Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

Seasonal variability in methane and nitrous oxide fluxes from tropical peatlands in the Western Amazon basin

Teh, Yit Arn[1*], Murphy, Wayne A.[2], Berrio, Juan-Carlos[2], Boom, Arnound[2], and Page, Susan E.[2]

[1] Institute of Biological and Environmental Sciences, University of Aberdeen

[2] Department of Geography, University of Leicester

* Author to whom all correspondence should be addressed; email: yateh@abdn.ac.uk

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

Biogeosciences Discussions Open Access

2. ABSTRACT

Here we report methane (CH_4) and nitrous oxide (N_2O) fluxes from lowland tropical peatlands in the Pastaza-Marañón foreland basin (PMFB) in Peru, one of the largest peatland complexes in the Amazon basin. Trace gas fluxes were sampled from the most numerically-dominant peatland vegetation types in the region: forested vegetation, forested (short pole) vegetation, *Mauritia flexuosa*-dominated palm swamp, and mixed palm swamp. Data were collected in both wet and dry seasons over the course of four field campaigns from 2012 to 2014. Peatlands in the PMFB were large and regionally significant sources of atmospheric CH_4, emitting 36.05 ± 3.09 mg CH_4-C m^{-2} d^{-1}. CH_4 emissions varied significantly among vegetation types and between seasons. CH_4 fluxes were greatest for mixed palm swamp (52.0 ± 16.0 mg CH_4-C m^{-2} d^{-1}), followed by *M. flexuosa* palm swamp (36.7 ± 3.9 mg CH_4-Cm^{-2} d^{-1}), forested (short pole) vegetation (31.6 ± 6.6 mg CH_4-Cm^{-2} d^{-1}), and forested vegetation (29.8 ± 10.0 mg CH_4-C m^{-2} d^{-1}). CH_4 fluxes also showed marked seasonality, with divergent seasonal flux patterns among ecosystems. Forested vegetation and mixed palm swamp showed significantly higher dry season (47.2 ± 5.4 mg CH_4-C m^{-2} d^{-1} and 85.5 ± 26.4 mg CH_4-C m^{-2} d^{-1}, respectively) compared to wet season emissions (6.8 ± 1.0 mg CH_4-C m^{-2} d^{-1} and 5.2 ± 2.7 mg CH_4-C m^{-2} d^{-1}, respectively). In contrast, forested (short pole) vegetation and *M. flexuosa* palm swamp showed the opposite trend, with dry season fluxes of 9.6 ± 2.6 and 25.5 ± 2.9 mg CH_4-C m^{-2} d^{-1}, respectively, versus wet season fluxes of 103.4 ± 13.6 and 53.4 ± 9.8 mg CH_4-C m^{-2} d^{-1}, respectively. Nitrous oxide fluxes were negligible (0.70 ± 0.34 μg N_2O-N m^{-2} d^{-1}), and did not vary significantly among ecosystems or between seasons.

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

KEYWORDS

methane, nitrous oxide, peat, tropical peatland, Amazonia, Peru

3. INTRODUCTION

The Amazon basin plays a critical role in the global atmospheric budgets of carbon (C) and greenhouse gases (GHGs) such as methane (CH_4) and nitrous oxide (N_2O). Recent basin-wide studies suggest that the Amazon as a whole accounts for approximately 7 % of global atmospheric CH_4 emissions (Wilson et al., 2016). N_2O emissions are of a similar magnitude, with emissions ranging from 2-3 Tg N_2O-N year^{-1} (or, approximately 12-18 % of global atmospheric emissions) (Huang et al., 2008;Saikawa et al., 2014;Saikawa et al., 2013). While we have a relatively strong understanding of the role that the Amazon plays in regional and global atmospheric budgets of these gases, one of the key gaps in knowledge is the contribution of specific ecosystem types to regional fluxes of GHGs (Huang et al., 2008;Saikawa et al., 2014;Saikawa et al., 2013). In particular, our understanding of the contribution of Amazonian wetlands to regional C and GHG budgets is weak, as the majority of past ecosystem-scale studies have focused on *terra firme* forests and savannas (D'Amelio et al., 2009;Saikawa et al., 2013;Wilson et al., 2016;Kirschke et al., 2013;Nisbet et al., 2014). Empirical studies of GHG fluxes from Amazonian wetlands are more limited in geographic scope and have focused on three major areas: wetlands in the state of Amazonas near the city of Manaus (Devol et al., 1990;Bartlett et al., 1990;Bartlett et al., 1988;Keller et al., 1986), the Pantanal region (Melack et al., 2004;Marani and Alvalá, 2007;Liengaard et al., 2013), and the Orinoco River basin (Smith et al., 2000;Lavelle et al., 2014). Critically, none of the ecosystems sampled in the past were peat-forming ones; rather, the habitats investigated were non-peat forming (i.e. mineral or organo-mineral soils), seasonally-inundated floodplain forests (i.e. *varzea*), rivers or lakes.

Peatlands are one of the major wetland habitats absent from current bottom-up GHG inventories for the Amazon basin, and are often grouped together with non-peat forming wetlands in regional atmospheric budgets (Wilson et al., 2016). Because we have little or no data on ecosystem-level land-atmosphere fluxes from these habitats (Lahteenoja et al., 2012;Lahteenoja et al., 2009b;Kirschke et al., 2013;Nisbet et al., 2014), it is difficult to ascertain if rates of GHG flux from these ecosystems are similar to or different from mineral soil wetlands. Given that underlying differences in plant community composition and soil properties are known to modulate the cycling and flux of GHGs in wetlands (Limpens et al., 2008;Melton et al., 2013;Belyea and Baird, 2006;Sjögersten et al., 2014), expanding our observations to include a wider range of wetland habitats is critical in order to improve our understanding of regional trace gas exchange, and also to determine if aggregating peat and mineral soil wetlands together in bottom-up emissions inventories are appropriate for regional budget calculations. Moreover, Amazonian peatlands are thought to account for a substantial land area (i.e. up to 150,000 km^2) (Schulman et al., 1999;Lahteenoja et al., 2012), and any differences in biogeochemistry among peat and mineral/organo-mineral soil wetlands may therefore have important implications for understanding and modelling the biogeochemical functioning of the Amazon basin as a whole.

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

Since the identification of extensive peat forming wetlands in the north (Lahteenoja et al., 2009a; Lahateenoja et al. 2009b; Lahteenoja and Page 2011) and south (Householder et al., 2012) of the Peruvian Amazon, several studies have been undertaken to better characterize these habitats, investigating vegetation composition and habitat diversity (Draper et al., 2014; Kelly et al., 2014; Householder et al., 2012; Lahteenoja and Page, 2011), vegetation history (Lahteenoja and Roucoux et al., 2010), C stocks (Lahteenoja et al., 2012; Draper et al., 2014), hydrology (Kelly et al., 2014), and peat chemistry (Lahteenoja et al., 2009a; Lahteenoja et al., 2009b). Most of the studies have focused on the Pastaza-Marañón foreland basin (PMFB), where one of the largest stretches of contiguous peatlands have been found (Lahteenoja et al 2009a; Lahteenoja and Page, 2011; Kelly et al, 2014), covering an estimated area of 35,600 ± 2,133 km^2 (Draper et al., 2014). Up to 90% of the peatlands in the PMFB lie in flooded backwater river margins on floodplains and are influenced by large, annual fluctuations in water table caused by the Amazonian flood pulse (Householder et al., 2012;Lahteenoja et al., 2009a). These floodplain systems are dominated by shallow (~3.9m) (Lahteenoja et al., 2009a) to deep (~12.9 m) (Householder et al., 2012) peat deposits. The remaining 10% of these peatlands are not directly influenced by river flow and form domed (i.e. raised) nutrient-poor bogs that likely only receive water and nutrients from rainfall (Lahteenoja et al., 2009b). These nutrient-poor bogs are dominated by large, C-rich forests (termed “pole forests”), that represent a very high density C store (total pool size of 1391 ± 710 Mg C ha^{-1}, which includes both above- and belowground stocks); exceeding in fact the C density of nearby floodplain systems (Draper et al., 2014). Even though the peats in these nutrient-poor bogs have a relatively high hydraulic conductivity, they act as natural stores of water because of high rainwater inputs (>3000 mm per annum), which help to maintain positive water tables, even during parts of the dry season (Kelly et al., 2014).

In order to improve our understanding of the biogeochemistry and rates of GHG exchange from Amazonian peatlands, we conducted a preliminary study of CH_4 and N_2O fluxes from forested peatlands in the PMFB. The main objectives of this research were to:

1. Quantify the magnitude and range of soil CH_4 and N_2O fluxes from a sub-set of peatlands in the PMFB that represent key dominant vegetation types
2. Determine seasonal patterns of trace gas exchange
3. Establish the relationship between trace gas fluxes and environmental variables

Sampling was concentrated on the four most dominant vegetation types in the area, based on prior work by the investigators (Lahteenoja and Page, 2011). Trace gas fluxes were captured from both floodplain systems and nutrient-poor bogs in order to account for underlying differences in biogeochemistry that may arise from variations in hydrology. Sampling was conducted during four field campaigns (two wet season, two dry season) over a 27-month period, extending from February 2012 to May 2014.

4. METHODS AND MATERIALS

4.1 Study site and sampling design

The study was carried out in the lowland tropical peatland forests of the PMFB, between 2 and 35 km south of the city of Iquitos, Peru (Lahteenoja et al., 2009a; Lahteenoja et al., 2009b) (Figure 1, Table 1). The mean annual temperature is 26 °C, annual precipitation is c. 3,100 mm, relative humidity ranges from 80-90 %, and altitude ranges from c. 90 to 130 m above sea level (Marengo 1998). The northwestern Amazon basin near Iquitos experiences pronounced seasonality, which is characterized by consistently high annual temperatures, but marked seasonal variation in precipitation (Tian et al., 1998), and an annual river flood pulse linked to seasonal discharge from the Andes (Junk et al., 1989). Precipitation events are frequent, intense and of significant duration during the wet season (November to May) and infrequent, intense and of short duration during the dry season (June to August). Catchments in this region receive no less than 100 mm of rain per month (Espinoza Villar et al., 2009a; Espinoza Villar et al., 2009b) and >3000 mm of rain per year. River discharge varies by season, with the lowest discharge between the dry season months of August and September. Peak discharge from the wet season flood pulse occurs between April and May, as recorded at the Tamshiyaku River gauging station (Espinoza Villar et al., 2009b).

Soils are classified as pure peat and pure peat with clay and sediment deposits, with an organic content of >50 %. The pH of the soils varied by site and ranged from 3.5 to 7.2 (Lahteenoja et al., 2009a; Lahteenoja et al., 2009b; this study). Study sites were classified as either nutrient-rich, intermediate, or nutrient-poor. The former tend to occur on floodplains and river margins, and account for approximately 90 % of the peatland cover in the PMFB, and receive water and nutrient inputs from the annual Amazon river flood pulse (Householder et al., 2012;Lahteenoja et al., 2009a). They are characterized by peat soils which contain higher inorganic mineral content, of which Ca is a dominant constituent (Lahteenoja et al., 2009b). In contrast, the nutrient-poor sites tend to occur further in-land (i.e. away from river margins and floodplains), and receive low or infrequent inputs of water and nutrients from the annual Amazon river flood pulse, and are almost entirely rain-fed (Lahteenoja et al., 2009b). These systems account for only about 10 % of peatland cover in the PMFB (Draper et al., 2014). Soil Ca concentrations are significantly lower in these sites compared to the nutrient-rich ones, with similar concentrations to that of rainwater (Lahteenoja et al., 2009b).

We established 229 sampling plots (~30 m^2 per plot) within five tropical peatland sites that captured four of the dominant vegetation types in the region (Draper et al., 2014;Householder et al., 2012;Kelly et al., 2014;Lahteenoja and Page, 2011), and which encompassed a range of nutrient availabilities (Figure 1, Table 1) (Lahteenoja and Page, 2011;Lahteenoja et al., 2009a). These four dominant vegetation types included: forested vegetation (nutrient-rich; n= 9 plots), forested (short pole) vegetation (nutrient-poor; n= 19 plots), *Mauritia flexuosa*-dominated palm swamp (intermediate fertility, n= 112 plots), and mixed palm swamp (nutrient-rich; n=8 plots) (Table 1). Four of the study sites (Buena Vista, Charo, Miraflores, and Quistococha) were dominated by single vegetation types, whereas San Jorge contained a mixture of *M. flexuosa* palm swamp and forested (short pole) vegetation (Table 1). As a consequence, both vegetation types were sampled in San Jorge to develop a more representative picture of GHG fluxes from this location. Sampling efforts were partially constrained by issues of site access; some locations were difficult to access (e.g. centre of the San Jorge peatland) due to water table height and navigability of river channels; as a consequence, sampling patterns were somewhat uneven, with higher sampling densities in some peatlands than in others (Table 1).

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

In each peatland site, transects were established from the edge of the peatland to its centre. Each transect varied in length from 2 to 5 km, depending on the relative size of the peatland. Randomly located sampling plots (~30 m^2 per plot) were established at 50 or 200 m intervals along each transect, from which GHG fluxes and environmental variables were measured concomitantly. The sampling interval (i.e. 50 or 200 m) was determined by the length of the transect or size of the peatland, with shorter sampling intervals (50 m) for shorter transects (i.e. smaller peatlands) and longer sampling intervals (200 m) for longer transects (i.e. larger peatlands).

4.2 Quantifying soil-atmosphere exchange

Soil-atmosphere fluxes (CH_4, N_2O) were determined in four campaigns over a two-year annual water cycle: February 2012 (wet season), June-August 2012 (dry season), June-July 2013 (dry season), and May-June 2014 (wet season). Gas exchange was quantified using a floating static chamber approach (Livingston and Hutchinson, 1995; Teh et al., 2011). Static flux measurements were made by enclosing a 0.225 m^2 area with a dark, single component, vented 10 L flux chamber. No chamber bases (collars) were used due to the highly saturated nature of the soils. In most cases, a standing water table was present at the soil surface, so chambers were placed directly onto the water. In the absence of a standing water table, a weighted skirt was applied to create an airtight seal. Under these drier conditions, chambers were placed carefully on the soil surface from a distance of no closer than 2 m in order to reduce the risk of pressure-induced ebullition or disruption to soil gas concentration profiles caused by the investigators' footfall. To promote even mixing within the headspace, chambers were fitted with small computer fans (Pumpanen et al., 2004). Headspace samples were collected from each flux chamber at five intervals over a 25 minute enclosure period using a gas tight syringe. Gas samples were stored in evacuated Exetainers® (Labco Ltd., Lampeter UK), shipped to the UK, and subsequently analysed for CH_4, CO_2 and N_2O concentrations using Thermo TRACE GC Ultra (Thermo Fischer Scientific Inc., Waltham, Massachusetts, USA) at the University of St. Andrews. Chromatographic separation was achieved using a Porapak-Q column, and gas concentrations determined using a flame ionization detector (FID) for CH_4, a methanizer-FID for CO_2, and an electron capture detector (ECD) for N_2O. Instrumental precision, determined from repeated analysis of standards, was < 5% for all detectors. Flux rates were determined by using the JMP IN version 11 (SAS Institute, Inc., Cary, North Carolina, USA) package to plot best-fit lines to the data for headspace concentration against time for individual flux chambers (Teh et al., 2014). Gas mixing ratios (ppm) were converted to areal fluxes by using the Ideal Gas Law to solve for the quantity of gas in the headspace (on a mole or mass basis) and normalized by the surface area of each static flux chamber (Livingston and Hutchinson, 1995).

4.3 Environmental variables

To investigate the effects of environmental variables on trace gas fluxes, we determined air temperature, soil temperature, chamber headspace temperature, soil pH, soil electrical conductivity (EC; μScm^{-2}), dissolved oxygen concentration of the soil pore water (DO; measured as percent saturation, %) in the top 15 cm of the peat column, and water table position concomitant with gas sampling. Air temperature and chamber headspace temperature were measured using a Check Temp probe and meter. Peat temperature, pH, DO and EC were measured at a depth of 15 cm below the peat surface and recorded *in situ*

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

with each gas sample using a HACH® rugged outdoor HQ30D multi meter and pH, LDO or EC probe. At sites where the water level was above the peat surface, the water depth was measured using a meter rule. Where the water table was at or below the peat surface, the water level was measured by auguring a hole to 1 m depth and measuring water table depth using a meter rule.

4.4 Statistical Analyses

Statistical analyses were performed using JMP IN version 11 (SAS Institute, Inc., Cary, North Carolina, USA). Box-Cox transformations were applied where the data failed to meet the assumptions of analysis of variance (ANOVA); otherwise, non-parametric tests were applied. ANOVA and analysis of co-variance (ANCOVA) were used to test for relationships between gas fluxes and vegetation type, season, and environmental variables. When determining the effect of vegetation type on gas flux, data from different study sites (e.g. San Jorge and Miraflores) were pooled together. Means comparisons were tested using a Fisher's Least Significant Difference (LSD) test.

5. RESULTS

5. 1 Differences in gas fluxes and environmental variables among vegetation types

All vegetation types were net sources of CH_4, with an overall mean (± standard error) flux of 36.1 ± 3.1 mg CH_4-C m^{-2} d^{-1}. Soil CH_4 fluxes varied significantly among the four vegetation types sampled in this study (two-way ANOVA with vegetation, season and their interaction, $F_{7,\,979}$ = 13.2, P<0.0001; Fig. 2a). However, the effect of vegetation was relatively weak (see ANCOVA results in the section 'Relationships between gas fluxes and environmental variables'), and a means comparison test on the pooled data was unable to determine which means differed significantly from the others (Fisher's LSD, P > 0.05). For the pooled data, the overall numerical trend was that mixed palm swamp showed the highest mean flux (52.0 ± 16.0 mg CH_4-C m^{-2} d^{-1}), followed by *M. flexuosa* palm swamp (36.7 ± 3.9 mg CH_4-Cm^{-2} d^{-1}), forested (short pole) vegetation (31.6 ± 6.6 mg CH_4-Cm^{-2} d^{-1}), and forested vegetation (29.8 ± 10.0 mg CH_4-C m^{-2} d^{-1}).

These study sites were also a weak net source of N_2O, with a mean flux of 0.70 ± 0.34 μg N_2O-N m^{-2} d^{-1}. Because of the high variance in N_2O flux among plots, analysis of variance indicated that mean N_2O flux did not differ significantly among vegetation types (two-way ANOVA, P > 0.5, Fig. 2b). However, when the N_2O flux data were grouped by vegetation type, we see that some vegetation types tended to function as net atmospheric sources, while others acted as atmospheric sinks (Fig. 2b, Table 3). For example, the highest N_2O emissions were observed from *M. flexuosa* palm swamp (1.11 ± 0.44 μg N_2O-N m^{-2} d^{-1}) and forested vegetation (0.20 ± 0.95 μg N_2O-N m^{-2} d^{-1}). In contrast, forested (short pole) vegetation and mixed palm swamp were weak sinks for N_2O, with mean fluxes of -0.01 ± 0.84 and -0.21 ± 0.70 μg N_2O-N m^{-2} d^{-1}, respectively.

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

Soil pH varied significantly among vegetation types (data pooled across all seasons; ANOVA, $P < 0.0001$, Table 2). Multiple comparisons tests indicated that mean soil pH was significantly different for each of the vegetation types (Fisher's LSD, $P < 0.0001$, Table 2), with the lowest pH in forested (short pole) vegetation (4.10 ± 0.04), followed by *M. flexuosa* palm swamp (5.32 ± 0.02), forested vegetation (6.15 ± 0.06), and the mixed palm swamp (6.58 ± 0.04).

Soil dissolved oxygen (DO) content varied significantly among vegetation types (data pooled across all seasons; Kruskal-Wallis, $P < 0.0001$, Table 2). Multiple comparisons tests indicated that mean DO was significantly different for each of the vegetation types (Fisher's LSD, $P < 0.05$, Table 2), with the highest DO in the forested (short pole) vegetation (25.2 ± 2.1 %), followed by the *M. flexuosa* palm swamp (18.1 ± 1.0 %), forested vegetation (11.8 ± 2.8 %), and the mixed palm swamp (0.0 ± 0.0 %).

Electrical conductivity (EC) varied significantly among vegetation types (data pooled across all seasons; Kruskal-Wallis, $P < 0.0001$, Table 2). Multiple comparison tests indicated that mean EC was significantly for each of the vegetation types (Fisher's LSD, $P < 0.05$; Table 2), with the highest EC in the mixed palm swamp (170.9 ± 6.0 µs m^{-2}), followed by forested vegetation (77.1 ± 4.2 µs m^{-2}), *M. flexuosa* palm swamp (49.7 ± 1.4 µs m^{-2}) and the forested (short pole) vegetation (40.9 ± 3.5 µs m^{-2}).

Soil temperature varied significantly among vegetation types (data pooled across all seasons; ANOVA, $P < 0.0001$, Table 2). Multiple comparisons tests indicated that soil temperature in

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

forested (short pole) vegetation was significantly lower than in the other vegetation types (Table 2); whereas the other vegetation types did not differ in temperature amongst themselves (Fisher's LSD, $P < 0.05$, Table 2).

Air temperature varied significantly among vegetation types (data pooled across all seasons; ANOVA, $P < 0.0001$, Table 2). Multiple comparisons tests indicated that soil temperature in *M. flexuosa* palm swamp was significantly lower than in the other vegetation types; whereas the other vegetation types did not differ in temperature amongst themselves (Fisher's LSD, $P < 0.05$, Table 2).

Water table depths varied significantly among vegetation types (data pooled across all seasons; ANOVA, $P < 0.0001$, Table 2). The highest mean water tables were observed in mixed palm swamp (59.6 ± 9.3 cm), followed by forested vegetation (34.0 ± 6.9 cm), *M. flexuosa* palm swamp (17.4 ± 1.2 cm), and forested (short pole) vegetation (3.5 ± 1.0 cm) (Fisher's LSD, $P < 0.0005$).

5.2 Seasonal variations in gas fluxes and environmental variables

The peatlands sampled in this study showed pronounced seasonal variability in CH_4 fluxes (two-way ANOVA, $F_{7, 979} = 13.2$, $P<0.0001$; Table 3). In contrast, N_2O fluxes showed no seasonal trends (two-way ANOVA, $P > 0.5$), and therefore will not be discussed further here. For CH_4 flux, the overall trend was towards significantly higher wet season (51.1 ± 7.0 mg CH_4-

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

C m^{-2} d^{-1}) compared to dry season (27.3 ± 2.7 mg CH_4-C m^{-2} d^{-1}) fluxes (data pooled across all vegetation types; t-Test, $P < 0.001$, Table 3). However, when the CH_4 fluxes were disaggregated by vegetation type, very different seasonal trends emerged. For example, both forested vegetation and mixed palm swamp showed significantly greater CH_4 fluxes during the *dry season* with net fluxes of 47.2 ± 5.4 mg CH_4-C m^{-2} d^{-1} and 64.2 ± 12.1 mg CH_4-C m^{-2} d^{-1}, respectively (Fisher's LSD, $P < 0.05$, Table 3). In contrast, *wet season* fluxes were 7-16 times lower, with net fluxes of 6.7 ± 1.0 mg CH_4-C m^{-2} d^{-1} and 6.1 ± 1.3 mg CH_4-C m^{-2} d^{-1}, respectively (Fisher's LSD, $P < 0.05$, Table 3). In contrast, forested (short pole) vegetation and *M. flexuosa* palm swamp showed seasonal trends consistent with the pooled data set; i.e. significantly higher fluxes during the wet season (46.7 ± 8.4 and 60.4 ± 9.1 mg CH_4-C m^{-2} d^{-1}, respectively) compared to the dry season (28.3 ± 2.6 and 18.8 ± 2.6 mg CH_4-C m^{-2} d^{-1}, respectively) (Fisher's LSD, $P < 0.05$, Table 3).

For the environmental variables, soil pH, DO, EC, water table depth, and soil temperature varied significantly between seasons, whereas air temperature did not. Thus, for sake of brevity, air temperature is not discussed further here. Mean soil pH was significantly lower during the wet season (5.18 ± 0.03) than the dry season (5.31 ± 0.04) (data pooled across all vegetation types; t-Test, $P < 0.05$, Table 2). When disaggregated by vegetation type, the overall trend was found to hold true for all vegetation types except forested (short pole) vegetation, which displayed higher pH during the wet season compared to the dry season (Table 2). A two-way ANOVA on Box-Cox transformed data using vegetation type, season and their interaction as explanatory variables indicated that vegetation type was the best

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

predictor of pH, with season and vegetation type by season playing a lesser role ($F_{7,\,1166}$ = 348.9, $P < 0.0001$).

For DO, the overall trend was towards significantly lower DO during the wet season (13.9 ± 1.0 %) compared to the dry season (19.3 ± 1.2 %) (data pooled across all vegetation types; Wilcoxon test, $P < 0.0001$, Table 2). However, when the data were disaggregated by vegetation type, we found that individual vegetation types showed distinct seasonal trends from each other. Forested vegetation and mixed palm swamp were consistent with the overall trend (i.e. lower wet season compared to dry season DO), whereas forested (short pole) vegetation and *M. flexuosa* palm swamp displayed the reverse trend (i.e. higher *wet season* compared to *dry season* DO) (Table 2). A two-way ANOVA on Box Cox transformed data using vegetation type, season and their interaction as explanatory variables indicated that vegetation type was the best predictor of DO, followed by a strong vegetation by season interaction; season itself played a lesser role than either of the other two explanatory variables ($F_{7,\,1166}$ = 57.0, $P < 0.0001$).

For EC, the overall trend was towards lower EC in the wet season (49.4 ± 1.8 µs m^{-2}) compared to the dry season (65.5 ± 2.2 µs m^{-2}) (data pooled across all vegetation types; Wilcoxon test, $P < 0.05$, Table 2). When the data were disaggregated by vegetation type, this trend was consistent for all the vegetation types except for forested vegetation, where differences between wet and dry season were not statistically significant (Wilcoxon, $P > 0.05$, Table 2).

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

Water table depths varied significantly between seasons (data pooled across all vegetation types; Wilcoxon test, $P < 0.0001$, Table 2). Mean water table level was significantly higher in the wet (54.1 ± 2.7 cm) than the dry (1.3 ± 0.8 cm) season. When disaggregated by vegetation type, the trend held true for individual vegetation types (Table 2). All vegetation types had negative dry season water tables (i.e. below the soil surface) and positive wet season water tables (i.e. water table above the soil surface), except for *M. flexuosa* palm swamp that had positive water tables in both seasons. Two-way ANOVA on Box-Cox transformed data using vegetation type, season and their interaction as explanatory variables indicated that all three factors explained water table depth, but that season accounted for the largest proportion of the variance in the model, followed by vegetation by season, and lastly by vegetation type ($F_{7, 1157} = 440.1$, $P < 0.0001$).

For soil temperature, the overall trend was towards slightly higher temperatures in the wet season (25.6 ± 0.0°C) compared to the dry season (25.1 ± 0.0°C) (t-Test, $P < 0.0001$). Analysis of the disaggregated data indicates this trend was consistent for individual vegetation types (Table 2). Two-way ANOVA on Box-Cox transformed data using vegetation type, season and their interaction as explanatory variables indicated that all three variables played a significant role in modulating soil temperature, although season accounted for the largest proportion of the variance whereas the other two factors accounted for a similar proportion of the variance ($F_{7, 1166} = 21.3$, $P < 0.0001$).

5.3 Relationships between gas fluxes and environmental variables

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

To explore the relationship between environmental variables and trace gas fluxes, we conducted an analysis of covariance (ANCOVA) on Box-Cox transformed gas flux data, using vegetation type, season, vegetation by season, and environmental variables as explanatory variables.

For CH_4, ANCOVA revealed that vegetation by season was the strongest predictor of CH_4 flux, followed by a strong season effect ($F_{13, 917}$ = 9.2, P<0.0001). Other significant drivers included soil temperature, water table depth, and a borderline-significant effect of vegetation type (P < 0.06). The strong effect of vegetation by season reflects the fact that different vegetation types showed seasonal differences in emission patterns, with forested vegetation and mixed palm swamp showing significantly higher dry season compared to wet season emissions, while forested (short pole) vegetation and *M. flexuosa* palm swamp showed the reverse trend (see above; Table 3). The positive relationships between soil temperature, water table depth and CH_4 flux indicate that warmer conditions or higher water tables both stimulate CH_4 flux. However, it is important to note that each of these environmental variables were only weakly correlated with CH_4 flux even if the relationships were statistically significant; when individual bivariate regressions were calculated, the r^2 values were less than 0.01 for each plot.

For N_2O, ANCOVA indicated that the best predictors of flux rates were dissolved oxygen and conductivity ($F_{13, 1014}$= 2.2, P < 0.0082). As was the case for CH_4 and CO_2, when the relationships between these environmental variables and N_2O flux were explored using individual bivariate regressions, r^2 values were found to be very low (e.g. less than $r^2 < 0.0009$) and not statistically significant.

6. DISCUSSION

6.1 Large and asynchronous CH_4 fluxes from peatlands in the Pastaza-Marañón foreland basin

The ecosystems sampled in this study were strong atmospheric sources of CH_4. Net CH_4 flux, averaged across all vegetation types, was 36.1 ± 3.1 mg CH_4-C m^{-2} d^{-1}, spanning a range from -99.8 to 1,509.7mg CH_4-C m^{-2} d^{-1}. This mean falls within the range of fluxes observed in Indonesian peatlands (3.7-87.8 mg CH_4-C m^{-2} d^{-1}) (Couwenberg et al., 2010) and other Amazonian wetlands (7.1-390.0 mg CH_4-C m^{-2} d^{-1}) (Bartlett et al., 1990;Bartlett et al., 1988;Devol et al., 1990;Devol et al., 1988). These data suggest that peatlands in the Pastaza-Marañón foreland basin may be strong contributors to the regional atmospheric CH_4 budget, given that the four vegetation types sampled here represent the dominant cover types in the PMFB (Draper et al., 2014;Householder et al., 2012;Kelly et al., 2014;Lahteenoja and Page, 2011)

The overall trend in the data was towards greater temporal (i.e. seasonal) variability in CH_4 fluxes rather than spatial (i.e. inter-site) variability. For the pooled dataset, CH_4 emissions were significantly greater during the wet season than the dry season, with fluxes falling by approximately half from one season to the other (i.e. 51.1 ± 7.0 to 27.3 ± 2.7 mg CH_4-C m^{-2} d^{-1}). This is in contrast to the data on CH_4 fluxes among study sites, where statistical analyses indicate that there was a weak effect of vegetation type on CH_4 flux, that was on the edge of statistical significance (i.e. ANCOVA; $P < 0.06$ for the vegetation effect term).

On face value, these data suggest two findings; first, the weak effect of vegetation type implies that patterns of CH_4 cycling are broadly similar among study sites. Second, the strong seasonal pattern suggests that – on the whole – these systems conform to our normative expectations of how peatlands function with respect to seasonal variations in hydrology and redox potential; i.e. enhanced CH_4 emissions during a more anoxic wet season, and reduced CH_4 emissions during a more oxic dry season when water tables fall. However, closer inspection of the data reveals that different vegetation types showed contrasting seasonal emission patterns (Table 3), challenging our basic assumptions about how these ecosystems function. For example, while forested (short pole) vegetation and *M. flexuosa* palm swamp conformed to expected seasonal trends for methanogenic wetlands (i.e. higher wet season compared to dry season emissions), forested vegetation and mixed palm swamp showed the opposite pattern, with significantly greater CH_4 emissions during the dry season. The disaggregated data thus imply that the process-based controls on CH_4 fluxes may vary significantly among these different ecosystems, rather than being similar, leading to a divergence in seasonal flux patterns.

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

What may explain this pattern of divergence? One explanation is that CH_4 emissions from forested vegetation and mixed palm swamp, compared to the other two ecosystems, may be more strongly transport-limited during the wet season than the dry season. This interpretation is partially supported by the field data; forested vegetation and mixed palm swamp had the highest wet season water table levels, measuring 110.8 ± 9.3 and 183.7 ± 1.7 cm, respectively (Table 2). In contrast, water table levels for forested (short pole) vegetation and *M. flexuosa* palm swamp in the wet season were 3-7 times lower, measuring only 26.9 ± 0.5 and 37.2 ± 1.7 cm, respectively (Table 2). The greater depth of overlying water in forested vegetation and mixed palm swamp may therefore have exerted a greater physical constraint on gas transport compared to the other two ecosystems. Although one could argue that the positive relationship between water table depth and CH_4 flux found in the ANCOVA contradicts this interpretation, the relationship between the two variables is so weak (i.e. r^2 = 0.005) that we believe it is unlikely that water table alone exerted a strong control over CH_4 fluxes.

However, transport limitation alone does not fully explain the difference in dry season CH_4 emissions among vegetation types. Forested vegetation and mixed palm swamp showed substantially higher dry season CH_4 emissions (47.2 ± 5.4 and 85.5 ± 26.4 mg CH_4-C m^{-2} d^{-1}, respectively) compared to forested (short pole) vegetation and *M. flexuosa* palm swamp (9.6 ± 2.6 and 25.5 ± 2.9 mg CH_4-C m^{-2} d^{-1}, respectively), pointing to underlying differences in CH_4 production and oxidation among these ecosystems. One possibility is that dry season methanogenesis in forested vegetation and mixed palm swamp was greater than in the other two ecosystems, potentially driven by higher rates of C flow (Whiting and Chanton, 1993).

This is plausible given that forested vegetation and mixed palm swamp tend to occur in more nutrient-rich parts of the Pastaza-Marañón foreland basin, whereas forested (short pole) vegetation and *M. flexuosa* palm swamp tend to dominate in more nutrient-poor areas (Lahteenoja et al., 2009a), leading to potential differences in rates of plant productivity. Moreover, it is possible that the nutrient-rich vegetation may be able to utilize the higher concentration of nutrients, deposited during the flood pulse, during the Amazonian dry season (Morton et al., 2014;Saleska et al., 2016), with implications for overall ecosystem C throughput and CH_4 emissions. Of course, this interpretation does not preclude other explanations, such as differences in CH_4 transport rates among ecosystems (e.g. due to plant-facilitated transport or ebullition) (Panagala et al., 2013), or varying rates of CH_4 oxidation (Teh et al., 2005); however, these possibilities cannot be explored further without recourse to more detailed process-level experiments. Forthcoming studies on the regulation of GHG fluxes at finer spatial scales (e.g. investigation of environmental gradients within individual study sites) or diurnal patterns of GHG exchange (Murphy *et al.*, in prep.) will further deepen our understanding of the process controls on soil GHG flux from these peatlands, and shed light on these questions.

Finally, while the trends described here are intriguing, it is important to acknowledge some of the potential limitations of our data. First, given the uneven sampling pattern, it is possible that the values reported here do not fully represent the entire range of fluxes for the more lightly sampled habitats. However, given the large and statistically significant differences in CH_4 fluxes during different seasons, it is likely that the main trends that we have identified here will hold true with more spatially-extensive sampling. Second, the data presented here represent a conservative estimate of CH_4 efflux because the low frequency sampling approach utilized in this study was unable to capture “hot moments” or erratic ebullition fluxes, which often result in much higher net CH_4 fluxes (McClain et al., 2003). Third and last, our data probably underestimate net CH_4 fluxes for the PMFB because we chose to include fluxes with strong negative values (i.e. more than -10 mg CH_4-C m^{-2} d^{-1}) in our calculation of mean flux rates. These observations are more negative than other values typically reported elsewhere in the tropical wetland literature (Bartlett et al., 1990;Bartlett et al., 1988;Devol et al., 1990;Devol et al., 1988;Couwenberg et al., 2010). However, they represent only a small proportion of our dataset (i.e. 7 %, or only 68 out of 980 measurements), and inspection of our field notes and the data itself did not produce convincing reasons to exclude these observations (e.g. we found no evidence of irregularities during field sampling, and any chambers that showed statistically insignificant changes in concentration over time were removed during our quality control procedures). While headspace concentrations for these measurements were often elevated above mean tropospheric levels (>2 ppm), this in itself is not unusual in reducing environments that contain strong local sources of CH_4 (Baldocchi et al., 2012). We did not see this as a reason to omit these values as local concentrations of CH_4 are likely to vary naturally in methanogenic forest environments because of poor mixing in the understory. Most importantly, exclusion of these data did not alter the overall statistical trends reported above, and only produced slightly higher estimates of mean CH_4 flux (41.6 ± 3.2 mg CH_4-C m^{-2} d^{-1} versus 36.1 ± 3.1 mg CH_4-C m^{-2} d^{-1}).

6.2 Western Amazonian peatlands as weak atmospheric sources of nitrous oxide

The ecosystems sampled in this study were negligible atmospheric sources of N_2O, emitting only 0.70 ± 0.34 μg N_2O-N m^{-2} d^{-1}, suggesting that peatlands in the Pastaza-Marañón foreland basin make little or no contribution to regional atmospheric budgets of N_2O. This is consistent with N_2O flux measurements from other forested tropical peatlands, where N_2O emissions were also found to be relatively low (Inubushi et al., 2003; Couwenberg et al., 2010). No statistically significant differences in N_2O flux were observed among study sites or between seasons, suggesting that these different peatlands may have similar patterns of N_2O cycling. Interestingly, differences in N_2O fluxes were not associated with the nutrient status of the peatland; i.e. more nutrient-rich ecosystems, such as forested vegetation and mixed palm swamp, did not show higher N_2O fluxes than their nutrient-poor counterparts, such as forested (short pole) vegetation and *M. flexuosa* palm swamp. This may imply that N availability, one of the principal drivers of nitrification, denitrification, and N_2O production (Groffman et al., 2009;Werner et al., 2007), may not be greater in nutrient-rich versus nutrient-poor ecosystems in this part of the Western Amazon. Alternatively, it is possible that even though N availability and N fluxes may differ between nutrient-rich and nutrient-poor systems, N_2O yield may also vary such that net N_2O emissions are not significantly different among study sites (Teh et al., 2014).

One potential source of concern are the negative N_2O fluxes that we documented here. While some investigators have attributed negative fluxes to instrumental error (Cowan et al., 2014;Chapuis-Lardy et al., 2007), others have demonstrated that N_2O consumption – particularly in wetland soils – is not an experimental artifact, but occurs due to the complex effects of redox, organic carbon content, nitrate availability, and soil transport processes on denitrification (Ye and Horwath, 2016;Yang et al., 2011;Wen et al., 2016;Schlesinger, 2013;Teh et al., 2014;Chapuis-Lardy et al., 2007). Given the low redox potential and high carbon content of these soils, it is plausible that microbial N_2O consumption is occurring, because these types of conditions have been found to be conducive for N_2O uptake elsewhere (Ye and Horwath, 2016;Teh et al., 2014;Yang et al., 2011).

7. CONCLUSIONS

These data suggest that peatlands in the Pastaza-Marañón foreland basin are strong sources of atmospheric CH_4 at a regional scale, and need to be better accounted for in CH_4 emissions inventories for the Amazon basin as a whole. In contrast, N_2O fluxes were negligible, suggesting that these ecosystems are weak regional sources at best. Most intriguing is the divergent seasonal emissions pattern for CH_4 among different vegetation types, which challenges our understanding and assumptions of how tropical peatlands function. These data highlight the need for more spatially-extensive sampling, in order to establish if this pattern is commonplace across peatlands of the Amazon basin, or if it is unique to the Pastaza-Marañón foreland basin. If CH_4 emission patterns for different peatlands in the Amazon are in fact asynchronous and decoupled from rainfall seasonality, then this may partially explain some of the heterogeneity in CH_4 source and sinks observed at the basin-wide scale (Wilson et al., 2016).

8. AUTHOR CONTRIBUTION

YAT secured the funding for this research, assisted in the planning and design of the experiment, and took the principal role in the analysis of the data and preparation of the manuscript. WAM planned and designed the experiment, collected the field data, analyzed the samples, and took a secondary role in data preparation, data analysis, and manuscript preparation. JCB, AB, and SEP supported the planning and design of the experiment, and provided substantive input into the writing of the manuscript.

9. ACKNOWLEDGEMENTS

The authors would like to acknowledge the UK Natural Environment Research Council for funding this research (NERC award number NE/I015469). We would like to thank MINAG and the Ministerio de Turismo in Iquitos for permits to conduct this research, the Instituto de Investigaciones de la Amazonía Peruana (IIAP) for logistical support, Peruvian rainforest villagers for their warm welcome and acceptance, Hugo Vasquez, Pierro Vasquez, Gian Carlo Padilla Tenazoa and Yully Rojas Reátegui for fieldwork assistance, Dr Outi Lahteenoja and Dr Ethan Householder for fieldwork planning, and Dr Paul Beaver of Amazonia Expeditions for lodging and logistical support. Our gratitude also goes to Alex Cumming for fieldwork support and laboratory assistance, Bill Hickin, Gemma Black, Adam Cox, Charlotte Langley, Kerry Allen, and Lisa Barber of the University of Leicester for all of their continued support. Thanks are also owed to Graham Hambley (St Andrews), Angus Calder (St Andrews), Viktoria Oliver (Aberdeen), Torsten Diem (Aberdeen), Tom Kelly (Leeds), and Freddie Draper Leeds) for their help in the laboratory and with fieldwork planning. TD, VO, and two anonymous referees provided very helpful and constructive comments on earlier drafts of this manuscript. This publication is a contribution from the Scottish Alliance for Geoscience, Environment and Society (http://www.sages.ac.uk) and the UK Tropical Peatland Working Group (https://tropicalpeat.wordpress.com).

10. REFERENCES

Baldocchi, D., Detto, M., Sonnentag, O., Verfaillie, J., Teh, Y. A., Silver, W., and Kelly, N. M.: The challenges of measuring methane fluxes and concentrations over a peatland pasture, Agric. For. Meteorol., 153, 177-187, http://dx.doi.org/10.1016/j.agrformet.2011.04.013, 2012.

Bartlett, K. B., Crill, P. M., Sebacher, D. I., Harriss, R. C., Wilson, J. O., and Melack, J. M.: METHANE FLUX FROM THE CENTRAL AMAZONIAN FLOODPLAIN, Journal of Geophysical Research-Atmospheres, 93, 1571-1582, 1988.

Bartlett, K. B., Crill, P. M., Bonassi, J. A., Richey, J. E., and Harriss, R. C.: METHANE FLUX FROM THE AMAZON RIVER FLOODPLAIN - EMISSIONS DURING RISING WATER, Journal of Geophysical Research-Atmospheres, 95, 16773-16788, 10.1029/JD095iD10p16773, 1990.

Belyea, L. R., and Baird, A. J.: Beyond "The limits to peat bog growth'': Cross-scale feedback in peatland development, Ecological Monographs, 76, 299-322, 2006.

Chapuis-Lardy, L., Wrage, N., Metay, A., Chotte, J.-L., and Bernoux, M.: Soils, a sink for N2O? A review, Global Change Biology, 13, 1-17, 10.1111/j.1365-2486.2006.01280.x, 2007.

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

Biogeosciences Discussions
Open Access

Couwenberg, J., Dommain, R., and Joosten, H.: Greenhouse gas fluxes from tropical peatlands in south-east Asia, Global Change Biology, 16, 1715-1732, 10.1111/j.1365-2486.2009.02016.x, 2010.

Cowan, N. J., Famulari, D., Levy, P. E., Anderson, M., Reay, D. S., and Skiba, U. M.: Investigating uptake of N₂O in agricultural soils using a high-precision dynamic chamber method, Atmos. Meas. Tech., 7, 4455-4462, 10.5194/amt-7-4455-2014, 2014.

D'Amelio, M. T. S., Gatti, L. V., Miller, J. B., and Tans, P.: Regional N2O fluxes in Amazonia derived from aircraft vertical profiles, Atmospheric Chemistry and Physics, 9, 8785-8797, 2009.

Devol, A. H., Richey, J. E., Clark, W. A., King, S. L., and Martinelli, L. A.: Methane emissions to the troposphere from the Amazon floodplain, Journal of Geophysical Research: Atmospheres, 93, 1583-1592, 10.1029/JD093iD02p01583, 1988.

Devol, A. H., Richey, J. E., Forsberg, B. R., and Martinelli, L. A.: SEASONAL DYNAMICS IN METHANE EMISSIONS FROM THE AMAZON RIVER FLOODPLAIN TO THE TROPOSPHERE, Journal of Geophysical Research-Atmospheres, 95, 16417-16426, 10.1029/JD095iD10p16417, 1990.

Draper, F. C., Roucoux, K. H., Lawson, I. T., Mitchard, E. T. A., Coronado, E. N. H., Lahteenoja, O., Montenegro, L. T., Sandoval, E. V., Zarate, R., and Baker, T. R.: The distribution and amount of carbon in the largest peatland complex in Amazonia, Environmental Research Letters, 9, 12, 10.1088/1748-9326/9/12/124017, 2014.

Groffman, P. M., Butterbach-Bahl, K., Fulweiler, R. W., Gold, A. J., Morse, J. L., Stander, E. K., Tague, C., Tonitto, C., and Vidon, P.: Challenges to incorporating spatially and temporally explicit phenomena (hotspots and hot moments) in denitrification models, Biogeochemistry, 93, 49-77, 10.1007/s10533-008-9277-5, 2009.

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

Householder, J. E., Janovec, J., Tobler, M., Page, S., and Lähteenoja, O.: Peatlands of the Madre de Dios River of Peru: Distribution, Geomorphology, and Habitat Diversity, Wetlands, 32, 359-368, 10.1007/s13157-012-0271-2, 2012.

Huang, J., Golombek, A., Prinn, R., Weiss, R., Fraser, P., Simmonds, P., Dlugokencky, E. J., Hall, B., Elkins, J., Steele, P., Langenfelds, R., Krummel, P., Dutton, G., and Porter, L.: Estimation of regional emissions of nitrous oxide from 1997 to 2005 using multinetwork measurements, a chemical transport model, and an inverse method, Journal of Geophysical Research-Atmospheres, 113, 1-19, D17313

10.1029/2007jd009381, 2008.

Keller, M., Kaplan, W. A., and Wofsy, S. C.: EMISSIONS OF N2O, CH4 AND CO2 FROM TROPICAL FOREST SOILS, Journal of Geophysical Research-Atmospheres, 91, 1791-1802, 10.1029/JD091iD11p11791, 1986.

Kelly, T. J., Baird, A. J., Roucoux, K. H., Baker, T. R., Honorio Coronado, E. N., Ríos, M., and Lawson, I. T.: The high hydraulic conductivity of three wooded tropical peat swamps in northeast Peru: measurements and implications for hydrological function, Hydrological Processes, 28, 3373-3387, 10.1002/hyp.9884, 2014.

Kirschke, S., Bousquet, P., Ciais, P., Saunois, M., Canadell, J. G., Dlugokencky, E. J., Bergamaschi, P., Bergmann, D., Blake, D. R., Bruhwiler, L., Cameron-Smith, P., Castaldi, S., Chevallier, F., Feng, L., Fraser, A., Heimann, M., Hodson, E. L., Houweling, S., Josse, B., Fraser, P. J., Krummel, P. B., Lamarque, J. F., Langenfelds, R. L., Le Quere, C., Naik, V., O'Doherty, S., Palmer, P. I., Pison, I., Plummer, D., Poulter, B., Prinn, R. G., Rigby, M., Ringeval, B., Santini, M., Schmidt, M., Shindell, D. T., Simpson, I. J., Spahni, R., Steele, L. P., Strode, S. A., Sudo, K., Szopa, S., van der Werf, G. R., Voulgarakis, A., van Weele, M., Weiss,

R. F., Williams, J. E., and Zeng, G.: Three decades of global methane sources and sinks, Nature Geoscience, 6, 813-823, 10.1038/ngeo1955, 2013.

Lahteenoja, O., Ruokolainen, K., Schulman, L., and Alvarez, J.: Amazonian floodplains harbour minerotrophic and ombrotrophic peatlands, Catena, 79, 140-145, 10.1016/j.catena.2009.06.006, 2009a.

Lahteenoja, O., Ruokolainen, K., Schulman, L., and Oinonen, M.: Amazonian peatlands: an ignored C sink and potential source, Global Change Biology, 15, 2311-2320, 10.1111/j.1365-2486.2009.01920.x, 2009b.

Lahteenoja, O., and Page, S.: High diversity of tropical peatland ecosystem types in the Pastaza-Maranon basin, Peruvian Amazonia, Journal of Geophysical Research-Biogeosciences, 116, 14, 10.1029/2010jg001508, 2011.

Lahteenoja, O., Reategui, Y. R., Rasanen, M., Torres, D. D., Oinonen, M., and Page, S.: The large Amazonian peatland carbon sink in the subsiding Pastaza-Maranon foreland basin, Peru, Global Change Biology, 18, 164-178, 10.1111/j.1365-2486.2011.02504.x, 2012.

Lavelle, P., Rodriguez, N., Arguello, O., Bernal, J., Botero, C., Chaparro, P., Gomez, Y., Gutierrez, A., Hurtado, M. D., Loaiza, S., Pullido, S. X., Rodriguez, E., Sanabria, C., Velasquez, E., and Fonte, S. J.: Soil ecosystem services and land use in the rapidly changing Orinoco River Basin of Colombia, Agriculture Ecosystems & Environment, 185, 106-117, 10.1016/j.agee.2013.12.020, 2014.

Liengaard, L., Nielsen, L. P., Revsbech, N. P., Priem, A., Elberling, B., Enrich-Prast, A., and Kuhl, M.: Extreme emission of N2O from tropical wetland soil (Pantanal, South America), Frontiers in Microbiology, 3, 13, 10.3389/fmicb.2012.00433, 2013.

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

Limpens, J., Berendse, F., Blodau, C., Canadell, J. G., Freeman, C., Holden, J., Roulet, N., Rydin, H., and Schaepman-Strub, G.: Peatlands and the carbon cycle: from local processes to global implications – a synthesis, Biogeosciences, 5, 1475–1491, 2008.

Marani, L., and Alvalá, P. C.: Methane emissions from lakes and floodplains in Pantanal, Brazil, Atmospheric Environment, 41, 1627-1633, http://dx.doi.org/10.1016/j.atmosenv.2006.10.046, 2007.

McClain, M. E., Boyer, E. W., Dent, C. L., Gergel, S. E., Grimm, N. B., Groffman, P. M., Hart, S. C., Harvey, J. W., Johnston, C. A., Mayorga, E., McDowell, W. H., and Pinay, G.: Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems, Ecosystems, 6, 301-312, 10.1007/s10021-003-0161-9, 2003.

Melack, J. M., Hess, L. L., Gastil, M., Forsberg, B. R., Hamilton, S. K., Lima, I. B. T., and Novo, E.: Regionalization of methane emissions in the Amazon Basin with microwave remote sensing, Global Change Biology, 10, 530-544, 10.1111/j.1529-8817.2003.00763.x, 2004.

Melton, J. R., Wania, R., Hodson, E. L., Poulter, B., Ringeval, B., Spahni, R., Bohn, T., Avis, C. A., Beerling, D. J., Chen, G., Eliseev, A. V., Denisov, S. N., Hopcroft, P. O., Lettenmaier, D. P., Riley, W. J., Singarayer, J. S., Subin, Z. M., Tian, H., Zurcher, S., Brovkin, V., van Bodegom, P. M., Kleinen, T., Yu, Z. C., and Kaplan, J. O.: Present state of global wetland extent and wetland methane modelling: conclusions from a model inter-comparison project (WETCHIMP), Biogeosciences, 10, 753-788, 10.5194/bg-10-753-2013, 2013.

Morton, D. C., Nagol, J., Carabajal, C. C., Rosette, J., Palace, M., Cook, B. D., Vermote, E. F., Harding, D. J., and North, P. R. J.: Amazon forests maintain consistent canopy structure and greenness during the dry season, Nature, 506, 221-224, 10.1038/nature13006 http://www.nature.com/nature/journal/v506/n7487/abs/nature13006.html - supplementary-information, 2014.

Nisbet, E. G., Dlugokencky, E. J., and Bousquet, P.: Methane on the Rise—Again, Science, 343, 493-495, 10.1126/science.1247828, 2014.

Saikawa, E., Schlosser, C. A., and Prinn, R. G.: Global modeling of soil nitrous oxide emissions from natural processes, Global Biogeochemical Cycles, 27, 972-989, 10.1002/gbc.20087, 2013.

Saikawa, E., Prinn, R. G., Dlugokencky, E., Ishijima, K., Dutton, G. S., Hall, B. D., Langenfelds, R., Tohjima, Y., Machida, T., Manizza, M., Rigby, M., O'Doherty, S., Patra, P. K., Harth, C. M., Weiss, R. F., Krummel, P. B., van der Schoot, M., Fraser, P. J., Steele, L. P., Aoki, S., Nakazawa, T., and Elkins, J. W.: Global and regional emissions estimates for N2O, Atmospheric Chemistry and Physics, 14, 4617-4641, 10.5194/acp-14-4617-2014, 2014.

Saleska, S. R., Wu, J., Guan, K., Araujo, A. C., Huete, A., Nobre, A. D., and Restrepo-Coupe, N.: Dry-season greening of Amazon forests, Nature, 531, E4-E5, 10.1038/nature16457, 2016.

Schlesinger, W. H.: An estimate of the global sink for nitrous oxide in soils, Global Change Biology, 19, 2929-2931, 10.1111/gcb.12239, 2013.

Schulman, L., Ruokolainen, K., and Tuomisto, H.: Parameters for global ecosystem models, Nature, 399, 535-536, 1999.

Sjögersten, S., Black, C. R., Evers, S., Hoyos-Santillan, J., Wright, E. L., and Turner, B. L.: Tropical wetlands: A missing link in the global carbon cycle?, Global Biogeochemical Cycles, 28, 1371-1386, 10.1002/2014GB004844, 2014.

Smith, L. K., Lewis, W. M., Chanton, J. P., Cronin, G., and Hamilton, S. K.: Methane emissions from the Orinoco River floodplain, Venezuela., Biogeochemistry, 51, 113-140, 2000.

Teh, Y. A., Silver, W. L., and Conrad, M. E.: Oxygen effects on methane production and oxidation in humid tropical forest soils, Global Change Biology, 11, 1283-1297, 10.1111/j.1365-2486.2005.00983.x, 2005.

Teh, Y. A., Diem, T., Jones, S., Huaraca Quispe, L. P., Baggs, E., Morley, N., Richards, M., Smith, P., and Meir, P.: Methane and nitrous oxide fluxes across an elevation gradient in the tropical Peruvian Andes, Biogeosciences, 11, 2325-2339, 10.5194/bg-11-2325-2014, 2014.

Wen, Y., Chen, Z., Dannenmann, M., Carminati, A., Willibald, G., Kiese, R., Wolf, B., Veldkamp, E., Butterbach-Bahl, K., and Corre, M. D.: Disentangling gross N2O production and consumption in soil, Sci Rep, 6, 8, 10.1038/srep36517, 2016.

Werner, C., Butterbach-Bahl, K., Haas, E., Hickler, T., and Kiese, R.: A global inventory of N2O emissions from tropical rainforest soils using a detailed biogeochemical model, Global Biogeochemical Cycles, 21, 1-18, Gb3010 10.1029/2006gb002909, 2007.

Whiting, G. J., and Chanton, J. P.: Primary production control of methane emission from wetlands., Nature, 364, 794-795, 1993.

Wilson, C., Gloor, M., Gatti, L. V., Miller, J. B., Monks, S. A., McNorton, J., Bloom, A. A., Basso, L. S., and Chipperfield, M. P.: Contribution of regional sources to atmospheric methane over the Amazon Basin in 2010 and 2011, Global Biogeochem. Cycles, 30, 400–420, 10.1002/2015GB005300, 2016.

Yang, W. H., Teh, Y. A., and Silver, W. L.: A test of a field-based N-15-nitrous oxide pool dilution technique to measure gross N2O production in soil, Global Change Biology, 17, 3577-3588, 10.1111/j.1365-2486.2011.02481.x, 2011.

Ye, R., and Horwath, W. R.: Nitrous oxide uptake in rewetted wetlands with contrasting soil organic carbon contents, Soil Biology and Biochemistry, 100, 110-117, http://dx.doi.org/10.1016/j.soilbio.2016.06.009, 2016.

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

11. TABLES AND FIGURES

Table 1. Site characteristics including field site location, nutrient status, plot and flux chamber replication

Vegetation type	Site name	Nutrient status*	Latitude (S)	Longitude (W)	Plots	Flux chambers
Forested	Buena Vista	Rich	4°14'45.60"	73°12'0.20"W	9	74
Forested (short pole)	San Jorge (centre)	Poor	4°03'35.95"S	73°12'01.13"W	3	26
Forested (short pole)	Miraflores	Poor	4°28'16.59"S	74° 4'39.95"W	16	142
M. flexuosa Palm Swamp	Quistococha	Intermediate	3°49'57.61"	73°12'01.13"	119	433
M. flexuosa Palm Swamp	San Jorge (edge)	Intermediate	4°03'18.83"S	73°10'16.80"W	6	81
Mixed palm swamp	Charo	Rich	4°16'21.80"S	73°15'27.80"W	8	56

*After Householder et al. 2012, Lahteenoja et al. 2009a, and Lahteenoja et al. 2009b

Table 2. Environmental variables for each vegetation type for the wet and dry season. Values reported here are means and standard errors. Lower case letters indicate significant differences among vegetation types within the wet or dry season (Fisher's LSD, *P* < 0.05).

Vegetation Type	Peat Temperature (°C)		Air Temperature (°C)		Conductivity ($\mu S\ m^{-2}$)		Dissolved Oxygen (%)		Water Table Level (cm)		pH	
	Wet Season	Dry Season	Wet Season	Dry Season	Wet Season	Dry Season	Wet Season	Dry Season	Wet Season	Dry Season	Wet Season	Dry Season
Forested	26.1 ± 0.1a	24.7 ± 0.0a	28.8 ± 0.7a	26.4 ± 0.3a	79.0 ± 5.9a	75.9 ± 5.7a	0.2 ± 0.1a	18.9 ± 4.4a	110.8 ± 9.3a	-13.2 ± 0.7a	5.88 ± 0.15a	6.31 ± 0.04a
Forested (short pole)	25.2 ± 0.0b	24.8 ± 0.1a	27.6 ± 0.1b	27.5 ± 0.1b	21.0 ± 0.0b	48.5 ± 4.8b	4.4 ± 0.0a	33.1 ± 2.6b	26.9 ± 0.5b	-4.7 ± 0.4b	4.88 ± 0.01b	3.8 ± 0.03b
M. flexuosa Palm Swamp	25.6 ± 0.6c	25.3 ± 0.1b	26.3 ± 0.1c	26.4 ± 0.1a	45.9 ± 2.1c	51.9 ± 1.8b	19.4 ± 1.3b	17.3 ± 1.5a	37.2 ± 1.7c	6.1 ± 1.3c	5.04 ± 0.03c	5.49 ± 0.03c
Mixed Palm Swamp	26.0 ± 0.0a	25.0 ± 0.1ab	26.1 ± 0.1c	28.2 ± 0.3b	100.0 ± 0.2d	206.4 ± 4.2c	0.0 ± 0.0a	0.0 ± 0.0c	183.7 ± 1.7d	-2.4 ± 0.3b	6.1 ± 0.03a	6.82 ± 0.02d

729 **Table 3.** Trace gas fluxes for each vegetation type for the wet and dry season. Values reported
730 here are means and standard errors. Upper case letters indicate significant differences in gas
731 flux between seasons with a vegetation type, while lower case letters indicate significant
732 differences among vegetation types within a season (Fisher's LSD, $P < 0.05$).

Vegetation Type	Methane Flux (mg CH_4-C m^{-2} d^{-1})		Nitrous Oxide Flux (µg N_2O-N m^{-2} d^{-1})	
	Wet Season	Dry Season	Wet Season	Dry Season
Forested	6.7 ± 1.0Aa	47.2 ± 5.4Ba	2.54 ± 1.48	-1.16 ± 1.20
Forested (short pole)	60.4 ± 9.1Ab	18.8 ± 2.6Bb	1.16 ± 0.54	-0.42 ± 0.90
M. flexuosa Palm Swamp	46.7 ± 8.4Ac	28.3 ± 2.6Bc	1.14 ± 0.35	0.92 ± 0.61
Mixed Palm Swamp	6.1 ± 1.3Aa	64.2 ± 12.1Ba	1.45 ± 0.79	-0.80 ± 0.79

733

Figure Captions

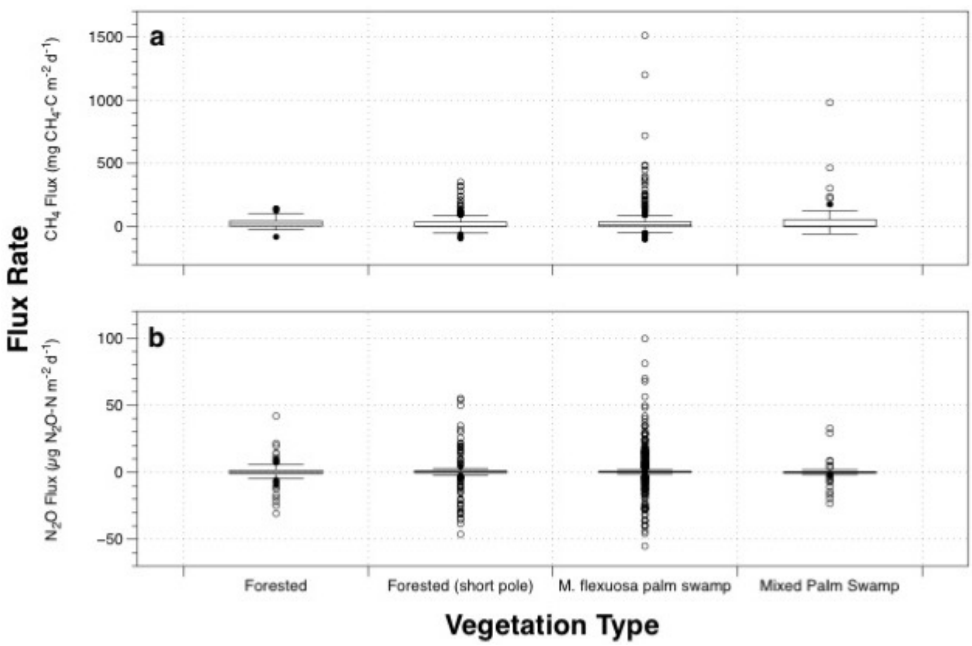
Figure 1. Map of the study region and field sites.

Figure 2. Net **(a)** CH_4 and **(b)** N_2O fluxes by vegetation type. Boxes enclose the interquartile range, whiskers indicate the 90th and 10th percentiles. The solid line in each box represents the median. Individual points represent potential outliers.

Biogeosciences Discuss., doi:10.5194/bg-2017-48, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 24 February 2017

740 **Figure 1**

741 **Figure 2**



742