

DETAILED RESPONSE TO REFEREES

On behalf of my co-authors, I would like to thank the Associate Editor and the two anonymous referees for their thoughtful and constructive comments on our manuscript. Please find enclosed a revised version of the text, where we have sought to address all the referees' concerns, in-line with the responses that we have provided to the referees during the discussion period for the paper. A detailed description of how we have responded to the referees comments is provided below.

RESPONSE TO REFEREE 1

1. Although the number of studies on trace gas fluxes from lowland tropical peatlands are steadily increasing, measurements are completely absent from some important large peatland areas. The peats in the foreland basin of Pastaza Marañon (PMFB) in Peru is an example of an important tropical peatland area from which we have no empirical studies on CH₄ and N₂O fluxes. As such, this study is timely and novel. The authors conducted chamber based CH₄ and N₂O fluxes stratified according to the four dominant vegetation types ranging from nutrient rich floodplains to nutrient poor bogs. While the spatial resolution of the sampling is good (see Table 1) the temporal resolution is restricted to four time sampling over a period of two years (sampling twice during the wet season and twice during a dry season). However, given the difficult accessibility and the fact that this is the first report on fluxes from this important peat area this is acceptable for this initial study. Furthermore, we do learn important controls since supporting variables were measured as well. Nevertheless if have several point that should be addressed before the manuscript can be accepted for publication.

Authors' response: The authors would like to thank the referee for his/her thoughtful and insightful comments on our manuscript. We welcome this opportunity to improve the manuscript for the wider readership of *Biogeosciences*, and hope that the changes we have produced will meet with your satisfaction..

2. In your introduction, I miss a section on the known controls of CH₄ and N₂O fluxes in peatlands. I think it is important to include this, since it is otherwise unclear why you

measured the environmental variables that you did. Are there some potentially important factors that you did not measure and if so, why was that the case?

Authors' response: In the revised version of the manuscript, the introduction has been modified to include a more thorough description of the controls on CH₄ and N₂O flux (lines 150-196).

With respect to potentially important factors that we did not measure: we did not quantify CH₄ emissions from woody plants nor did we specifically seek to quantify ebullition. While plant-mediated fluxes are believed to be important in tropical wetland ecosystems (Pangala et al., 2013), we did not have enough data on floristic composition or individual plant identities within our plots to come-up with a sampling design that would adequately represent plant-mediated fluxes from our study sites. Likewise, ebullition is often characterized by high spatial and temporal variability. In order to develop representative measures of ebullition, we would have to use quasi-continuous, automated flux chambers or an inverted "flux funnel" approach (Strack et al., 2005). However, we lacked the resources to implement either of these approaches in this study. In the revised text, we have expanded the discussion of ebullition in order to meet the concerns raised in points 4 and 5 (see below). We have also revised the text to include an expanded discussion of our study's limitations in the discussion (lines 780-830).

For N₂O, even though inorganic N is thought to be one of the major drivers of N₂O flux, we did not collect data on inorganic N (NH₄⁺, NO₃⁻), because the relatively modest budget for this project did not accommodate costs for inorganic N analysis.

3. *In l.142 and l.147 you mention soil Ca, it remains a mystery in which form this Ca occurs. Please provide more details, is Ca an important environmental control on CH₄ or N₂O fluxes?*

Authors' response: The Ca in these systems occurs as dissolved inorganic Ca²⁺ associated with the soil or peat exchange complex, or Ca found in secondary minerals (Lahteenoja et al., 2009; Lahteenoja and Page, 2011). As far as we are aware, Ca has no direct effect on CH₄

or N₂O fluxes, although Ca may indirectly influence trace gas exchange by influencing plant productivity and organic matter decay. We have revised the text to clarify this point (lines 264-272).

4. You describe your chambers as floating static chambers (l. 179). You furthermore write that chamber were placed on the soil surface from a distance of no closer than 2m to reduce the risk of ebullition (l. 186). For me it is hard to believe that ebullition was completely excluded and I also cannot understand how you can place these chambers at a distance of 2 m? Nobody has arms that long (at least I don't), so how was this done in detail? And, especially, how did you take the gas samples from your chambers using syringes without causing ebullition?

Authors' response: The referee is correct that we were unable to entirely exclude ebullition from our dataset. We did in fact find evidence of ebullition, with 164 of the 1181 chamber observations (13.9 %) showing signs of ebullition (e.g. abrupt, non-linear changes in headspace concentrations). Of these 164 observations, 83 (7.0 %) showed net CH₄ efflux (or, net ebullition), while a further 81 (6.9 %) showed very high rates of net CH₄ uptake. The latter we termed "ebullition-driven CH₄ uptake," due to the fact that very high rates of CH₄ uptake were observed following a putative bubble event. For these data, ebullition fluxes were calculated in one of two ways: for chambers showing steep non-linear increases, we fitted the data to a quadratic regression equation ($P < 0.05$), and fluxes were determined from the steep initial rise in CH₄ concentrations. For chambers showing abrupt stochastic increases, fluxes were determined by calculating the total CH₄ production over the course of the bubble event, in-line with the approach used by the investigators in other studies (Teh et al., 2011). The text has now been amended to include a more thorough description of how these ebullition data were handled and interpreted in the methods (lines 377-400), results and discussion (lines 432-453, lines 456-458, lines 524-567, lines 661-706, Table 2).

With respect to chamber placement; this was achieved by using a 2-m long pole to lower the flux chambers onto the water or saturated soil. Gas samples were collected with syringes using >2 m lengths of Tygon® tubing, after thoroughly purging the dead volumes in

the sample lines. The text has now been revised to provide these additional details on chamber placement and sampling technique (lines 358-362).

5. Ebullition is relatively easy to detect e.g. if you start with very high concentrations or if you detect abrupt increases in CH₄ concentration. Can you give us information on how you dealt with such data and how many of your chamber measurements were potentially affected by ebullition? Is there a correlation of flux strength and the potential occurrence of ebullition? You also mention in your discussion that you measured occasionally high CH₄ uptake values (l. 477). Is it possible that this was related to high CH₄ concentrations at the beginning of chamber closure, potentially caused by ebullition? Did you find a correlation between initial CH₄ concentration and calculated CH₄ uptake values? I was also wondering whether the contrasting seasonal emission patterns that you discuss (l. 417 and further) could be related to ebullition. As you see, I think you don't give use sufficient information about the potential occurrence of ebullition and you should clearly improve this.

Authors' response: Please see point 4 above. We did in fact see evidence of greater ebullition in higher emission environments. For example, ebullition was more common in Mixed Palm Swamp and *M. flexuosa* palm swamp (12.2 and 16.7 % of observations for those vegetation types, respectively), which are the two vegetation types that showed the highest CH₄ fluxes. In contrast, forested (short pole) and forested vegetation, which showed the lowest CH₄ fluxes, saw the lowest occurrence of ebullition (i.e. 6.9 and 10.5 % of observations, respectively). We also observed greater ebullition fluxes in the wet season, though the trend for ebullition-driven uptake was less clear. Due to the high variance in both ebullition and ebullition-driven uptake fluxes, we did not observe statistically significant differences in either of these rates among vegetation types, or between seasons. The manuscript has now been revised to incorporate this information (lines 377-400, lines 432-453, lines 456-458, lines 524-567, lines 661-706, Table 2).

Regarding chambers that showed high oxidation rates; these high fluxes were in fact related to high initial concentrations, and we cannot exclude the possibility that these chambers could have been affected by ebullition, even if we did not see empirical evidence for this

over the course of our chamber measurements (e.g. ebullition could have occurred immediately after chamber placement and before the first sample was taken). The text has now been revised to incorporate this information (lines 798-830).

6. I have no problem with the fact that you measured negative N₂O fluxes, since we see more and more evidence that globally this is quite an important process. However, some of the negative fluxes seem to be quite high in your figure 2. How do your N₂O uptake rates compare to other published values and is it possible that this may also somehow related to ebullition? Also, here I would be interested if your negative values correlate with the initially measured concentration in your chambers. If ebullition played a role for negative CH₄ and N₂O fluxes, you may expect that both strong CH₄ uptake and N₂O uptake would occur in the same chamber measurement. Did you check this?

Authors' response: Relative to other environments we have studied elsewhere in Peru (e.g. Kosñipata Valley, Manu National Park) and in the literature from upland environments, these uptake fluxes are very low; at least one order of magnitude lower than uptake fluxes observed in upland ecosystems (Teh et al., 2014). We believe it is highly unlikely that ebullition caused these trends, because we saw very little evidence of ebullition-driven N₂O fluxes (only 3 out of 1181 observations, or 0.3 %), and these data were filtered to remove these three observations from the analysis presented here. We also saw no evidence that strong CH₄ uptake was correlated with N₂O uptake. The text has been amended to acknowledge that we saw only limited evidence of N₂O ebullition (lines 456-458).

7. You probably measured your fluxes at different time of the day. Did you find any diurnal pattern in GHG fluxes? If yes, what could explain these observed differences and how would this affect your estimate of emission strength?

Authors' response: We did in fact conduct a subsidiary study to investigate if gas fluxes showed evidence of diurnal variability, but did not find strong evidence of diurnal trends in fluxes. The text has now been revised to provide this information (lines 348-351 and lines 529-530).

8. *The potential role of CH₄ oxidation is remarkable absent from your discussion. Why is that the case? Do you think this is not important for the total measured CH₄ fluxes?*

Authors' response: For sake of brevity, we did not go discuss the potential role of gross CH₄ oxidation in modulating net CH₄ efflux. This is not because we did not believe gross CH₄ oxidation was unimportant; rather, it was because we did not have the tools or the experimental design to make clear inferences about what proportion of produced CH₄ was consumed prior to atmospheric egress. We do in fact believe that gross CH₄ oxidation is very important, as demonstrated by past work in tropical systems that have used isotope tracers to deconvolve gross CH₄ production and oxidation fluxes (von Fischer and Hedin, 2002; von Fischer and Hedin, 2007; Teh et al., 2005). For example, work by the lead author has demonstrated that gross methanotrophy may consume upwards of 48 % of produced CH₄ in tropical soils (Teh et al., 2005). Follow-up experiments at these study sites could explore this question in the future. We will revise the manuscript to include this information.

9 *The version of the map in Fig. 1 that I saw did not have a very good quality. Can you provide a map where the four vegetation types that you used for stratification are included? The impression of Fig. 1 is that the total peat area is larger than what can be seen in the map. Can you adjust Fig. 1 in such a way that we see all of (or most of) the PMFB peatland area?*

Authors' response: Figure 1 has now been revised to better illustrate the distribution of peat-rich areas across the study site.

RESPONSE TO REFEREE 2

10. *The investigations by Teh et al. on CH₄ and N₂O emissions from tropical peatlands are recently of major interest. Particularly for the study region in the Amazon basin, knowledge on magnitude, pattern and controls of greenhouse gas fluxes is scarce. As this region is a potentially huge source of CH₄, it is important to close this knowledge gap. This study could contribute to this process.*

Authors' response: The authors would like to thank the referee for his/her kind and very supportive remarks.

11. *The findings of large CH₄ and negligible N₂O emissions might have been anticipated while the asynchronous CH₄ fluxes with higher fluxes during the dry season for two of the four investigated vegetation types might not. Potential explanations for this result are discussed. However, there is plenty of literature on mechanisms and controls of peatland CH₄ and N₂O fluxes but appropriate references are missing in the introduction as well as in the discussion part. For example, it has been reported that CH₄ fluxes do not increase or even decline when sites are inundating and that highest emissions occur for water levels close to the surface (e.g. Couwenberg et al., 2011, Hydrobiologia 674, 67-89).*

Authors' response: Please see point 2 above. We also thank the referee for the suggested reference, and have incorporated the findings from this work into the new version of the manuscript.

12. *Furthermore, I strongly recommend to revise the abstract and the presentation of results. The abstract mainly lists the results but doesn't tell anything about motivation, objective and main conclusions of the study. The two figures are of poor quality and Fig. 2 is not very helpful for interpretation of results due to the huge amounts of outliers. I would recommend to rather show columns with standard errors or maxima/minima. And why was the data shown in the figure grouped for vegetation type but not for different seasons? Also, figures that visualize the relationships between GHG fluxes and the measured environmental*

variables would be interesting. Although the relationships might be very weak, this would give the reader a better idea of the dataset.

Authors' response: Thank you for these suggestions. The abstract (lines 10-60) and Figure 2 have now been revised in-line with the referee's suggestions. With respect to seasonal trends, we made the decision to show this information in a table rather than as a figure to show seasonal differences (see Table 4 in the revised text). We believe that a tabular format shows seasonal trends with greater clarity than a more complex figure showing both site and seasonal differences.

With respect to the relationship between GHG fluxes and environmental variables (e.g. scatterplots of environmental variables versus gas flux), we have now generated scatter plots for some of the key variables discussed in the results section (see Supplementary Online Materials Figures S1 to S4).

13. P4, L60: *Peatlands are not necessarily peat-forming. In contrast, many peatlands have been drained for utilization purposes which turns them into significant C sources and in regions like Central Europe, only a few percent of peatlands are still in a natural condition and thus peat-forming. Please be more specific about the state of peatlands in the study region.*

Authors' response: The peatlands in the PMFB are unmanaged and have not been affected by human disturbance, unlike their counterparts in SE Asia. In the wider Amazon basin, only peatlands in the Madre de Dios region have been heavily affected by human activity. The revised text now includes this additional information (lines 98-102).

14. P4, L61-65: *Are you talking about peatlands in general or about peatlands in the Amazon basin? If you mean peatlands in general, your statements are not correct as there are several studies on peatland GHG emissions but most of them were conducted in the boreal or temperate zone.*

Authors' response: We were referring to peatlands in the Amazon basin; the focus of past research in the region has been on mineral soil wetlands. The text has now been revised to clarify this point (lines 102-105).

15. P5, L90: *I wouldn't classify a peat depth of 3.9 m as shallow. Following the international definition, peatlands are defined by a minimum of 20 cm of peat deposit, which could be classified as shallow. It seems that peat deposits in the study region are all very deep.*

Authors' response: The text has now been revised so that we simply refer to the depth range of the peat (lines 132-133).

16. P7, L127-128: *You do not mention the months of September and October. Are they neither wet season nor dry season?*

Authors' response: September and October represent a transitional period between the wet and dry seasons, and the text has now been revised to clarify this point (lines 226-228).

17. P7, L135: *"Pure peat" is not a soil classification! Please use World reference base (2015) to classify your sites. Qualifiers should be used to characterize the soils more precisely.*

Authors' response: The referee's concern is duly noted, and we have now revised the text accordingly (lines 235-272).

18. P7, L136: *The pH values given are not in line with Table 2. Are these values from preliminary measurements?*

Authors' response: The values reported on line 136 represent the range of values observed in prior studies, whereas the values reported in Table 2 reflect more specific data from our study plots. We have made this clearer in the revised version of the text (lines 237-239).

19. P8, L150: *The number of plots remains unclear to me. You mention 229 plots but the numbers below summarize to 148 plots and in Table 1 you list 161 plots. Please clarify.*

Authors' response: The total number of plots should be 239, with the following breakdown by vegetation type:

Forested: 21 plots

Forested (short pole): 47 plots

M. Flexuosa palm swamp: 153 plots

Mixed palm swamp: 18 plots

The revised version of the text (lines 313-320) and Table 1 have been corrected accordingly.

20. P9, L177: *Please clarify the procedure of the measurement campaigns. How long were these campaigns, did you sample each plot only once, several times per day or also on different days?*

Authors' response: The duration of the campaign for each study site varied depending on its size. Each study site was generally sampled only once for each campaign. The revised text has been updated accordingly (lines 348-351).

21. P9, L178: *What about the wet season in 2013? Why didn't you measure the fluxes during that period?*

Authors' response: Due to personal circumstances, we were unable to collect data during the 2013 wet season.

22. P9, L186: *How is it possible to place the chamber in a distance of 2 m? I cannot imagine how this practically works. And what about the sampling procedure? You have to get quite close to the chambers for that. Please clarify.*

Authors' response: Please see point 4 above.

23. P10, L199: *Does it mean that fluxes were calculated from linear or non-linear regressions depending on the individual concentration trend against time? It is important to clarify this as linear regression can lead to substantial underestimation of fluxes as a consequence of decreasing concentration gradients over time. And which quality criteria have been used to ensure the reliability of computed fluxes?*

Authors' response: The referee is correct; the revised manuscript has been altered to clarify this point (lines 377-400).

24. P13, L268: *The paragraphs for the results of different variables always have the same wording, which gives a quite uninspired impression.*

Authors' response: We strove for clarity of expression in this section of the text, and believe that this reporting format achieves this goal.

25. P14, L281: *I don't find it very meaningful to do statistics on measurements of air temperature. Also, you would have to compare exactly the same periods, otherwise the results could be misleading.*

Authors' response: Air temperature measurements can be useful because they provide an indication of overall climatic variability, not only between seasons but among ecosystems, which may have different amounts of canopy closure. We have therefore provided this information to provide the reader a sense of overall patterns in climate variability among study sites.

26. P16, L325: *Several different statistical tests were applied but not mentioned in the statistical analyses section.*

Authors' response: We did not specifically mention the Wilcoxon signed-rank test in the statistics section; however, we did indicate that non-parametric tests were used under certain circumstances (lines 422-423). The revised text has also been update to provide specific detail on what non-parametric tests were employed (line 423).

27. P19, L398: *It has to be considered that conclusions on that can only be drawn when annual CH₄ budgets can be estimated from regular or automatic measurements in high temporal resolution.*

Authors' response: The sentence referred to by the referee includes a qualifier (i.e. “may be”) to denote that we believe that it is highly likely that this region is an important regional contributor to CH₄ flux, but do not necessarily claim that this is entirely proven. Although we agree with the referee that regular or higher frequency measurements would be required to reach a more definitive conclusion, we believe that the weight of evidence supports our qualitative claim, including findings not only from this paper but from regional atmospheric sampling studies (Wilson et al., 2016).

28. P20, L 416: *The water tables of the studied sites do in my opinion not allow the definition of oxic conditions as the water tables reported were quite high even in the dry season. Particularly non-degraded peat has a high water holding capacity, thus also when the water table drops below the soil surface, water filled pore space remains high in the top soil, still preventing CH₄ oxidation.*

Authors' response: The sentence referred to by the referee includes a qualifier (i.e. “more”) to indicate that we are comparing oxygen availability during the wet and dry season, rather than making a statement about absolute oxygen content. The data provided in Table 2 demonstrate that most of the vegetation types, with the exception of Mixed Palm Swamp, show elevated dissolved oxygen levels during the dry season, supporting the idea that the soils contained more oxygen than during the wet season.

29. P21, L 438: *No references are given in this section. The weak relationship is probably a result of the overall high water levels as the general assumption that CH₄ emissions increase with water level is based on measurements from sites with huge drainage gradients. Generally, CH₄ emissions increase exponentially when the water level passes a threshold of roughly 20 – 30 cm below ground. For water levels close to or above the surface, CH₄ fluxes are often extremely variable. Some references would be very helpful here for the*

interpretation of your results. Also, methodological issues should be discussed as CH₄ emissions mainly occur in terms of erratic ebullition when water tables are above the soil surface. This might be difficult to detect with small chambers during a short period of enclosure.

Authors' response: The text has been revised to include the point raised here and the additional citations suggested the referee (lines 724-738, Supplementary Online Materials Figure S2) (Couwenberg et al., 2010; Couwenberg et al., 2011). Moreover, the text has now been heavily revised to include a wider discussion of ebullition, in-line with the first referee's concerns (see points 4 and 5 above).

30. P23, L479: *Where negative CH₄ fluxes also measured for water tables above ground? This would be rather unreliable in my opinion as one would not expect CH₄ uptake in water saturated soil or even open water. Also, I assume that there should be more recent literature on CH₄ exchange in tropical peatlands.*

Authors' response: No negative CH₄ fluxes were observed when water tables were above the soil surface, only when water tables were below the soil surface.

31. P24, L505-508: *It is for me very unlikely that the different ecosystems do not differ in N availability. This conclusion cannot be drawn from equally low N₂O emissions as there are probably other reasons for negligible N₂O fluxes also in the nutrient-rich ecosystems. For example, there might be a higher N uptake by productive plant species at the nutrient-rich sites, competing with the potentially N₂O producing microbes or N compounds are completely reduced to N₂ during denitrification because of permanently anoxic conditions.*
Technical corrections P2, L9: The numbering of sections starts with 2.

Authors' response: We do not disagree with the referee; we simply indicated that this may be one possible explanation for the trends in our data.

32. P5, L99: *Replace "positive water tables" by "high water tables" or "water tables above ground".*

Authors' response: Editorial suggestion taken.

33. P10, L197: *I assume that the instrumental precision was > 95 % or the instrumental noise was < 5 %.*

Authors' response: Yes.

34. P10, L210: *In which height was the air temperature measured?*

Authors' response: Approximately 1.3 m above the surface; the revised text has been modified accordingly (line 407).

35. P10, L211: *Please add manufacturer.*

Authors' response: Editorial suggestion taken.

36. P13, L270: *add "different" after "significantly".*

Authors' response: Editorial suggestion taken.

37. P14, L282: *"Soil temperature" has to be replaced by "air temperature"*

Authors' response: Editorial suggestion taken.

38. P15, L314: *Add "during" before "the dry season".*

Authors' response: Editorial suggestion taken.

39. P18, L364: *Plural: relationships*

Authors' response: Editorial suggestion taken.

40. *P18, L372: Results should not be interpreted in the "Results" section.*

Authors' response: Editorial suggestion taken; interpretive text was deleted.

41. *P18, L382: Add "electrical" before "conductivity".*

Authors' response: Editorial suggestion taken.

42. *P18, L383: Why do you mention CO₂ here? No results on CO₂ were shown.*

Authors' response: Editorial suggestion taken.

43. *P19, L394: Please round up to 1510.*

Authors' response: Editorial suggestion taken

44. *P25, L526: Replace "these data" by "our data".*

Authors' response: Editorial suggestion taken.

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1 **1. TITLE PAGE**

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

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9 2. ABSTRACT

10 The Amazon plays a critical role in global atmospheric budgets of methane (CH₄) and nitrous
11 oxide (N₂O). However, while we have a relatively good understanding of the continental-scale
12 flux of these greenhouse gases (GHGs), one of the key gaps in knowledge is the specific
13 contribution of peatland ecosystems to the regional budgets of these GHGs. Here we report
14 CH₄ and N₂O fluxes from lowland tropical peatlands in the Pastaza-Marañón foreland basin
15 (PMFB) in Peru, one of the largest peatland complexes in the Amazon basin. The goal of this
16 research was to: quantify the range and magnitude of CH₄ and N₂O fluxes from this region;
17 assess seasonal trends in trace gas exchange; and determine the role of different
18 environmental variables in driving GHG flux. Trace gas fluxes were determined from the most
19 numerically-dominant peatland vegetation types in the region: forested vegetation, forested
20 (short pole) vegetation, *Mauritia flexuosa*-dominated palm swamp, and mixed palm swamp.
21 Data were collected in both wet and dry seasons over the course of four field campaigns from
22 2012 to 2014. Diffusive CH₄ emissions averaged 36.05 ± 3.09 mg CH₄-C m⁻² d⁻¹ across the
23 entire dataset, with diffusive CH₄ flux varying significantly among vegetation types and
24 between seasons. The ebullition flux of CH₄ averaged 973.3 ± 161.4 mg CH₄-C m⁻² d⁻¹, and did
25 not vary significantly among vegetation types nor between seasons. Diffusive CH₄ flux was,
26 greatest for mixed palm swamp (52.0 ± 16.0 mg CH₄-C m⁻² d⁻¹), followed by *M. flexuosa* palm
27 swamp (36.7 ± 3.9 mg CH₄-C m⁻² d⁻¹), forested (short pole) vegetation (31.6 ± 6.6 mg CH₄-C m⁻²
28 d⁻¹), and forested vegetation (29.8 ± 10.0 mg CH₄-C m⁻² d⁻¹). Diffusive CH₄ flux also showed
29 marked seasonality, with divergent seasonal patterns among ecosystems. Forested
30 vegetation and mixed palm swamp showed significantly higher dry season (47.2 ± 5.4 mg CH₄-
31 C m⁻² d⁻¹ and 85.5 ± 26.4 mg CH₄-C m⁻² d⁻¹, respectively) compared to wet season emissions

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47 (6.8 ± 1.0 mg CH₄-C m⁻² d⁻¹ and 5.2 ± 2.7 mg CH₄-C m⁻² d⁻¹, respectively). In contrast, forested
48 (short pole) vegetation and *M. flexuosa* palm swamp showed the opposite trend, with dry
49 season flux of 9.6 ± 2.6 and 25.5 ± 2.9 mg CH₄-C m⁻² d⁻¹, respectively, versus wet season flux
50 of 103.4 ± 13.6 and 53.4 ± 9.8 mg CH₄-C m⁻² d⁻¹, respectively. These divergent seasonal trends
51 may be linked to very high water tables (>1 m) in forested vegetation and mixed palm swamp
52 during the wet season, which may have constrained CH₄ transport across the soil-atmosphere
53 interface. Diffusive N₂O flux was very low (0.70 ± 0.34 μg N₂O-N m⁻² d⁻¹), and did not vary
54 significantly among ecosystems nor between seasons. We conclude that peatlands in the
55 PMFB are large and regionally significant sources of atmospheric CH₄, that need to be better
56 accounted for in regional emissions inventories. In contrast, N₂O flux was negligible,
57 suggesting that this region does not make a significant contribution to regional atmospheric
58 budgets of N₂O. The divergent seasonal pattern in CH₄ flux among vegetation types challenges
59 our underlying assumptions of the controls on CH₄ flux in tropical peatlands, and emphasizes
60 the need for more process-based measurements during high water table periods.

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63 KEYWORDS

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

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73 **3. INTRODUCTION**

74 The Amazon basin plays a critical role in the global atmospheric budgets of carbon (C) and
75 greenhouse gases (GHGs) such as methane (CH₄) and nitrous oxide (N₂O). Recent basin-wide
76 studies suggest that the Amazon as a whole accounts for approximately 7 % of global
77 atmospheric CH₄ emissions (Wilson et al., 2016). N₂O emissions are of a similar magnitude,
78 with emissions ranging from 2-3 Tg N₂O-N year⁻¹ (or, approximately 12-18 % of global
79 atmospheric emissions) (Huang et al., 2008;Saikawa et al., 2014;Saikawa et al., 2013). While
80 we have a relatively strong understanding of the role that the Amazon plays in regional and
81 global atmospheric budgets of these gases, one of the key gaps in knowledge is the
82 contribution of specific ecosystem types to regional fluxes of GHGs (Huang et al.,
83 2008;Saikawa et al., 2014;Saikawa et al., 2013). In particular, our understanding of the
84 contribution of Amazonian wetlands to regional C and GHG budgets is weak, as the majority
85 of past ecosystem-scale studies have focused on *terra firme* forests and savannas (D'Amelio
86 et al., 2009;Saikawa et al., 2013;Wilson et al., 2016;Kirschke et al., 2013;Nisbet et al., 2014).
87 Empirical studies of GHG fluxes from Amazonian wetlands are more limited in geographic
88 scope and have focused on three major areas: wetlands in the state of Amazonas near the
89 city of Manaus (Devol et al., 1990;Bartlett et al., 1990;Bartlett et al., 1988;Keller et al., 1986),
90 the Pantanal region (Melack et al., 2004;Marani and Alvalá, 2007;Liengaard et al., 2013), and
91 the Orinoco River basin (Smith et al., 2000;Lavelle et al., 2014). Critically, none of the
92 ecosystems sampled in the past were peat-forming ones; rather, the habitats investigated
93 were non-peat forming (i.e. mineral or organo-mineral soils), seasonally-inundated floodplain
94 forests (i.e. *varzea*), rivers or lakes.

95

96 Peatlands are one of the major wetland habitats absent from current bottom-up GHG
97 inventories for the Amazon basin, and are often grouped together with non-peat forming
98 wetlands in regional atmospheric budgets (Wilson et al., 2016). Unlike their Southeast Asian
99 counterparts, most peatlands in the Amazon basin are unaffected by human activity at the
100 current time (Lahteenoja et al., 2009a; Lahteenoja et al. 2009b; Lahteenoja and Page 2011),
101 except for ecosystems in the Madre de Dios region in southeastern Peru, which are impacted
102 by gold mining (Householder et al., 2012). Because we have little or no data on ecosystem-
103 level land-atmosphere fluxes from Amazonian peatlands (Lahteenoja et al., 2012; Lahteenoja
104 et al., 2009b; Kirschke et al., 2013; Nisbet et al., 2014), it is difficult to ascertain if rates of GHG
105 flux from these ecosystems are similar to or different from mineral soil wetlands (e.g. varzea).
106 Given that underlying differences in plant community composition and soil properties are
107 known to modulate the cycling and flux of GHGs in wetlands (Limpens et al., 2008; Melton et
108 al., 2013; Belyea and Baird, 2006; Sjögersten et al., 2014), expanding our observations to
109 include a wider range of wetland habitats is critical in order to improve our understanding of
110 regional trace gas exchange, and also to determine if aggregating peat and mineral soil
111 wetlands together in bottom-up emissions inventories are appropriate for regional budget
112 calculations. Moreover, Amazonian peatlands are thought to account for a substantial land
113 area (i.e. up to 150,000 km²) (Schulman et al., 1999; Lahteenoja et al., 2012), and any
114 differences in biogeochemistry among peat and mineral/organo-mineral soil wetlands may
115 therefore have important implications for understanding and modelling the biogeochemical
116 functioning of the Amazon basin as a whole.

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119 Since the identification of extensive peat forming wetlands in the north (Lahteenoja et al.,
120 2009a; Lahteenoja et al. 2009b; Lahteenoja and Page 2011) and south (Householder et al.,
121 2012) of the Peruvian Amazon, several studies have been undertaken to better characterize
122 these habitats, investigating vegetation composition and habitat diversity (Draper et al., 2014;
123 Kelly et al., 2014; Householder et al., 2012; Lahteenoja and Page, 2011), vegetation history
124 (Lahteenoja and Roucoux et al., 2010), C stocks (Lahteenoja et al., 2012; Draper et al., 2014),
125 hydrology (Kelly et al., 2014), and peat chemistry (Lahteenoja et al., 2009a; Lahteenoja et al.,
126 2009b). Most of the studies have focused on the Pastaza-Marañón foreland basin (PMFB),
127 where one of the largest stretches of contiguous peatlands have been found (Lahteenoja et
128 al 2009a; Lahteenoja and Page, 2011; Kelly et al, 2014), covering an estimated area of 35,600
129 $\pm 2,133 \text{ km}^2$ (Draper et al., 2014). Up to 90% of the peatlands in the PMFB lie in flooded
130 backwater river margins on floodplains and are influenced by large, annual fluctuations in
131 water table caused by the Amazonian flood pulse (Householder et al., 2012; Lahteenoja et al.,
132 2009a). These floodplain systems are dominated by peat deposits that range in depth from
133 $\sim 3.9 \text{ m}$ (Lahteenoja et al., 2009a) to $\sim 12.9 \text{ m}$ (Householder et al., 2012). The remaining 10%
134 of these peatlands are not directly influenced by river flow and form domed (i.e. raised)
135 nutrient-poor bogs that likely only receive water and nutrients from rainfall (Lahteenoja et
136 al., 2009b). These nutrient-poor bogs are dominated by large, C-rich forests (termed “pole
137 forests”), that represent a very high density C store (total pool size of $1391 \pm 710 \text{ Mg C ha}^{-1}$,
138 which includes both above- and belowground stocks); exceeding in fact the C density of
139 nearby floodplain systems (Draper et al., 2014). Even though the peats in these nutrient-poor
140 bogs have a relatively high hydraulic conductivity, they act as natural stores of water because
141 of high rainwater inputs (>3000 mm per annum), which help to maintain high water tables,
142 even during parts of the dry season (Kelly et al., 2014).

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150 CH₄ flux in tropical soils are regulated by the complex interplay among multiple factors that
 151 regulate CH₄ production, oxidation, and transport. Key factors include: redox/water table
 152 depth (Couwenberg et al., 2010;Couwenberg et al., 2011;Silver et al., 1999;Teh et al.,
 153 2005;von Fischer and Hedin, 2007), plant productivity (von Fischer and Hedin, 2007;Whiting
 154 and Chanton, 1993), soil organic matter lability (Wright et al., 2011), competition for C
 155 substrates among anaerobes (Teh et al., 2008;Teh and Silver, 2006;von Fischer and Hedin,
 156 2007), and presence of plants capable of facilitating atmospheric egress (Pangala et al., 2013).
 157 Of all these factors, fluctuation in soil redox conditions, as mediated by variations in water
 158 table depth, is perhaps most critical in regulating CH₄ dynamics (Couwenberg et al.,
 159 2010;Couwenberg et al., 2011), because of the underlying physiology of the microbes that
 160 produce and consume CH₄. Methanogenic archaea are obligate anaerobes that only produce
 161 CH₄ under anoxic conditions (Conrad, 1996); as a consequence, they are only active in stably
 162 anoxic soil microsites or soil layers, where they are protected from the effects of strong
 163 oxidants such as oxygen or where competition for reducing equivalents (e.g. acetate, H₂) from
 164 other anaerobic microorganisms is eliminated (Teh et al., 2008;Teh and Silver, 2006;Teh et
 165 al., 2005;von Fischer and Hedin, 2002;von Fischer and Hedin, 2007). CH₄ oxidation, on the
 166 other hand, is thought to be driven primarily by aerobic methanotrophic bacteria in tropical
 167 soils (Hanson and Hanson, 1996;Teh et al., 2005;Teh et al., 2006;von Fischer and Hedin,
 168 2002;von Fischer and Hedin, 2007), with anaerobic CH₄ oxidation playing a quantitatively
 169 smaller role (Blazewicz et al., 2012). Thus, fluctuations in redox or water table depth play a
 170 fundamental role in directing the flow of C among different anaerobic pathways (Teh et al.,
 171 2008;Teh and Silver, 2006;von Fischer and Hedin, 2007), and shifting the balance between

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173 production and consumption of CH₄ (Teh et al., 2005; von Fischer and Hedin, 2002). Moreover,
174 water table or soil moisture fluctuations are also thought to profoundly influence CH₄
175 transport dynamics throughout the soil profile, changing the relative partitioning of CH₄
176 among different transport pathways such as diffusion, ebullition, and plant-facilitated
177 transport (Whalen, 2005; Jungkunst and Fiedler, 2007).

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179 Controls on N₂O flux are also highly complex (Groffman et al., 2009), with N₂O originating
180 from as many as four separate sources (e.g. bacterial ammonia oxidation, archaeal ammonia
181 oxidation, denitrification, dissimilatory nitrate reduction to ammonium), each with different
182 environmental controls (Baggs, 2008; Morley and Baggs, 2010; Firestone and Davidson,
183 1989; Firestone et al., 1980; Pett-Ridge et al., 2013; Silver et al., 2001; Prosser and Nicol, 2008).

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184 Key factors regulating soil N₂O flux include: redox, soil moisture content or water table depth,
185 temperature, pH, labile C availability, and labile N availability (Groffman et al., 2009). As is the
186 case for CH₄, variations in redox/water table depth plays an especially prominent role in
187 regulating N₂O flux in tropical peatland ecosystems, because all of the processes that produce
188 N₂O are redox-sensitive, with bacterial or archaeal ammonia oxidation occurring under
189 aerobic conditions (Prosser and Nicol, 2008; Firestone and Davidson, 1989; Firestone et al.,
190 1980) whereas nitrate-reducing processes (i.e. denitrification, dissimilatory nitrate reduction
191 to ammonium) are anaerobic ones (Firestone and Davidson, 1989; Firestone et al.,
192 1980; Morley and Baggs, 2010; Silver et al., 2001). Moreover, for nitrate reducing processes,
193 which are believed to be the dominant source of N₂O in wet systems, the extent of
194 anaerobiosis also controls the relative proportion of N₂O or N₂ produced during dissimilatory

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195 metabolism (Firestone and Davidson, 1989; Firestone et al., 1980; Morley and Baggs,
196 2010; Silver et al., 2001).

197

198 In order to improve our understanding of the biogeochemistry and rates of GHG exchange
199 from Amazonian peatlands, we conducted a preliminary study of CH₄ and N₂O fluxes from
200 forested peatlands in the PMFB. The main objectives of this are to:

- 201 1. Quantify the magnitude and range of soil CH₄ and N₂O fluxes from a sub-set of
202 peatlands in the PMFB that represent dominant vegetation types
- 203 2. Determine seasonal patterns of trace gas exchange
- 204 3. Establish the relationship between trace gas fluxes and environmental variables

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

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213 **4. MATERIALS AND METHODS**

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214 **4.1 Study site and sampling design**

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

234
 235 Histosols form the dominant soil type for peatlands in this region (Andriess, 1988; Lahteenoja
 236 and Page, 2011). Study sites are broadly classified as nutrient-rich, intermediate, or nutrient-
 237 poor (Lahteenoja and Page, 2011), with pH ranging from 3.5 to 7.2 (Lahteenoja and Page,
 238 2011; Lahteenoja et al., 2009a; Lahteenoja et al., 2009b). More specific data on pH for our plots
 239 are presented in Table 3. Nutrient-rich (i.e. minerotrophic) sites tend to occur on floodplains

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| Deleted: (Andriess, 1988; Lahteenoja and Page, 2011) 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 and Page, 2011; Lahteenoja et al., 2009a; Lahteenoja et al., 2009b) (Lahteenoja et al., 2009a; Lahteenoja et al., 2009b; this study). |
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252 and river margins, and account for at least 60 % of the peatland cover in the PMFB (Lahteenoja
 253 and Page, 2011;Draper et al., 2014). They receive water, sediment, and nutrient inputs from
 254 the annual Amazon river flood pulse (Householder et al., 2012;Lahteenoja and Page, 2011),
 255 leading to higher inorganic nutrient content, of which Ca and other base cations form major
 256 constituents (Lahteenoja and Page, 2011). Many of the soils in these nutrient-rich areas are
 257 fluvaquentic Tropofibrists (Andriessse, 1988), and contain thick mineral layers or minerogenic
 258 intrusions, reflective of episodic sedimentation events in the past (Lahteenoja and Page,
 259 2011). In contrast, nutrient-poor (i.e. oligotrophic) sites tend to occur further in-land
 260 (Lahteenoja and Page, 2011;Draper et al., 2014). They are almost entirely rain-fed, and
 261 receive low or infrequent inputs of water and nutrients from streams and rivers, (Lahteenoja
 262 and Page, 2011). These ecosystems account for 10 to 40 % of peatland cover in the PMFB,
 263 though precise estimates vary depending on the land classification scheme employed
 264 (Lahteenoja and Page, 2011;Draper et al., 2014). Soil Ca and base cation concentrations are
 265 significantly lower in these sites compared to nutrient-rich ones, with similar concentrations
 266 to that of rainwater (Lahteenoja and Page, 2011). Soils are classified as typic or hydric
 267 Tropofibrists (Andriessse, 1988). Even though Ca and base cations themselves play no direct
 268 role in modulating CH₄ and N₂O fluxes, underlying differences in soil fertility may indirectly
 269 influence CH₄ and N₂O flux by influencing the rate of labile C input to the soil, the
 270 decomposability of organic matter, and the overall throughput of C and nutrients through the
 271 plant-soil system (Firestone and Davidson, 1989;Groffman et al., 2009;von Fischer and Hedin,
 272 2007;Whiting and Chanton, 1993).

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Deleted: {Householder, 2012 #4168;Lahteenoja, 2009 #1200;Lahteenoja, 2011 #4173;Draper, 2014 #4162;Householder, 2012 #4168;Lahteenoja, 2011 #4173}. They are characterized by peat soils which contain higher inorganic mineral content, of which Ca is a dominant constituent (Lahteenoja et al., 2009b)(Lahteenoja and Page, 2011).

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297 We established 239 sampling plots (~30 m² per plot) within five tropical peatland sites that
298 captured four of the dominant vegetation types in the region (Draper et al.,
299 2014;Householder et al., 2012;Kelly et al., 2014;Lahteenoja and Page, 2011), and which
300 encompassed a range of nutrient availabilities (Figure 1, Table 1) (Lahteenoja and Page,
301 2011;Lahteenoja et al., 2009a). These four dominant vegetation types included: forested
302 vegetation (nutrient-rich; n= 21 plots), forested (short pole) vegetation (nutrient-poor; n= 47
303 plots), *Mauritia flexuosa*-dominated palm swamp (intermediate fertility, n= 153 plots), and
304 mixed palm swamp (nutrient-rich; n=18 plots) (Table 1). Four of the study sites (Buena Vista,
305 Charo, Miraflores, and Quistococha) were dominated by only one vegetation type, whereas
306 San Jorge contained a mixture of *M. flexuosa* palm swamp and forested (short pole)
307 vegetation (Table 1). As a consequence, both vegetation types were sampled in San Jorge to
308 develop a more representative picture of GHG fluxes from this location. Sampling efforts were
309 partially constrained by issues of site access; some locations were difficult to access (e.g.
310 centre of the San Jorge peatland) due to water table height and navigability of river channels;
311 as a consequence, sampling patterns were somewhat uneven, with higher sampling densities
312 in some peatlands than in others (Table 1).

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314 In each peatland site, transects were established from the edge of the peatland to its centre.
315 Each transect varied in length from 2 to 5 km, depending on the relative size of the peatland.
316 Randomly located sampling plots (~30 m² per plot) were established at 50 or 200 m intervals
317 along each transect, from which GHG fluxes and environmental variables were measured
318 concomitantly. The sampling interval (i.e. 50 or 200 m) was determined by the length of the
319 transect or size of the peatland, with shorter sampling intervals (50 m) for shorter transects

326 (i.e. smaller peatlands) and longer sampling intervals (200 m) for longer transects (i.e. larger
327 peatlands).

328

329 4.2 Quantifying soil-atmosphere exchange

330 Soil-atmosphere fluxes (CH₄, N₂O) were determined in four campaigns over a two-year annual
331 water cycle: February 2012 (wet season), June-August 2012 (dry season), June-July 2013 (dry
332 season), and May-June 2014 (wet season). The duration of the campaign for each study site

333 varied depending on its size. Each study site was generally sampled only once for each
334 campaign, except for a sub-set of plots within each vegetation type where diurnal studies
335 were conducted to determine if CH₄ and N₂O fluxes varied over daily time steps. Gas exchange

336 was quantified using a floating static chamber approach (Livingston and Hutchinson, 1995;
337 Teh et al., 2011). Static flux measurements were made by enclosing a 0.225 m² area with a
338 dark, single component, vented 10 L flux chamber. No chamber bases (collars) were used due

339 to the highly saturated nature of the soils. In most cases, a standing water table was present
340 at the soil surface, so chambers were placed directly onto the water. In the absence of a
341 standing water table, a weighted skirt was applied to create an airtight seal. Under these drier

342 conditions, chambers were placed carefully on the soil surface. In order to reduce the risk of
343 pressure-induced ebullition or disruption to soil gas concentration profiles caused by the
344 investigators' footfall, flux chambers were lowered from a distance of 2-m away using a 2-m

345 long pole. Gas samples were collected with syringes using >2 m lengths of Tygon® tubing,
346 after thoroughly purging the dead volumes in the sample lines. To promote even mixing
347 within the headspace, chambers were fitted with small computer fans (Pumpanen et al.,

348 2004). Headspace samples were collected from each flux chamber at five intervals over a 25

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352 minute enclosure period using a gas tight syringe. Gas samples were stored in evacuated
353 Exetainers® (Labco Ltd., Lampeter UK), shipped to the UK, and subsequently analysed for CH₄,
354 CO₂ and N₂O concentrations using Thermo TRACE GC Ultra (Thermo Fischer Scientific Inc.,
355 Waltham, Massachusetts, USA) at the University of St. Andrews. Chromatographic separation
356 was achieved using a Porapak-Q column, and gas concentrations determined using a flame
357 ionization detector (FID) for CH₄, a methanizer-FID for CO₂, and an electron capture detector
358 (ECD) for N₂O. Instrumental precision, determined from repeated analysis of standards, was
359 < 5% for all detectors.

360
361 Diffusive fluxes were determined by using the JMP IN version 11 (SAS Institute, Inc., Cary,
362 North Carolina, USA) statistical package to plot best-fit lines to the data for headspace
363 concentration against time for individual flux chambers, with fluxes calculated from linear or
364 non-linear regressions depending on the individual concentration trend against time (Teh et
365 al., 2014). Gas mixing ratios (ppm) were converted to areal fluxes by using the Ideal Gas Law
366 to solve for the quantity of gas in the headspace (on a mole or mass basis) and normalized by
367 the surface area of each static flux chamber (Livingston and Hutchinson, 1995). Ebullition-
368 derived CH₄ fluxes were also quantified in our chambers where evidence of ebullition was
369 found. This evidence consisted of either: (i) rapid, non-linear increases in CH₄ concentration
370 over time; (ii) abrupt, stochastic increases in CH₄ concentration over time; or (iii) an abrupt
371 stochastic increase in CH₄ concentration, followed by a linear decline in concentration. For
372 observations following pattern (i), flux was calculated by fitting a quadratic regression
373 equation to the data ($P < 0.05$), and CH₄ flux determined from the initial steep rise in CH₄
374 concentration. For data following pattern (ii), the ebullition rate was determined by

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379 calculating the total CH₄ production over the course of the bubble event, in-line with prior
380 work conducted by the investigators (Teh et al., 2011). Last, for data following pattern (iii), a
381 best-fit line was plotted to the CH₄ concentration data after the bubble event, and a net rate
382 of CH₄ uptake calculated from the gradient of the line. Observations following patterns (i) and
383 (ii) were categorized as “ebullition” (i.e. net efflux) whereas observations following pattern
384 (iii) were categorized as “ebullition-driven CH₄ uptake” (i.e. net influx).

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386 4.3 Environmental variables

387 To investigate the effects of environmental variables on trace gas fluxes, we determined air
388 temperature, soil temperature, chamber headspace temperature, soil pH, soil electrical
389 conductivity (EC; μScm^{-2}), dissolved oxygen concentration of the soil pore water (DO;
390 measured as percent saturation, %) in the top 15 cm of the peat column, and water table
391 position concomitant with gas sampling. Air temperature (measured 1.3 m above the soil)
392 and chamber headspace temperature were measured using a Checktemp[®] probe and meter
393 (Hanna Instruments LTD, Leighton Buzzard, UK). Peat temperature, pH, DO and EC were
394 measured at a depth of 15 cm below the peat surface and recorded *in situ* with each gas
395 sample using a HACH[®] rugged outdoor HQ30D multi meter and pH, LDO or EC probe. At sites
396 where the water level was above the peat surface, the water depth was measured using a
397 meter rule. Where the water table was at or below the peat surface, the water level was
398 measured by auguring a hole to 1 m depth and measuring water table depth using a meter
399 rule.

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403 4.4 Statistical Analyses

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

412

413

414 5. RESULTS

415 5.1 Differences in gas fluxes and environmental variables among vegetation types

416 All vegetation types were net sources of CH₄, with an overall mean (± standard error) diffusive
417 flux of 36.1 ± 3.1 mg CH₄-C m⁻² d⁻¹ and a mean ebullition flux of 973.3 ± 161.4 mg CH₄-C m⁻²
418 d⁻¹ (Figure 2, Table 2). We also saw examples of ebullition-driven CH₄ uptake (i.e. a sudden or
419 stochastic increase in CH₄ concentration, followed immediately by a rapid linear decline in
420 concentration), with a mean rate of -504.1 ± 84.4 mg CH₄-C m⁻² d⁻¹ (Table 2). Diffusive fluxes
421 of CH₄ accounted for the majority of observations (83.3 to 93.1 %), while ebullition or
422 ebullition-driven uptake of CH₄ accounted for a much smaller proportion of observations (6.9
423 to 16.7 %; Table 2).

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427 Diffusive CH₄ flux varied significantly among the four vegetation types sampled in this study

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428 (two-way ANOVA with vegetation, season and their interaction, $F_{7, 979} = 13.2$, $P < 0.0001$; Fig.

429 2a). However, the effect of vegetation was relatively weak (see ANCOVA results in the section

430 'Relationships between gas fluxes and environmental variables'), and a means comparison

431 test on the pooled data was unable to determine which means differed significantly from the

432 others (Fisher's LSD, $P > 0.05$). For the pooled data, the overall numerical trend was that mixed

433 palm swamp showed the highest mean flux (52.0 ± 16.0 mg CH₄-C m⁻² d⁻¹), followed by *M.*

434 *flexuosa* palm swamp (36.7 ± 3.9 mg CH₄-C m⁻² d⁻¹), forested (short pole) vegetation ($31.6 \pm$

435 6.6 mg CH₄-C m⁻² d⁻¹), and forested vegetation (29.8 ± 10.0 mg CH₄-C m⁻² d⁻¹). CH₄ ebullition

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436 and ebullition-driven CH₄ uptake did not vary significant among vegetation types nor between

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437 seasons (Table 2).

438

439 These study sites were also a weak net source of N₂O, with a mean diffusive flux of 0.70 ± 0.34

440 $\mu\text{g N}_2\text{O-N m}^{-2} \text{d}^{-1}$. We saw only limited evidence of ebullition of N₂O, with only three chambers

441 out of 1181 (0.3 % of observations) showing evidence of N₂O ebullition. These data were

442 omitted from the analysis of diffusive flux of N₂O. Because of the high variance in diffusive

443 N₂O flux among plots, analysis of variance indicated that mean diffusive N₂O flux did not differ

444 significantly among vegetation types (two-way ANOVA, $P > 0.5$, Fig. 2b). However, when the

445 N₂O flux data were grouped by vegetation type, we see that some vegetation types tended

446 to function as net atmospheric sources, while others acted as atmospheric sinks (Fig. 2b, Table

447 3). For example, the highest N₂O emissions were observed from *M. flexuosa* palm swamp

448 (1.11 ± 0.44 $\mu\text{g N}_2\text{O-N m}^{-2} \text{d}^{-1}$) and forested vegetation (0.20 ± 0.95 $\mu\text{g N}_2\text{O-N m}^{-2} \text{d}^{-1}$). In

451 contrast, forested (short pole) vegetation and mixed palm swamp were weak sinks for N₂O,
452 with a mean flux of -0.01 ± 0.84 and $-0.21 \pm 0.70 \mu\text{g N}_2\text{O-N m}^{-2} \text{d}^{-1}$, respectively.

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453

454 Soil pH varied significantly among vegetation types (data pooled across all seasons; ANOVA,
455 $P < 0.0001$, Table 3). Multiple comparisons tests indicated that mean soil pH was significantly
456 different for each of the vegetation types (Fisher's LSD, $P < 0.0001$, Table 3), with the lowest
457 pH in forested (short pole) vegetation (4.10 ± 0.04), followed by *M. flexuosa* palm swamp
458 (5.32 ± 0.02), forested vegetation (6.15 ± 0.06), and the mixed palm swamp (6.58 ± 0.04).

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459

460 Soil dissolved oxygen (DO) content varied significantly among vegetation types (data pooled
461 across all seasons; Kruskal-Wallis, $P < 0.0001$, Table 3). Multiple comparisons tests indicated
462 that mean DO was significantly different for each of the vegetation types (Fisher's LSD, $P <$
463 0.05 , Table 3), with the highest DO in the forested (short pole) vegetation ($25.2 \pm 2.1 \%$),
464 followed by the *M. flexuosa* palm swamp ($18.1 \pm 1.0 \%$), forested vegetation ($11.8 \pm 2.8 \%$),
465 and the mixed palm swamp ($0.0 \pm 0.0 \%$).

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466

467 Electrical conductivity (EC) varied significantly among vegetation types (data pooled across all
468 seasons; Kruskal-Wallis, $P < 0.0001$, Table 3). Multiple comparison tests indicated that mean
469 EC was significantly different for each of the vegetation types (Fisher's LSD, $P < 0.05$; Table 3),
470 with the highest EC in the mixed palm swamp ($170.9 \pm 6.0 \mu\text{s m}^{-2}$), followed by forested
471 vegetation ($77.1 \pm 4.2 \mu\text{s m}^{-2}$), *M. flexuosa* palm swamp ($49.7 \pm 1.4 \mu\text{s m}^{-2}$) and the forested
472 (short pole) vegetation ($40.9 \pm 3.5 \mu\text{s m}^{-2}$).

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480

481 Soil temperature varied significantly among vegetation types (data pooled across all seasons;

482 ANOVA, $P < 0.0001$, Table 3). Multiple comparisons tests indicated that soil temperature in

483 forested (short pole) vegetation was significantly lower than in the other vegetation types

484 (Table 3); whereas the other vegetation types did not differ in temperature amongst

485 themselves (Fisher's LSD, $P < 0.05$, Table 3).

486

487 Air temperature varied significantly among vegetation types (data pooled across all seasons;

488 ANOVA, $P < 0.0001$, Table 3). Multiple comparisons tests indicated that air temperature in *M.*

489 *flexuosa* palm swamp was significantly lower than in the other vegetation types; whereas the

490 other vegetation types did not differ in temperature amongst themselves (Fisher's LSD, $P <$

491 0.05 , Table 3).

492

493 Water table depths varied significantly among vegetation types (data pooled across all

494 seasons; ANOVA, $P < 0.0001$, Table 3). The highest mean water tables were observed in mixed

495 palm swamp (59.6 ± 9.3 cm), followed by forested vegetation (34.0 ± 6.9 cm), *M. flexuosa*

496 palm swamp (17.4 ± 1.2 cm), and forested (short pole) vegetation (3.5 ± 1.0 cm) (Fisher's LSD,

497 $P < 0.0005$).

498

499 **5.2 Temporal variations in gas fluxes and environmental variables**

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508 The peatlands sampled in this study showed pronounced seasonal variability in diffusive CH₄
509 flux (two-way ANOVA, $F_{7, 979} = 13.2$, $P < 0.0001$; Table 4). For ebullition of CH₄ and ebullition-
510 driven uptake of CH₄, mean fluxes varied between seasons, but high variability meant that
511 these differences were not statistically significant ((two-way ANOVA, $P > 0.8$; Table 2).

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512 Diffusive N₂O flux showed no seasonal trends (two-way ANOVA, $P > 0.5$), and therefore will
513 not be discussed further here. Diurnal studies suggest that neither diffusive fluxes of CH₄ nor
514 N₂O varied over the course of a 24-hour period.

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515
516 For diffusive CH₄ flux, the overall trend was towards significantly higher wet season ($51.1 \pm$

517 $7.0 \text{ mg CH}_4\text{-C m}^{-2} \text{ d}^{-1}$) compared to dry season ($27.3 \pm 2.7 \text{ mg CH}_4\text{-C m}^{-2} \text{ d}^{-1}$) flux (data pooled

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518 across all vegetation types; t-Test, $P < 0.001$, Table 4). However, when diffusive CH₄ flux was

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519 disaggregated by vegetation type, very different seasonal trends emerged. For example, both

520 forested vegetation and mixed palm swamp showed significantly greater diffusive CH₄ flux

521 during the *dry season* with net fluxes of $47.2 \pm 5.4 \text{ mg CH}_4\text{-C m}^{-2} \text{ d}^{-1}$ and $64.2 \pm 12.1 \text{ mg CH}_4\text{-C}$

522 $\text{m}^{-2} \text{ d}^{-1}$, respectively (Fisher's LSD, $P < 0.05$, Table 3). In contrast, *wet season* flux was 7-16

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523 times lower, with net fluxes of $6.7 \pm 1.0 \text{ mg CH}_4\text{-C m}^{-2} \text{ d}^{-1}$ and $6.1 \pm 1.3 \text{ mg CH}_4\text{-C m}^{-2} \text{ d}^{-1}$,

524 respectively (Fisher's LSD, $P < 0.05$, Table 3). In contrast, forested (short pole) vegetation and

525 *M. flexuosa* palm swamp showed seasonal trends consistent with the pooled data set; i.e.

526 significantly higher flux during the wet season (46.7 ± 8.4 and $60.4 \pm 9.1 \text{ mg CH}_4\text{-C m}^{-2} \text{ d}^{-1}$,

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527 respectively) compared to the dry season (28.3 ± 2.6 and $18.8 \pm 2.6 \text{ mg CH}_4\text{-C m}^{-2} \text{ d}^{-1}$,

528 respectively) (Fisher's LSD, $P < 0.05$, Table 3).

529

543 Even though seasonal trends in CH₄ ebullition and ebullition-driven uptake were not
544 statistically significant, we will briefly describe the overall patterns for the different
545 vegetation types as they varied among ecosystems (Table 2). Forested vegetation showed no
546 evidence of ebullition at all, while ebullition-driven uptake was greater during the dry season.
547 For forested (short pole) vegetation, ebullition was generally greater during the wet season,
548 while ebullition-driven uptake was higher during the dry season. For *M. flexuosa* palm swamp,
549 both ebullition and ebullition-driven uptake were greater during the wet season. Lastly, for
550 mixed palm swamp, both ebullition and ebullition-driven uptake were greater during the dry
551 season.

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553 For the environmental variables, soil pH, DO, EC, water table depth, and soil temperature
554 varied significantly between seasons, whereas air temperature did not. Thus, for sake of
555 brevity, air temperature is not discussed further here. Mean soil pH was significantly lower
556 during the wet season (5.18 ± 0.03) than during the dry season (5.31 ± 0.04) (data pooled
557 across all vegetation types; t-Test, $P < 0.05$, Table 2). When disaggregated by vegetation type,
558 the overall trend was found to hold true for all vegetation types except forested (short pole)
559 vegetation, which displayed higher pH during the wet season compared to the dry season
560 (Table 2). A two-way ANOVA on Box-Cox transformed data using vegetation type, season and
561 their interaction as explanatory variables indicated that vegetation type was the best
562 predictor of pH, with season and vegetation type by season playing a lesser role ($F_{7, 1166} =$
563 $348.9, P < 0.0001$).

564

565 For DO, the overall trend was towards significantly lower DO during the wet season ($13.9 \pm$
566 1.0%) compared to the dry season ($19.3 \pm 1.2 \%$) (data pooled across all vegetation types;
567 Wilcoxon test, $P < 0.0001$, Table 2). However, when the data were disaggregated by
568 vegetation type, we found that individual vegetation types showed distinct seasonal trends
569 from each other. Forested vegetation and mixed palm swamp were consistent with the
570 overall trend (i.e. lower wet season compared to dry season DO), whereas forested (short
571 pole) vegetation and *M. flexuosa* palm swamp displayed the reverse trend (i.e. higher *wet*
572 *season* compared to *dry season* DO) (Table 2). A two-way ANOVA on Box Cox transformed
573 data using vegetation type, season and their interaction as explanatory variables indicated
574 that vegetation type was the best predictor of DO, followed by a strong vegetation by season
575 interaction; season itself played a lesser role than either of the other two explanatory
576 variables ($F_{7,1166} = 57.0$, $P < 0.0001$).

577

578 For EC, the overall trend was towards lower EC in the wet season ($49.4 \pm 1.8 \mu\text{s m}^{-2}$) compared
579 to the dry season ($65.5 \pm 2.2 \mu\text{s m}^{-2}$) (data pooled across all vegetation types; Wilcoxon test,
580 $P < 0.05$, Table 2). When the data were disaggregated by vegetation type, this trend was
581 consistent for all the vegetation types except for forested vegetation, where differences
582 between wet and dry season were not statistically significant (Wilcoxon, $P > 0.05$, Table 2).

583

584 Water table depths varied significantly between seasons (data pooled across all vegetation
585 types; Wilcoxon test, $P < 0.0001$, Table 2). Mean water table level was significantly higher in
586 the wet ($54.1 \pm 2.7 \text{ cm}$) than the dry ($1.3 \pm 0.8 \text{ cm}$) season. When disaggregated by vegetation

587 type, the trend held true for individual vegetation types (Table 2). All vegetation types had
588 negative dry season water tables (i.e. below the soil surface) and positive wet season water
589 tables (i.e. water table above the soil surface), except for *M. flexuosa* palm swamp that had
590 positive water tables in both seasons. Two-way ANOVA on Box-Cox transformed data using
591 vegetation type, season and their interaction as explanatory variables indicated that all three
592 factors explained water table depth, but that season accounted for the largest proportion of
593 the variance in the model, followed by vegetation by season, and lastly by vegetation type ($F_{7,1157} = 440.1, P < 0.0001$).

595

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

604

605 5.3 Relationships between gas fluxes and environmental variables

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

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610 variables. We did not analyze trends between ebullition and ebullition-driven uptake and
611 environmental variables because of the limitations in the sampling methodology and the
612 limited number of observations.

613

614 For diffusive CH₄ flux, ANCOVA revealed that vegetation by season was the strongest
615 predictor of CH₄ flux, followed by a strong season effect ($F_{13, 917} = 9.2, P < 0.0001$). Other
616 significant drivers included soil temperature, water table depth, and a borderline-significant
617 effect of vegetation type ($P < 0.06$). However, it is important to note that each of these
618 environmental variables were only weakly correlated with CH₄ flux even if the relationships
619 were statistically significant; for example, when individual bivariate regressions were
620 calculated, the r^2 values were less than 0.01 for each plot (see Supplementary Online
621 Materials, Figures S1 and S2).

622

623 For diffusive N₂O flux, ANCOVA indicated that the best predictors of flux rates were dissolved
624 oxygen and electrical conductivity ($F_{13, 1014} = 2.2, P < 0.0082$). As was the case for CH₄, when
625 the relationships between these environmental variables and N₂O flux were explored using
626 individual bivariate regressions, r^2 values were found to be very low (e.g. less than $r^2 < 0.0007$)
627 or not statistically significant (see Supplementary Online Materials, Figures S3 and S4).

628

629

630 **6. DISCUSSION**

Deleted: 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 CH₄ flux indicate that warmer conditions or higher water tables both stimulate CH₄ flux.

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643 **6.1 Large and asynchronous CH₄ fluxes from peatlands in the Pastaza-Marañón foreland**
644 **basin**

645 The ecosystems sampled in this study were strong atmospheric sources of CH₄. Diffusive CH₄
646 flux, averaged across all vegetation types, was 36.1 ± 3.1 mg CH₄-C m⁻² d⁻¹, spanning a range
647 from -100 to 1,510 mg CH₄-C m⁻² d⁻¹. This mean falls within the range of other diffusive fluxes
648 observed in Indonesian peatlands (3.7-87.8 mg CH₄-C m⁻² d⁻¹) (Couwenberg et al., 2010) and
649 other Amazonian wetlands (7.1-390.0 mg CH₄-C m⁻² d⁻¹) (Bartlett et al., 1990; Bartlett et al.,
650 1988; Devol et al., 1990; Devol et al., 1988). Although the ebullition data must be treated with
651 caution because of the sampling methodology (see below), we observed an average ebullition
652 flux of 973.3 ± 161.4 mg CH₄-C m⁻² d⁻¹, spanning a range of 27 to 8,082 mg CH₄-C m⁻² d⁻¹.
653 While data on ebullition from Amazonian wetlands are sparse, these values are broadly in-
654 line with riverine and lake ecosystems sampled elsewhere (Bastviken et al., 2010; Smith et al.,
655 2000; Sawakuchi et al., 2014). Ebullition-driven CH₄ uptake is not a commonly reported
656 phenomena in other peatland studies because it is likely an artefact of chamber sampling
657 methods; as a consequence, we do not discuss these data further here. To summarize, these
658 data on diffusive CH₄ flux and ebullition suggest that peatlands in the Pastaza-Marañón
659 foreland basin are strong contributors to the regional atmospheric budget of CH₄, given that
660 the four vegetation types sampled here represent the dominant cover types in the PMFB
661 (Draper et al., 2014; Householder et al., 2012; Kelly et al., 2014; Lahteenoja and Page, 2011)

662
663 The overall trend in the diffusive flux data was towards greater temporal (i.e. seasonal)
664 variability in diffusive CH₄ flux, rather than strong spatial (i.e. inter-site) variability. For the
665 pooled dataset, diffusive CH₄ emissions were significantly greater during the wet season than

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679 the dry season, with emissions falling by approximately half from one season to the other (i.e.
680 51.1 ± 7.0 to 27.3 ± 2.7 mg CH₄-C m⁻² d⁻¹). This is in contrast to the data on diffusive CH₄ flux
681 among study sites, where statistical analyses indicate that there was a weak effect of
682 vegetation type on CH₄ flux, that was only on the edge of statistical significance (i.e. ANCOVA;
683 $P < 0.06$ for the vegetation effect term). For the ebullition data, while there was no significant
684 difference among vegetation types nor between seasons, it is interesting to note that
685 ebullition was more common for the two vegetation types – Mixed Palm Swamp and *M.*
686 *flexuosa* palm swamp – that showed the highest rates of diffusive CH₄ flux (Figure 2, Table 2).
687 In contrast, forested (short pole) and forested vegetation, which showed the lowest rates of
688 diffusive CH₄ flux, also showed the lowest occurrence of ebullition (Figure 2, Table 2). This is
689 broadly consistent with the notion that Mixed Palm Swamp and *M. flexuosa* palm swamp may
690 produce more CH₄ than the other vegetation types.

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691
692 On face value, these data on diffusive CH₄ flux suggest two findings; first, the relatively weak
693 effect of vegetation type on diffusive CH₄ flux implies that patterns of CH₄ cycling are broadly
694 similar among study sites. Second, the strong overall seasonal pattern suggests that – on the
695 whole – these systems conform to our normative expectations of how peatlands function
696 with respect to seasonal variations in hydrology and redox potential; i.e. enhanced CH₄
697 emissions during a more anoxic wet season (i.e. when water tables rise), and reduced CH₄
698 emissions during a more oxic dry season (i.e. when water tables fall). However, closer
699 inspection of the data reveals that different vegetation types showed contrasting seasonal
700 emission patterns (Table 3), challenging our basic assumptions about how these ecosystems
701 function. For example, while forested (short pole) vegetation and *M. flexuosa* palm swamp

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705 conformed to expected seasonal trends for methanogenic wetlands (i.e. higher wet season
706 compared to dry season emissions), forested vegetation and mixed palm swamp showed the
707 opposite pattern, with significantly greater CH₄ emissions during the dry season. The
708 disaggregated data thus imply that the process-based controls on CH₄ fluxes may vary
709 significantly among these different ecosystems, rather than being similar, leading to a
710 divergence in seasonal flux patterns.

711

712 What may explain this pattern of seasonal divergence in CH₄ flux? One explanation is that CH₄
713 emissions from forested vegetation and mixed palm swamp, compared to the other two
714 ecosystems, may be more strongly transport-limited during the wet season than the dry
715 season. This interpretation is supported by the field data; forested vegetation and mixed palm
716 swamp had the highest wet season water table levels, measuring 110.8 ± 9.3 and 183.7 ± 1.7
717 cm, respectively (Table 2). In contrast, water table levels for forested (short pole) vegetation
718 and *M. flexuosa* palm swamp in the wet season were 3-7 times lower, measuring only 26.9 ±
719 0.5 and 37.2 ± 1.7 cm, respectively (Table 2). Moreover, a scatter plot of diffusive CH₄ flux
720 against water table depth shows a peak in diffusive CH₄ emissions when water tables are
721 between 30 to 40 cm above the surface, after which CH₄ emissions decline precipitously
722 (Supplementary Online Materials Figure S2). Thus, the greater depth of overlying water in
723 forested vegetation and mixed palm swamp may have exerted a much greater physical
724 constraint on gas transport compared to the other two ecosystems. This interpretation is
725 broadly consistent with studies from other ecosystems, which indicate that high or positive
726 water tables may suppress CH₄ emissions from wetlands above a system-specific threshold
727 (Couwenberg et al., 2010; Couwenberg et al., 2011).

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Deleted: Although one could argue that the positive relationship between water table depth and CH₄ 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 CH₄ fluxes.

737 However, transport limitation alone does not fully explain the difference in dry season CH₄
738 emissions among vegetation types. Forested vegetation and mixed palm swamp showed
739 substantially higher dry season CH₄ emissions (47.2 ± 5.4 and 85.5 ± 26.4 mg CH₄-C m⁻² d⁻¹,
740 respectively) compared to forested (short pole) vegetation and *M. flexuosa* palm swamp (9.6
741 ± 2.6 and 25.5 ± 2.9 mg CH₄-C m⁻² d⁻¹, respectively), pointing to underlying differences in CH₄
742 production and oxidation among these ecosystems. One possibility is that dry season
743 methanogenesis in forested vegetation and mixed palm swamp was greater than in the other
744 two ecosystems, potentially driven by higher rates of C flow (Whiting and Chanton, 1993).
745 This is plausible given that forested vegetation and mixed palm swamp tend to occur in more
746 nutrient-rich parts of the Pastaza-Marañón foreland basin, whereas forested (short pole)
747 vegetation and *M. flexuosa* palm swamp tend to dominate in more nutrient-poor areas
748 (Lahteenoja et al., 2009a), leading to potential differences in rates of plant productivity and
749 belowground C flow. Moreover, it is possible that the nutrient-rich vegetation may be able to
750 utilize the higher concentration of nutrients, deposited during the flood pulse, during the
751 Amazonian dry season (Morton et al., 2014; Saleska et al., 2016), with implications for overall
752 ecosystem C throughput and CH₄ emissions. Of course, this interpretation does not preclude
753 other explanations, such as differences in CH₄ transport rates among ecosystems (e.g. due to
754 plant-facilitated transport or ebullition) (Panagala et al., 2013), or varying rates of CH₄
755 oxidation (Teh et al., 2005). However, these other possibilities cannot be explored further
756 without recourse to more detailed process-level experiments. Forthcoming studies on the
757 regulation of GHG fluxes at finer spatial scales (e.g. investigation of environmental gradients
758 within individual study sites) or detailed diurnal studies of GHG exchange (Murphy *et al.*, in

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761 prep.) will further deepen our understanding of the process controls on soil GHG flux from
762 these peatlands, and shed light on these questions.

763

764 Finally, while the trends described here are intriguing, it is important to acknowledge some
765 of the potential limitations of our data. First, given the uneven sampling pattern, it is possible

766 that the values reported here do not fully represent the entire range of diffusive flux rates,

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767 especially for the more sparsely sampled habitats. However, given the large and statistically

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768 significant differences in CH₄ emissions between seasons, it is likely that the main trends that

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769 we have identified will hold true with more spatially-extensive sampling. Second, the data

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770 presented here represent a conservative underestimate of CH₄ emissions, because the low

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771 frequency, static chamber sampling approach that we utilized was unable to fully capture

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772 erratic ebullition events representatively (McClain et al., 2003). Although we attempted to

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773 quantify CH₄ ebullition within our static flux chambers, the sampling approach that we utilized

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774 was not the best-suited for representatively quantifying ebullition. Given the erratic or

775 stochastic nature of ebullition, automated chamber measurements or an inverted "flux

776 funnel" approach would have provided better estimates of ebullition (Strack et al., 2005).

777 However, we lacked the resources to implement these approaches here. We also did not

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778 measure CH₄ emissions from the stems of woody plants, even though woody plants have been

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779 recently identified as an important point of atmospheric egress (Pangala et al., 2013). We did

Deleted: which often result in much higher net CH₄ fluxes (McClain et al., 2003). (Strack et al., 2005)

780 not have enough data on floristic composition or individual plant identities within our plots

781 to develop a sampling design that would adequately represent plant-mediated fluxes from

782 our study sites, nor the resources to implement a separate study of stem fluxes. Third and

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783 last, our data probably underestimate net CH₄ fluxes for the PMFB because we chose to

798 include fluxes with strong negative values (i.e. more than $-10 \text{ mg CH}_4\text{-C m}^{-2} \text{ d}^{-1}$) in our
799 calculation of mean diffusive flux rates. These observations are more negative than other
800 values typically reported elsewhere in the tropical wetland literature (Bartlett et al.,
801 1990; Bartlett et al., 1988; Devol et al., 1990; Devol et al., 1988; Couwenberg et al., 2010).
802 However, they represent only a small proportion of our dataset (i.e. 7 %, or only 68 out of 980
803 measurements), and inspection of our field notes and the data itself did not produce
804 convincing reasons to exclude these observations (e.g. we found no evidence of irregularities
805 during field sampling, and any chambers that showed statistically insignificant changes in
806 concentration over time were removed during our quality control procedures). While
807 headspace concentrations for these measurements were often elevated above mean
808 tropospheric levels ($>2 \text{ ppm}$), this in itself is not unusual in reducing environments that
809 contain strong local sources of CH_4 (Baldocchi et al., 2012). We did not see this as a reason to
810 omit these values as local concentrations of CH_4 are likely to vary naturally in methanogenic
811 forest environments due to poor mixing in the understory and episodic ebullition events.
812 Importantly, exclusion of these data did not alter the overall statistical trends reported above,
813 and only produced slightly higher estimates of diffusive CH_4 flux ($41.6 \pm 3.2 \text{ mg CH}_4\text{-C m}^{-2} \text{ d}^{-1}$
814 versus $36.1 \pm 3.1 \text{ mg CH}_4\text{-C m}^{-2} \text{ d}^{-1}$).

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816 **6.2 Western Amazonian peatlands as weak atmospheric sources of nitrous oxide**

817 The ecosystems sampled in this study were negligible atmospheric sources of N_2O , emitting
818 only $0.70 \pm 0.34 \text{ } \mu\text{g N}_2\text{O-N m}^{-2} \text{ d}^{-1}$, suggesting that peatlands in the Pastaza-Marañón foreland
819 basin make little or no contribution to regional atmospheric budgets of N_2O . This is consistent
820 with N_2O flux measurements from other forested tropical peatlands, where N_2O emissions

824 were also found to be relatively low (Inubushi et al., 2003; Couwenberg et al., 2010). No
825 statistically significant differences in N₂O flux were observed among study sites or between
826 seasons, suggesting that these different peatlands may have similar patterns of N₂O cycling.
827 Interestingly, differences in N₂O fluxes were not associated with the nutrient status of the
828 peatland; i.e. more nutrient-rich ecosystems, such as forested vegetation and mixed palm
829 swamp, did not show higher N₂O fluxes than their nutrient-poor counterparts, such as
830 forested (short pole) vegetation and *M. flexuosa* palm swamp. This may imply that N
831 availability, one of the principal drivers of nitrification, denitrification, and N₂O production
832 (Groffman et al., 2009; Werner et al., 2007), may not be greater in nutrient-rich versus
833 nutrient-poor ecosystems in this part of the Western Amazon. Alternatively, it is possible that
834 even though N availability and N fluxes may differ between nutrient-rich and nutrient-poor
835 systems, N₂O yield may also vary such that net N₂O emissions are not significantly different
836 among study sites (Teh et al., 2014).

837

838 One potential source of concern are the negative N₂O fluxes that we documented here. While
839 some investigators have attributed negative fluxes to instrumental error (Cowan et al.,
840 2014; Chapuis-Lardy et al., 2007), others have demonstrated that N₂O consumption –
841 particularly in wetland soils – is not an experimental artifact, but occurs due to the complex
842 effects of redox, organic carbon content, nitrate availability, and soil transport processes on
843 denitrification (Ye and Horwath, 2016; Yang et al., 2011; Wen et al., 2016; Schlesinger,
844 2013; Teh et al., 2014; Chapuis-Lardy et al., 2007). Given the low redox potential and high
845 carbon content of these soils, it is plausible that microbial N₂O consumption is occurring,
846 because these types of conditions have been found to be conducive for N₂O uptake elsewhere
847 (Ye and Horwath, 2016; Teh et al., 2014; Yang et al., 2011).

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850 **7. CONCLUSIONS**

851 Our data suggest that peatlands in the Pastaza-Marañón foreland basin are strong sources of
 852 atmospheric CH₄ at a regional scale, and need to be better accounted for in CH₄ emissions
 853 inventories for the Amazon basin as a whole. In contrast, N₂O fluxes were negligible,
 854 suggesting that these ecosystems are weak regional sources at best. Divergent or
 855 asynchronous seasonal emissions pattern for CH₄ among different vegetation types was
 856 intriguing, and challenges our underlying expectations of how tropical peatlands function.
 857 These data highlight the need for greater wet season sampling, particularly from ecosystems
 858 near river margins that may experience very high water tables (i.e. >40 cm). Moreover, these
 859 data also emphasize the need for more spatially-extensive sampling across both the Pastaza-
 860 Marañón foreland basin and the wider Amazon region as a whole, in order to establish if these
 861 asynchronous seasonal emission patterns are commonplace or specific to peatlands in the
 862 PMFB region. If CH₄ emission patterns for different peatlands in the Amazon are in fact
 863 asynchronous and decoupled from rainfall seasonality, then this may partially explain some
 864 of the heterogeneity in CH₄ source and sinks observed at the basin-wide scale (Wilson et al.,
 865 2016).

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868 **8. AUTHOR CONTRIBUTION**

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885 YAT secured the funding for this research, assisted in the planning and design of the
886 experiment, and took the principal role in the analysis of the data and preparation of the
887 manuscript. WAM planned and designed the experiment, collected the field data, analyzed
888 the samples, and took a secondary role in data preparation, data analysis, and manuscript
889 preparation. JCB, AB, and SEP supported the planning and design of the experiment, and
890 provided substantive input into the writing of the manuscript. AB in particular took a lead role
891 in developing the maps of our study sites in the PMFB.

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914 **10. REFERENCES**

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1142

1143 **11. TABLES AND FIGURES**

1144 **Table 1.** Site characteristics including field site location, nutrient status, plot and flux chamber
 1145 replication

| Vegetation type | Site name | Nutrient status* | Latitude (S) | Longitude (W) | Plots | Flux chambers |
|------------------------|--------------------|------------------|--------------|---------------|-------|---------------|
| Forested | Buena Vista | Rich | 4°14'45.60"S | 73°12'0.20"W | 21 | 105 |
| Forested (short pole) | San Jorge (centre) | Poor | 4°03'35.95"S | 73°12'01.13"W | 6 | 28 |
| Forested (short pole) | Miraflores | Poor | 4°28'16.59"S | 74° 4'39.95"W | 41 | 204 |
| M. flexuosa Palm Swamp | Quistococha | Intermediate | 3°49'57.61"S | 73°12'01.13"W | 135 | 668 |
| M. flexuosa Palm Swamp | San Jorge (edge) | Intermediate | 4°03'18.83"S | 73°10'16.80"W | 18 | 86 |
| Mixed palm swamp | Charo | Rich | 4°16'21.80"S | 73°15'27.80"W | 18 | 90 |

1146 *After Householder et al. 2012, Lahteenoja et al. 2009a, and Lahteenoja et al. 2009b

| Vegetation type | Site name |
|------------------------|--------------------|
| Forested | Buena Vista |
| Forested (short pole) | San Jorge (centre) |
| Forested (short pole) | Miraflores |
| M. flexuosa Palm Swamp | Quistococha |
| M. flexuosa Palm Swamp | San Jorge (edge) |
| Mixed palm swamp | Charo |

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1149 **Table 2. Proportion of observations for each vegetation type that showed evidence of**
 1150 **ebullition, mean rates of ebullition and ebullition-driven CH₄ uptake. Values represent**
 1151 **means and standard errors.**

| Vegetation Type | Percentage of observations (%) | Ebullition (mg CH ₄ -C m ⁻² d ⁻¹) | | Ebullition-driven uptake (mg CH ₄ -C m ⁻² d ⁻¹) | |
|-------------------------------|--------------------------------|---|---------------|---|----------------|
| | | Wet Season | Dry Season | Wet Season | Dry Season |
| Forested | 10.5 | 0 | 0 | 0 | -136.4 ± 0.1 |
| Forested (short pole) | 6.9 | 994.6 ± 293.2 | 512.5 ± 153.0 | -95.8 ± 0.0 | -245.5 ± 48.9 |
| <i>M. flexuosa</i> Palm Swamp | 16.7 | 1192.0 ± 305.7 | 994.3 ± 237.3 | -869.4 ± 264.8 | -401.4 ± 59.9 |
| Mixed Palm Swamp | 12.2 | 0 | 733.6 ± 313.1 | 0 | -464.4 ± 565.9 |

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1153 **Table 3.** Environmental variables for each vegetation type for the wet and dry season.

1154 Values reported here are means and standard errors. Lower case letters indicate significant

1155 differences among vegetation types within the wet or dry season (Fisher's LSD, $P < 0.05$).

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| Vegetation Type | Peat Temperature (°C) | | Air Temperature (°C) | | Conductivity ($\mu\text{S m}^{-2}$) | | 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 | 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 |
| 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 |

| Vegetation Type | Peat Temperature (°C) | | Air Temperature (°C) | |
|-----------------------|-----------------------|--------------|----------------------|-------------|
| | 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 |
| Forested (short pole) | 25.2 ± 0.0b | 24.8 ± 0.1a | 27.6 ± 0.1b | 27.5 ± 0.1b |
| M. flexuosa | 25.6 ± 0.6c | 25.3 ± 0.1b | 26.3 ± 0.1c | 26.4 ± 0.1a |
| Palm Swamp | 26.0 ± 0.0a | 25.0 ± 0.1ab | 26.1 ± 0.1c | 28.2 ± 0.3b |

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1159 **Table 4.** Trace gas fluxes for each vegetation type for the wet and dry season. Values reported
 1160 here are means and standard errors. Upper case letters indicate significant differences in gas
 1161 flux between seasons with a vegetation type, while lower case letters indicate significant
 1162 differences among vegetation types within a season (Fisher's LSD, $P < 0.05$).

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| Vegetation Type | Methane Flux (mg CH ₄ -C m ⁻² d ⁻¹) | | Nitrous Oxide Flux (µg N ₂ O-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 |
| <i>M. flexuosa</i> 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 |

1163

| Vegetation Type | Methane Flux (mg CH ₄ -C m ⁻² d ⁻¹) | |
|-------------------------------|--|---------------|
| | Wet Season | Dry Season |
| Forested | 6.7 ± 1.0Aa | 47.2 ± 5.4Ba |
| Forested (short pole) | 60.4 ± 9.1Ab | 18.8 ± 2.6Bb |
| <i>M. flexuosa</i> Palm Swamp | 46.7 ± 8.4Ac | 28.3 ± 2.6Bc |
| Mixed Palm Swamp | 6.1 ± 1.3Aa | 64.2 ± 12.1Ba |

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1166 **Figure Captions**

1167 **Figure 1.** Map of the study region and field sites. The colour scale to the right of the map
1168 denotes elevation in meters above sea level (m a.s.l.). Tan and brown tones indicate peatland
1169 areas.

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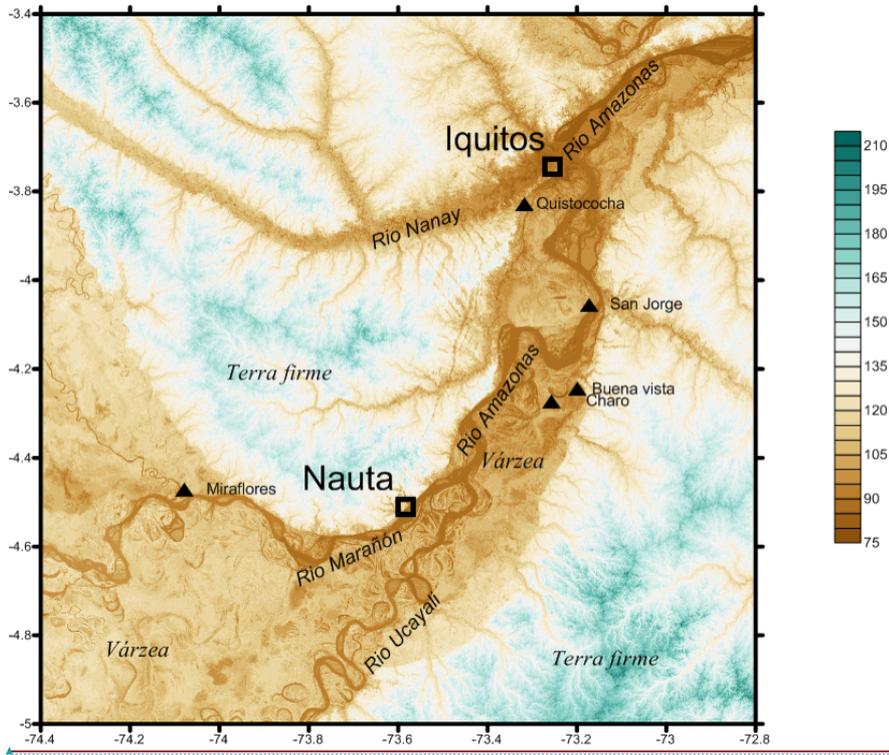
1171 **Figure 2.** Net diffusive (a) methane (CH₄) and (b) nitrous oxide (N₂O) fluxes by vegetation type.

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1172 Error bars denote standard errors.

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1176 **Figure 1**

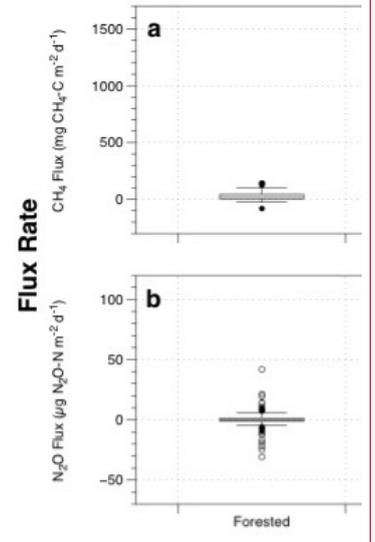
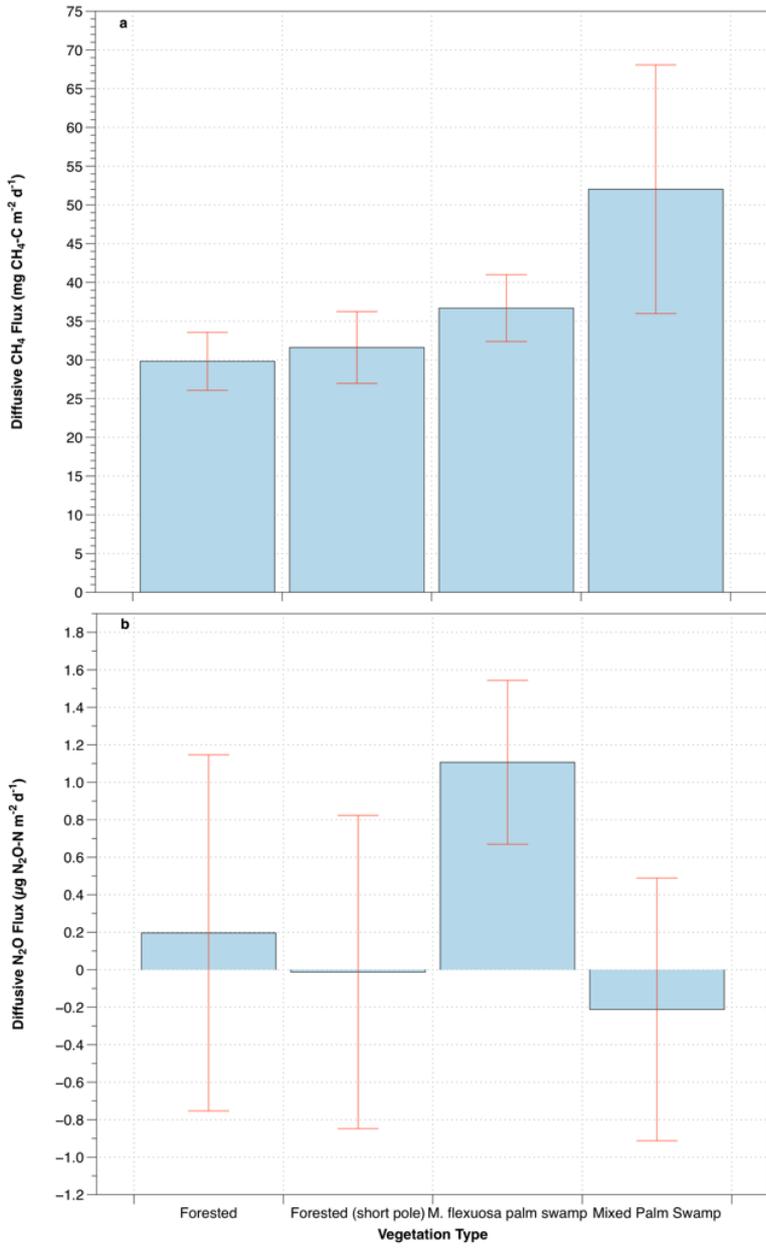


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