $CO_2$ NEE values above include the so-called $CO_2$ open-path senor self-heating correction of Burba et al., (2008). When these corrections are not applied, the annual $CO_2$ NEE is estimated at −552 g C $m^{-2}$ $y^{-1}$ and −546 g C $m^{-2}$ $y^{-1}$ for 2018 and 2019, respectively. We note here that the sensor self-heating correction factors are highly uncertain for any given site due to site-specific variability in IRGA heat fluxes, and ambient temperature-specific IRGA measurement bias that both are unaccounted for in the correction framework (Deventer et al., 2020). It is, however, noteworthy that despite these large uncertainties, the differences in annual budget estimates calculated with and without applying the correction differ by ~85 g $m^{-2}$ $y^{-1}$ (~18 %), fall within the respective uncertainty bounds, and thus do not alter the conclusion that this palm swamp peatland is a large $CO_2$ sink.

The annual $CH_4$ NEE budget for 2019 was estimated to be a source of 22 (20 to 24) g $CH_4$-C $m^{-2}$ $y^{-1}$, according to the monthly Laplace distribution analyses. Here, the uncertainty in parentheses was propagated from the range of the mean monthly values. The annual $CH_4$ NEE budget, based on the ANN approach was 17 (12 to 23) g $CH_4$-C $m^{-2}$ $y^{-1}$. However, since the ANN budget approach was characterized by low predictive power (i.e. $R^2 < 0.1$) we make use of the Laplace distribution analyses. Monthly $CH_4$ emissions ranged from 1.0 to 2.7 g $CH_4$-C $m^{-2}$ $month^{-1}$ (Figure S14). Maximum monthly $CH_4$ emissions were generally correlated with monthly precipitation. The $CH_4$ NEE budget of the Quistococha palm swamp forest is in excellent agreement with chamber based estimates (14.5 to 31.9 g $CH_4$-C $m^{-2}$ $y^{-1}$) within the park over the period April 2015 to March 2018 (Hergoualc'h et al., 2020). Methane emissions from the Quistococha site are larger than our mean budget estimate for a sub-boreal peatland (10.7 to 15.1 g $CH_4$-C $m^{-2}$ $y^{-1}$) in Minnesota, USA (Deventer et al., 2019; Olson et al., 2013) and northern peatlands (Table 2) and substantially larger than that extrapolated from two months of wet season measurements (8.8 g $CH_4$-C $m^{-2}$ $y^{-1}$) over a tropical peat forest in Sarawak, Malaysian Borneo (Tang et al., 2018). Further, our annual budget estimate is in excellent agreement with chamber-based estimates (28.6 ± 9.7 g $CH_4$-C $m^{-2}$ $y^{-1}$) from intact peat swamp forests in Southeast Asia (Hergoualc'h and Verchot, 2014). A recent synthesis of global eddy covariance $CH_4$ flux measurements revealed that tropical wetlands were extremely underrepresented in the global database (Knox et al., 2019). They reported only three sites (freshwater marsh site, USA; swamp Maludam, Malaysia; and brackish marsh, USA) with an estimated mean annual emission of 43.2 ± 11.2 g $CH_4$-C $m^{-2}$ $y^{-1}$.

The $CO_2$ sink strength of the Quistococha site was substantially higher than that of a tropical peat swamp forest in Sarawak, Malaysia, (mean of -136 ± 51 g C $m^{-2}$ $y^{-1}$) over the period 2011 to 2014 (Kiew et al., 2018) and a peat swamp forest in Indonesia (mean of +174 ± 203 g C $m^{-2}$ $y^{-1}$) over the period 2004 to 2008 (Hirano et al., 2012). Our review of tropical forest $CO_2$ budgets (Table 3) and comparison with the mean $CO_2$ NEE derived by Luyssaert et al., (2007) (see their Table 3, mean NEE = −403 ± 102 g C $m^{-2}$ $y^{-1}$) indicates that the Quistococha site is a relatively large $CO_2$ sink, but within the range of reported values for other tropical forests. Previous studies have argued that the spatial and temporal patterns of the annual $CO_2$ budget in Amazonian forests can be large, ranging from sink to source depending on climate and disturbance factors (Saleska et al., 2003). Further, a recent synthesis examining the impacts of El Niño/La Niña on the carbon balance of tropical ecosystems provides strong evidence that the drier conditions associated with El Niño are likely to reduce their carbon sink strength through a reduction in photosynthetic fluxes (Gloor et al., 2018; Koren et al., 2018; Malhi et al., 2018). In the western Amazon, El Niño/La Niña events may be less important than the influence of warm tropical NTA-SST anomalies on climate (Chen et al., 2015; Lilleskov et al., 2019), which have been shown to increase drought and fire frequency in the region. Model simulations by Wang et al., (2018) suggest that the peatlands of the Pastaza-Marañon Foreland Basin are susceptible to changing from a carbon sink to a carbon source if conditions continue to get warmer and drier within the region. Our observations and analyses for an underrepresented Amazonian palm swamp peatland in the Pastaza-Marañon Foreland Basin strongly support these findings.

The current rate of carbon accumulation, as measured from EC, cannot be compared directly to the long-term apparent rate of carbon accumulation (LARCA) as derived from peat core data (Ratcliffe et al., 2018; Young et al., 2019) because carbon accumulated in the current year has undergone less decomposition than older peats, which continue to lose carbon for thousands of years (Clymo et al., 1998). In fact, most of the recently accumulated carbon will not become part of the long-term peat. This is why the contemporary carbon balance of the Quistococha palm swamp forest is large (average sink = 464 g C $m^{-2}$ $y^{-1}$) relative to the long-term apparent peat carbon accumulation rate (LARCA = 74 g C $m^{-2}$ $y^{-1}$). Additional reasons for this disparity could also be related to: 1) a short record of EC measurements that do not capture the potential range of inter-annual variability of NEE at this site; 2) the dynamic history of paleo-vegetation; and 3) potential carbon losses in the form of disturbance and/or lateral DOC/DIC exports. Paleoecological evidence shows that the vegetation has changed dramatically at this site over the past 200 years (Lähteenoja et al., 2009) suggesting a potential for periods of disturbance and net carbon losses (Saleska et al., 2003). The site is located in close proximity to the Amazon river network so that channel meandering and avulsion have the potential to cause disturbances by removing or burying peat carbon (Salo et al., 1986). Drainage likely represents a significant carbon export from this watershed. Hastie et al., (2019) have shown that there is large inter-annual variability in the net carbon export from Amazonian river flood plains, which represents a significant fraction of carbon fixed by these forest ecosystems. Indeed, our energy balance measurements indicated that annual evaporation accounted for only 36% of the annual precipitation, which implies that drainage and runoff are significant. Measurements of DOC/DIC transport, however, have not yet been estimated for these palm swamp peatlands and this represents a potentially large uncertainty in our carbon accounting.

A global warming potential (GWP) analysis, based on the annual budgets of contemporary $CO_2$ and $CH_4$ flux measurements, does not necessarily reflect the long-term carbon dynamics of a peatland or the temporal dynamics and equilibrium response times of radiative forcing associated with changes in atmospheric burdens of $CO_2$ and $CH_4$ (Frolking et al., 2006; Neubauer, 2014). Here, we estimate the GWP to help assess the relative importance of contemporary $CH_4$ emissions versus $CO_2$ uptake on the climate system. The GWP, on a 100-year time horizon, for $CH_4$ is estimated at 28 with no carbon cycle feedbacks and 34 when including these feedbacks (Myhre et al., 2013). Therefore, based on the above annual budget estimates, the $CO_2$ equivalence of the $CH_4$ emissions is estimated to be 821 to 997 g $CO_{2eq}$ m$^{-2}$ y$^{-1}$, indicating that this Amazonian palm swamp peatland has a net negative radiative forcing effect in terms of its $CO_2$ budget (i.e. after converting from $CO_2$-C to $CO_2$, 1705 g $CO_2$ m$^{-2}$ y$^{-1}$ and 1694 g $CO_2$ m$^{-2}$ y$^{-1}$) and $CH_4$ budgets. However, this does not include the potential impacts of DIC/DOC transport and cycling offsite. Further, the sensitivity of NEE $CO_2$ to warmer and drier conditions implies that the carbon sink of these palm swamp peatlands could be reduced substantially by increasing tropical temperatures (Gloor et al., 2018) or through the increased intensity or frequency of drought events. Such feedbacks require longer-term observations to help understand the potential role of acclimation in these systems.

## 4. Conclusions

Our research has provided the first observations and analyses of the energy, $CO_2$, and $CH_4$ balance of an Amazonian palm swamp forested peatland. The results suggest that these peatlands may be an important $CO_2$ sink and a $CH_4$ source. While light-response analyses and flux partitioning support that photosynthetic activity in these systems is inhibited by high photosynthetic photon flux density, air temperatures, and vapor pressure deficits, latent heat flux appeared to be insensitive to these climate drivers. There is also evidence for increased ecosystem respiration under drier conditions and lower water table positions. Methane emissions were enhanced during the wet season, but did not show a significant diel pattern or temperature dependence. Overall, the $CH_4$ NEE budget was similar to that reported for other tropical peatlands and generally larger than sub-boreal and northern peatlands. Considering the global warming potential of $CH_4$ on a 100-year time horizon, we estimate that these ecosystems have a net radiative cooling effect in terms of their carbon budget. Further research is required to reduce the uncertainties in the annual carbon budget, carbon losses associated with runoff and drainage, and the processes controlling $CH_4$ production, consumption, and transport between the ecosystem and atmosphere. This is a very challenging environment for conducting long-term eddy covariance observations, but such measurements are critical to understanding the longer-term feedbacks associated with changes in hydrometeorological forcings.

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**Table 1.** Summary of canopy-scale light-response analyses

| Data Selection | $A_{max}$ (μmol $m^{-2}$ $s^{-1}$) | Alpha (unitless) | $R_d$ (μmol $m^{-2}$ $s^{-1}$) | Fit |
|---|---|---|---|---|
| All data | 43.0 (41.7 to 44.4) | 0.09 (0.08 to 0.11) | 11.9 (10.6 to 13.2) | $R^2$ = 0.44; df = 5882 |
| $T_{air}$ < 25 °C | 57.8 (44.0 to 71.5) | 0.07 (0.05 to 0.09) | 11.6 (9.6 to 13.7) | $R^2$ = 0.35; df = 1176 |
| $T_{air}$ > 25 °C | 40.6 (39.1 to 42.1) | 0.09 (0.07 to 0.11) | 10.7 (8.9 to 12.4) | $R^2$ = 0.39; df = 4703 |
| Wet 2018 | 58.0 (52.0 to 64.0) | 0.10 (0.07 to 0.14) | 13.5 (9.4 to 17.6) | $R^2$ = 0.51; df = 616 |
| Dry 2018 | 37.8 (33.8 to 41.7) | 0.06 (0.04 to 0.08) | 9.2 (6.4 to 12.0) | $R^2$ = 0.41; df = 797 |
| Wet 2019 | 45.5 (41.9 to 49.1) | 0.09 (0.06 to 0.12) | 10.7 (7.8 to 13.7) | $R^2$ = 0.51; df = 820 |
| Dry 2019 | 40.0 (34.4 to 45.7) | 0.06 (0.03 to 0.08) | 10.6 (6.9 to 14.3) | $R^2$ = 0.38; df = 637 |

*numbers in parentheses indicate the 95% confidence intervals (lower, upper)

**Table 2.** Summary of net ecosystem $CH_4$ exchange and soil $CH_4$ emissions of select peatland and wetland sites

| Site | Years | Ecosystem | Climate | Flux (g C $m^{-2}$ $y^{-1}$) | Reference |
|---|---|---|---|---|---|
| Iquitos, Peru, QFR 73° 19' 08.1" W; 3° 50' 03.9" S | 2019 | palm swamp peat forest | 3000 mm; 26 °C | 22[a] | this study |
| Iquitos, Peru, Quistococha Regional Reserve | 2015-2018 | intact palm swamp peat forest | 3087 mm; 27 °C | 14.5 to 31.9[b] | Hergoualc'h et al., 2020 |
| Maludam National Park, Sarawak, Malaysia 111° 8' E 1° 27' N | 2014-2015 | peat swamp forest | 2540 mm 27.1 °C | 9.2[a] | Wong et al., 2018 |
| Maludam National Park, Sarawak, Malaysia 111° 8' E 1° 27' N | 2013 | peat swamp forest | not reported for time period | 8.8[a] | Tang et al., 2018 |
| Meta-analysis of sites from Southeast Asia | 1990s-2010 | intact peat swamp forest | 26.3 °C | 28.6[b,c] | Hergoualc'h and Verchot, 2014 |
| Winous Point Marsh Conservancy, Lake Erie, Ohio, USA 82° 59' 45.02" W; 41° 27' 51.28" N | 2011-2013 | fresh water marsh | 840 mm; 9.2 °C | 42.3 to 57.0[a] | Chu et al., 2014 |
| Sacromento-San Joaquin Delta, CA, USA, 121.7650° W; 38.0498° N | 2012-2013 | restored young wetland | 390 mm; 15 °C | 53[a] | Knox et al., 2015 |
| Marcell Experimental Forest, Minnesota, USA -93.489° W 45.505° N | 2015-2017 | sub-boreal fen | 770 mm 3 °C | 10.7 to 15.1[a] | Deventer et al., 2019 Olson et al., 2013 |
| North Slope, Barrow, Alaska, USA 156° 36' 33.04" W; 71° 19' 21.10" N | 2013-2014 | wet sedge tundra | Not reported for time period | 4.5[a] | Goodrich et al., 2016 |
| Lena River Delta, Siberia, Russia 126° 30' E; 72° 22' N | 2003-2004 | arctic tundra | 319 mm; -14.7 | 2.4[a] | Wille et al., 2008 |

* note that a positive NEE value indicates a $CH_4$ source; Climate statistics represent mean annual values. [a]annual estimate of $CH_4$ NEE derived from eddy covariance data; [b]annual estimate of soil $CH_4$ emissions derived from chamber data; [c]annual mean derived from all available site data.

**Table 3.** Summary of net ecosystem $CO_2$ exchange of select tropical forest sites

| Site | Years | Ecosystem | Climate | NEE (g C $m^{-2}$ $y^{-1}$) | Reference |
|---|---|---|---|---|---|
| Iquitos, Peru, QFR 73° 19' 08.1" W; 3° 50' 03.9" S | 2018 to 2019 | palm swamp peat forest | 3000 mm; 26 ℃ | range of -462 to -465 | this study |
| Sarawak, Malaysia 111° 24' E 1° 23' N | 2011 to 2014 | peat swamp forest | 26.5 ℃ | range of -207 to -98 | Kiew et al., 2018 |
| Palangkaraya, Indonesia | July 2004 to July 2008 | peat swamp secondary forest | 2452 mm 26 ℃ | range of -27 to +443 | Hirano et al., 2012 |
| Pasoh Forest Reserve, Peninsular Malaysia 102° 18' E; 2° 58' N | 2003 to 2005 | lowland tropical evergreen forest | 1804 mm | -147 to -79 | Kosugi et al., 2008 |
| French Guiana, South America 52° 54' W; 5° 16' N | 2004 to 2005 | pristine tropical wet forest | 3041 mm; 26.5 ℃ | -157 to -142 | Bonal et al., 2008 |
| Tapajós National Forest, Pará, Brazil 54° 58' W 2° 51' S | 2002 to 2005 | evergreen old growth tropical rain forest | 2200 mm 26 ℃ | range of -221 to +2677 | Hutyra et al., 2007 |
| Tapajós National Forest, Pará, Brazil 54° 58' W 2° 51' S 54° 56' W 3° 54' S Sites KM 67 and KM 83 | July 2000 to August 2003 | Evergreen old growth tropical rain forest | 25 ℃ 1920 mm | range of +0 to +2300 | Saleska et al., 2003 |
| Cuieiras Forest Reserve, near Manaus, Brazil 60° 06' 55" W; 2° 35' 22" S | Sept 1, 1995 to Aug 31, 1996 | lowland terra firme tropical rain forest | 2200 mm | -590 | Malhi et al., 1998 |
| Reserva, Jaru, Rondonia, Brazil, 61° 56' W; 10° 84' S | Sept 1992; April to June 1993 | old growth tropical rain forest | 1997 mm 25 ℃ | -102[a] | Grace et al., 1995 |
| Reserva Florestal Ducke, near Manaus, Brazil 59° 57' W; 2° 57' S | April 22 to May 8, 1987 | old tropical rain forest | 1415 mm 27 ℃ | -220[b] | Fan et al., 1990 |

* note that a negative NEE value indicates a $CO_2$ sink; [a]annual estimate derived from a model parameterized with site data; [b]annual estimate based on mean flux value;

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**Figure 1.** Research site location and eddy covariance tower flux footprint climatology. The flux footprint was estimated using the model of Kljun et al., (2015). The isopleths indicate the cumulative probability of particle contribution to the total flux. The dashed lines indicate the wind sector that was used to filter out the influence of the lake on the tower flux measurements. The yellow triangle indicates an area of moderate ecosystem disturbance caused by palm fruit harvesting.

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**Figure 6.** Evaporative fraction - latent heat flux as a function of net radiation. a) color bar indicates vapor pressure deficit (hPa); b) color bar indicates air temperature ($^{o}$C).

**Figure 7.** Diel patterns of net ecosystem $CO_2$ exchange. a) all data; b) wet season and dry season in 2018; c) wet season and dry season in 2019; d) transition season in 2018 and 2019.

**Figure 8.** Canopy scale light-response $CO_2$ NEE analyses. a) Combining all available data for 2018 and 2019 where the color bar indicates water table position (m); b) All data combined where color bar indicates vapor pressure deficit (hPa); c) All data combined where color bar indicates air temperature ($^{o}$C). Note that a minimum PAR threshold of 25 $\mu$mol m$^{-2}$ s$^{-1}$ was used and that NEE data are plotted as -1 × NEE.

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**Figure 10.** Diel patterns of gross ecosystem photosynthesis (GEP). a) all data; b) wet season and dry season in 2018; c) wet season and dry season in 2019; d) transition season in 2018 and 2019.

**Figure 11.** Diel patterns of ecosystem respiration (RE). a) all data; b) wet season and dry season in 2018; c) wet season and dry season in 2019; d) transition season in 2018 and 2019.

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**Figure 13.** Relationships between net ecosystem methane exchange averaged over 7-day periods for environmental drivers including: a) soil temperature; b) air temperature; c) net ecosystem $CO_2$ exchange,

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**Figure 14.** Cumulative net ecosystem $CO_2$ exchange (NEE) in 2018 and 2019. Note that the uncertainty estimates were derived from a Monte Carlo approach that assesses the impact of the gap-filling approach on the cumulative NEE.