Reponse to Reviewer 1

We would like to thank reviewer 1 for taking the time to provide a useful critique of the manuscript. We have responded to their concerns in blue and copied their original comments in black for ease of reference.

Wolf et al. (2011) got a deeper insight into the soil "black box" by conducting incubations of soil samples from different soil horizons. Finally, they identified a stratification of CH4-uptake activity within the soil profile that highlights the heterogeneity of methane cycling processes in organic soils of tropical montane forests. After such a study by Wolf et al. (2011), it would be nice to identify hot spots of CH4 consumption and/or production within soils of their region and how that correlates with available nitrate, ammonium, oxygen etc

We whole-heartedly agree with reviewer 1 that overcoming the inherent difficulties posed to sampling strategies in attempting to study hot spot activity remains a particularly interesting facet of understanding fine scale heterogeneity within tropical soils (see Hall et al. (2013) for a nice example).

Furthermore, the discussion about N-inhibition or N-limitation of CH4 consumption and/or production is very speculative without having any information about present methanotrophic or methanogenic community composition and/or activity, especially when the results are so different. Other processes, as well, may eventually lead to the observed positive correlation between net CH4 flux and nitrate concentrations. Dependent on the nutrient status of the respective forest type, increased soil nitrate availability may stimulate plant growth that accelerates organic carbon availability via root exudation for methanogens and other microorganisms and finally lead to an increase of CH4 production in anoxic microsites and a decrease of net CH4 consumption (see Bodelier et al. 2011)

We remain speculative as conceptual models linking CH_4 exchange and N availability are complicated and we are limited to inferring possible causes in terms of changes in net exchange and field conditions. The apparent differences between Indonesia, Ecuador and Peru discussed do indeed seem to suggest a better understanding of patterns in the underlying gross processes is required. We attempt to investigate, albeit at a crude scale, the potential for microsite methanogenic activity in influencing net exchange through measurement of bulk soil O_2 and net CO_2 fluxes. We have extended the text on Page 12 to accommodate the reviewer's good suggestion: *"However, we may also have expected increases in available NO_3^- to competitively suppress methanogenic activity (Chidthaisong and Conrad, 2000). This is counter to the observation that net CH_4 is positively correlated to available NO_3^- and that emissions are most prevalent in the premontane forest. Greater below-ground productivity at lower elevations (Girardin et al., 2010), potentially driven by greater nutrient availability and temperature, may also stimulate CH_4 production in the rhizosphere through the supply of labile substrates to methanogenic communities or maintenance of anaerobic microsites through the O_2 demand of heterotrophic respiration (Bodelier, 2011). Such a mechanism, not observed in this data, might be supported by a positive relationship between net CH_4 and CO_2 fluxes (Verchot et al., 2000)."*

What is with phosphorus (see Wolf et al. 2011)? I think that nutrient status of the diverse vegetation including the deep roots within organic-rich soils of tropical montane forests may play an important role in structuring microbial community composition and activity that may be as important as soil structure and precipitation.

In addition to available nitrate and ammonium, phosphate and nitrite data were also obtained from the resin bags. No significant relationship was found between nitrite and net CH_4 flux, whilst, a significant negative relationship was identified between phosphate. However, this relationship was less robust than those which form the main focus of our discussion (i.e. soil temperature, available nitrate and water-filled pore space). As understanding the influence of variations in microbial functional diversity is beyond the scope of our work we omitted these data for the sake of clarity. They will however be available when the dataset is archived with CEDA.

I would remove the word significantly throughout the text. It is in almost every sentence of the "Results" section. I think it is enough if you say that A is higher than B or A influences B. If something is not significant there is no difference or influence. Additionally, you define statistical significance at $p<0.05$. That is enough, I think.

Following this advice, we have altered the text of results section accordingly.

Page 7, Line 5+6: How did you measure particle density and porosity

We have added this information to Page 7: *"Plot bulk densities were determined from the weight of volumetric soil samples after oven drying at 105 °C for 24 hours. Forest type particle density was determined from measurement of bulked plot samples using a 10 ml pyncometer (Klute and others, 1986)."*

Page 4+5: Could you clarify how many plots were installed, in total

A total of 9 plots were installed; three plots were installed in each of the three forest types. See Page 5, Line 8 – 13:

"Within each forest type three plots of 20 by 20 m were established approximately three months prior to the start of reported measurements in an attempt to minimise the effects of disturbances involved with installing sampling equipment (Varner et al., 2003). Within forest types the distance between plots ranged from ~ 100 to 1000 m. The plots in the premontane forest were each situated on a ridge, slope and flat feature between elevations of 1070 to 1088 m asl. Similarly, the lower montane forest plots were established on ridge, slope and flat features between elevations of 1532 to 1768 m asl. In the upper montane forest two plots were situated on slopes and the third on a ridge at elevations between 2811 to 2962 m asl."

Page 9, Line 22 and Table 3; Figure 4: As far as I understand, you have 3 plots per elevation (these are your independent samples if you say they were randomly selected; n=3). Now, you can do linear regression between your variables of interest among these three points but in my opinion you are not allowed to do linear regression among all samples (9 plot means) of the elevation gradient because they are not independent! You can check whether your forest type means differ from each other but not a linear regression among 9 plot means.

Reviewer 2 also raised this point and we have copied this response there. Our decision to treat measurement plots within a 'forest type' (or elevation band) as independent replicates of net CH_4 exchange is based on the assumption that spatial autocorrelation is limited to short distances (i.e. operating at sub- plot scales of ~ 1 to 10s of m). The plots in our study were more than 100 m apart. We treat our observations as longitudinal data to investigate the possible drivers of the relationship between net CH_4 flux and elevation within our study area. In an attempt to synthesise this information, we then discuss CH_4 exchange in terms of the ecosystem transitions (or 'forest types') seen across the landscape. This approach is adopted from the literature, for example, across montane forest landscapes (Purbopuspito et al., 2006, p.3) and more recently across lowland tropical forest landscapes (Hassler et al., 2015). We state our approach in the manuscript on Page 6, Line 19 – 21: *"Despite the three plots within each forest type broadly occurring within the same forest stand they were considered independent replicates of forest type as spatial correlations between net CH_4 fluxes in tropical forests are small (Ishizuka et al., 2005a; Purbopuspito et al., 2006)".* However, we acknowledge the concerns of both reviewers. The use of site (n = 3) or plot (n = 9) means in correlation tests does not fundamentally change the pattern or effect size of the relationships which form the basis of our discussion in section 4.2. For example, focussing on the most robust relationships identified between CH_4 exchange and environmental conditions (Table 3 (Pearson's $r > 0.8$, $p < 0.05$, $n = 9$) and then graphed in Figure 4): $n = 3$, net CH_4 flux vs. elevation (Pearson's $r = -0.85$, $p = 0.35$), soil temperature (Pearson's $r = 0.86$, $p = 0.34$), WFPS (Pearson's $r = 0.99$, $p = 0.10$) and NO3 (Pearson's $r = 0.92$, $p = 0.25$). In an attempt to minimise confusion caused by the text, we have altered the somewhat unclear use of 'site' on Page 4 to fall into line with the way we treat the data and how the experimental approach along this transect has previously been described (e.g. Teh et al., 2014, p.2)

References

Hall, S. J., McDowell, W. H. and Silver, W. L.: When wet gets wetter: decoupling of moisture, redox biogeochemistry, and greenhouse gas fluxes in a humid tropical forest soil, Ecosystems, 16(4), 576–589, 2013.

Hassler, E., Corre, M. D., Tjoa, A., Damris, M., Utami, S. R. and Veldkamp, E.: Soil fertility controls soil–atmosphere carbon dioxide and methane fluxes in a tropical landscape converted from lowland forest to rubber and oil palm plantations, Biogeosciences, 12(19), 5831–5852, doi:10.5194/bg-12-5831-2015, 2015.

Purbopuspito, J., Veldkamp, E., Brumme, R. and Murdiyarso, D.: Trace gas fluxes and nitrogen cycling along an elevation sequence of tropical montane forests in Central Sulawesi, Indonesia, Global Biogeochemical Cycles, 20(3), doi:10.1029/2005GB002516, 2006.

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

Reponse to Reviewer 2

We would like to thank Reviewer 2 for taking the time to provide a useful critique of the manuscript and in particular for providing detailed suggestions for improving the clarity of the discussion. We have responded to their concerns in blue and copied their original comments in black for ease of reference.

Pg 11, lines 6-8: this sentence is rather vague - can you rephrase it to state specifically what you think is occurring (perhaps with a reference)?

We have simplified the statement on Page 11: *"This may impart reflect the fact that seasonal variations in rainfall and temperature become more pronounced with elevation across this transect (Fig. 1)."* The issue is more appropriately discussed with reference to temporal relationship between net flux and WFPS in the following section. Page 12, Line ~16

Pg 11, line 15: can you suggest what you might have done differently?

We have expanded the text on Page 11: *"Emissions were more prevalent in the premontane forest, accounting for 29 % of fluxes, suggesting that emission hotspots are possible in these soils but may not have been captured by our sampling strategy (Delmas et al., 1992; Silver et al., 1999). Assessing and studying the potential for emissions from these ecosystems is likely to require higher resolution observations to capture spatial and temporal variability (Liptzin et al., 2011; Silver et al., 1999) combined with experimental manipulations (Hall et al., 2013) and a better understanding of below-ground CH_4 cycling (von Fischer and Hedin, 2007; Teh et al., 2005)."*

Pg 11, line 32:'dissimilarities' is vague - please rephrase this sentence to explain specifically what you mean.

We have reworded the text on Page 11: *"Notably, this relationship appears to be driven by decreased WFPS and increased CH_4 uptake in the upper montane forest plot during the dry season."*

Pg 12, line 11-12: the purpose of this sentence is unclear, please rephrase and/or expand on what you are trying to say here.

We have expanded on text on Page 11: *"However, we may also have expected increases in available NO_3^- to competitively suppress methanogenic activity (Chidthaisong and Conrad, 2000). This is counter to the observation that net CH_4 is positively correlated to available NO_3^- and that emissions are most prevalent in the premontane forest. Greater below-ground productivity at lower elevations (Girardin et al., 2010), potentially driven by greater nutrient availability and temperature, may also stimulate CH_4 production in the rhizosphere through the supply of labile substrates to methanogenic communities or maintenance of anaerobic microsites through the O_2 demand of heterotrophic respiration (Bodelier, 2011). Such a mechanism, not observed in this data, might be supported by a positive relationship between net CH_4 and CO_2 fluxes (Verchot et al., 2000)."*

Pg 13, line 10: discussed where? Are you referring to Pg. 11? If so, this is again quite vague. Can you suggest another possible driver?

We have expanded the text on Page 13: *"From these contrasts, it is possible to suggest that relationships with temperature identified here, as discussed with reference to spatial correlations across the Peruvian transect in the previous section, and in Ecuador (Wolf et al., 2012) result from covariance with other drivers like soil moisture or nutrient availability rather than as a result of the temperature sensitivity of CH_4 uptake."*

Pg 13, line 17: what mechanism? You comment on differences and go on to suggest they may be related to soil structure, but can you specifically describe a possible mechanism?
We have expanded the text on Page 13: *" Increased WFPS, a function of decreasing soil porosity and increasing precipitation across the transition from upper montane to premontane forests, appears to limit CH_4 uptake in Peru through diffusional constraints on the supply of CH_4 to methanotrophic communities. Whilst a similar pattern in soil porosity with elevation can be inferred from the presence organic horizons in montane forests studied in Ecuador (Wolf et al., 2012), the alignment between increasing precipitation and decreasing CH_4 uptake across this transect might suggest that diffusional constraints, in response to changes in soil moisture, might provide a generalised explanation for the patterns observed. Indeed, Veldkamp et al. (2013) invoke gas diffusional control to explaining positive correlation between net annual CH4 fluxes and rainfall in a meta-analysis of 7 tropical forests above 800 m elevation."*

Figure 4: Double-check your statistical theory here, but as they are currently presented, I don't think these graphs should have regression lines. I believe that once you choose to treat the 3 elevations as forest replicates, the within-elevation replicates would need to be averaged in order to avoid pseudoreplication.

Reviewer 2 also raised this point and we have copied our response here. Reviewer 2 also raised this point and we have copied this response there. Our decision to treat measurement plots within a 'forest type' (or elevation band) as independent replicates of net CH_4 exchange is based on the assumption that spatial autocorrelation is limited to short distances (i.e. operating at sub- plot scales of ~ 1 to 10s of m). The plots in our study were more than 100 m apart. We treat our observations as longitudinal data to investigate the possible drivers of the relationship between net CH_4 flux and elevation within our study area. In an attempt to synthesise this information, we then discuss CH_4 exchange in terms of the ecosystem transitions (or 'forest types') seen across the landscape. This approach is adopted from the literature, for example, across montane forest landscapes (Purbopuspito et al., 2006, p.3) and more recently across lowland tropical forest landscapes (Hassler et al., 2015). We state our approach in the manuscript on Page 6, Line 19 – 21: *"Despite the three plots within each forest type broadly occurring within the same forest stand they were considered independent replicates of forest type as spatial correlations between net CH_4 fluxes in tropical forests are small (Ishizuka et al., 2005a; Purbopuspito et al., 2006)"*. However, we acknowledge the concerns of both reviewers. The use of site (n = 3) or plot (n = 9) means in correlation tests does not fundamentally change the pattern or effect size of the relationships which form the basis of our discussion in section 4.2. For example, focussing on the most robust relationships identified between CH_4 exchange and environmental conditions (Table 3 (Pearson's $r > 0.8$, $p < 0.05$, n = 9) and then graphed in Figure 4): n = 3, net CH_4 flux vs. elevation (Pearson's $r = -0.85$, $p = 0.35$), soil temperature (Pearson's $r = 0.86$, $p = 0.34$), WFPS (Pearson's $r = 0.99$, $p = 0.10$) and NO3 (Pearson's $r = 0.92$, $p = 0.25$).
In an attempt to minimise confusion caused by the text, we have altered the somewhat unclear use of 'site' on Page 4 to fall into line with the way we treat the data and how the experimental approach along this transect has previously been described (e.g. Teh et al., 2014, p.2)

Throughout the paper (most mistakes occur in the discussion) use only past tense rather than mixing past and present.

Done, thanks.

When citing references, it is more helpful for the reader if you put references directly behind the information they refer to instead of grouping them at the end of the sentence (i.e. Pg 11, line 5, Pg 12, line 3, Pg 13, line 21).

Done, thanks.

To avoid unnecessary confusion, consider using 'efflux' or 'emissions' to refer specifically to positive fluxes. For example, on Pg. 8, line 3, one could argue that larger fluxes actually occurred at the higher elevations.

Done, thanks.

Pg 8, line 3,16: at lower 'elevations'

Done, thanks.

Pg 8, line 11: use consistent language. Rather than saying 'negative fluxes', use 'uptake' as you do elsewhere.

Done, thanks.

Pg 9, line 2, Pg 10, line 31, Pg 13, line 13: A semi-colon is used to join two related (complete) sentences. Whilst or while are conjunctions, which can be used to compare two (normally contrasting) ideas in a single sentence.

Done, thanks.

Pg 9, line 14: by 'species' do you mean 'forest type'?

Changed to 'compounds'.

Pg 9, line 28: plot 'means'

Done, thanks.

Pg 10, line 2,8: delete 'for example'

Done, thanks.

Pg 10, line 28: delete 'together'

Done, thanks.

Pg 10, line 30: did you do this statistical comparison over time or only comparing wet vs dry season? If the latter is true, then you can't say "with the procession of"

We have reworded the text on Page 10: *" However, the time-series of net CH_4 flux (Fig. 2 a) for the upper montane forest does suggest that CH_4 uptake increases with the procession of the dry season; ultimately equating to a ~ 30 % difference in uptake between dry and wet season. Our inability to detect a statistically significant difference between seasons at this site (Table 2) may reflect interannual variability, and the fact that environmental conditions change gradually across seasonal transitions (Clark et al., 2014)."*

Pg 11, line 1: 'differences', the fact 'that'

Done, thanks.

Pg 11, lines 12-13, Pg 12, line 32: 'source activity' is awkward. Change to 'emissions' or 'efflux'.

We have reworded the text on Page 11: *"Indeed, emissions represented only 1 – 2 % of fluxes in the upper and lower montane forests of this study."*

Pg 11, line 32: 'underpinned' sounds awkward here, perhaps 'supported'?

Done, thanks.

Pg 11, line 29-33 (and elsewhere): This part of the discussion would be improved if you indicated which tables/figures correspond to the results you are discussing.

Agreed, thanks.

Pg 12, line 17: 'Similar' to

Done, thanks.

Pg 12, lines 20, 26: 'the' positive correlations, 'the' wet and dry seasons

Done, thanks.

Pg 13, line 1: 'constrained' seems odd in this context, do you mean 'understood'?

Done, thanks .

Pg 13, line 4: move the reference to Table 5 from line 1 to here, after 'for these studies'

Done, thanks.

Pg 13, line 5: 'in this respect' doesn't fit here, can you reword?

We have reworded the text on Page 13: *"The soils of the montane forests in these three studies are differentiated from those of the premontane forests by the presence of thick organic horizons at the surface*."

References

Hall, S. J., McDowell, W. H. and Silver, W. L.: When wet gets wetter: decoupling of moisture, redox biogeochemistry, and greenhouse gas fluxes in a humid tropical forest soil, Ecosystems, 16(4), 576–589, 2013.

Hassler, E., Corre, M. D., Tjoa, A., Damris, M., Utami, S. R. and Veldkamp, E.: Soil fertility controls soil–atmosphere carbon dioxide and methane fluxes in a tropical landscape converted from lowland forest to rubber and oil palm plantations, Biogeosciences, 12(19), 5831–5852, doi:10.5194/bg-12-5831-2015, 2015.

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

Drivers of atmospheric methane uptake by montane forest soils in the southern Peruvian Andes

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Abstract. The soils of tropical montane forests can act as sources or sinks of atmospheric methane (CH_4). Understanding this activity is important in regional atmospheric CH_4 budgets, given that these ecosystems account for substantial portions of the landscape in mountainous areas like the Andes. Here we investigated the drivers of net CH_4 fluxes from premontane, lower and upper montane forests, experiencing a seasonal climate, in southeastern Peru. Between February 2011 and June 2013, these soils all functioned as net sinks for atmospheric CH_4. Mean (standard error) net CH_4 fluxes for the dry and wet season were -1.6 (0.1) and -1.1 (0.1) mg CH_4 - C m^{-2} d^{-1} in the upper montane forest, -1.1 (0.1) and -1.0 (0.1) mg CH_4 - C m^{-2} d^{-1} in the lower montane forest, and -0.2 (0.1) and -0.1 (0.1) mg CH_4 - C m^{-2} d^{-1} in the premontane forest. Variations among forest types were best explained by available nitrate and water-filled pore space, indicating that nitrate inhibition of oxidation or diffusional constraints imposed by changes in water-filled pore space on methanotrophic communities represent important controls on soil-atmosphere CH_4 exchange. Seasonality in CH_4 exchange varied among forests types with increased dry season an increase in wet season net CH_4 uptakeflux only apparent in the upper montane forest. Variation across these forests was best explained by available nitrate and water-filled pore space indicating that nitrate inhibition of oxidation or diffusional constraints imposed by changes in water-filled pore space on methanotrophic communities may represent important controls on soil-atmosphere CH_4 exchange. Net CH_4 flux was inversely related to elevation; a pattern that differs to that observed in Ecuador, the only other extant study site of soil-atmosphere CH_4 exchange in the tropical Andes. This may result from differences in rainfall patterns between the regions, suggesting that attention should be paid to the role of rainfall and soil moisture dynamics in modulating CH_4 uptake by the organic-rich soils typical of high elevation tropical forests.

1 Introduction

Methane (CH_4) is an important greenhouse gas, accounting for at least a fifth of the climate forcing associated with increases in the atmospheric concentration of well-mixed greenhouse gases since the industrial revolution (Cicerone and Oremland, 1988; Myhre et al., 2013)~~(Cicerone and Oremland, 1988; Myhre et al., 2013).~~ Despite the importance of tropical landscapes in the global CH_4 budget, the comparison of satellite retrievals of the atmospheric ~~-~~ concentration of CH_4 with source-sink inventories and bottom-up process based models indicates that these landscapes are poorly characterised (Bergamaschi et al., 2009; Bloom et al., 2010; Frankenberg et al., 2005)~~(Bergamaschi et al., 2009; Bloom et al., 2010; Frankenberg et al., 2005)~~. This likely reflects ~~a~~a historic imbalance in field observations~~,~~ when compared to the northern hemisphere. Soils play a key role in controlling atmospheric CH_4 concentrations~~,~~ with emissions from inundated tropical wetland soils representing the largest natural source of atmospheric CH_4, whilst well-drained soils represent the largest ~~net~~ biological sink (Ciais et al., 2013)~~(Ciais et al., 2013)~~. As s~~S~~oils are ~~, being~~ capable of acting as both globally significant sources or sinks for atmospheric CH_4, they are ~~are~~ of particular interest in refining our understanding of CH_4 exchange across tropical landscapes (Dutaur and Verchot, 2007; Spahni et al., 2011)~~(Dutaur and Verchot, 2007; Spahni et al., 2011)~~.

The function of a soil as source or sink for atmospheric CH_4 is the net result of consumption and production by aerobic methanotrophic bacteria and anaerobic methanogenic archaea ~~respectively~~ (Conrad, 1996; Le Mer and Roger, 2001)~~(Conrad, 1996; Le Mer and Roger, 2001)~~. Well-drained soils are typically thought to act as ~~a~~ net sinks for atmospheric CH_4 because aerated soils support communities of high-affinity methanotrophic bacteria that oxidise CH_4 at near-ambient concentrations (Bender and Conrad, 1992)~~(Bender and Conrad, 1992; Teh et al., 2006)~~. In such soils, variations in the net flux of CH_4 between soil and atmosphere are expected to be strongly influenced by constraints on the diffusional supply of CH_4 to methanotrophs imposed by the structure of the soil pore network and the difference between gaseous and aqueous phase mass transfer of CH_4 (Bender and Conrad, 1992; Conrad, 1996; Smith et al., 2003)~~(Bender and Conrad, 1992; Smith et al., 2003)~~. This reliance on diffusion indicates that high-affinity methanotrophs are likely to occupy well-connected pore spaces, and as such uptake of atmospheric CH_4 is also sensitive to water limitation under drier conditions (von Fischer et al., 2009) ~~(von Fischer et al., 2009)~~. Additionally, methanotrophic activity may be inhibited by the presence of inorganic nitrogen; for example, through competition between CH_4 and ammonium (NH_4^+) for the active sites of the enzyme facilitating oxidation (Reay and Nedwell, 2004; Steudler et al., 1989)~~(Reay and Nedwell, 2004; Steudler et al., 1989)~~. However, well-drained soils may also support anaerobic processes, concurrent with oxic conditions in the bulk soil matrix, within anoxic microsites (Conrad, 1996; Sexstone et al., 1985; Teh et al., 2005)~~(Conrad, 1996; Sexstone et al., 1985; Teh et al., 2005)~~. ~~-~~These anoxi~~e microsites~~c zones form as a result of physical limitations on the rate of O_2 diffusion imposed by aggregate structure or saturation of soil pores both of which may promote the development of radial O_2 gradients around ~~these~~ occluded microsites (Burgin et al., 2011; Sexstone et al., 1985)~~(Burgin et al., 2011; Sexstone et al., 1985)~~. Where biological O_2 demand outstrips diffusional supply, these gradients can result in localise~~d~~ d anoxia within such microsites (Burgin et al., 2011; Verchot et al.,

2000)(Burgin et al., 2011; Verchot et al., 2000). Under wet conditions and high O_2 demand, anaerobic metabolic activity can be significant and potentially lead to CH_4 emissions (Silver et al., 1999; Teh et al., 2005; Verchot et al., 2000)(Silver et al., 1999; Teh et al., 2005; Verchot et al., 2000). In these environments, methanotrophy can consume the majority of CH_4 produced in-situ through the activity of low affinity communities utilising elevated CH_4 concentrations at the interface of anoxic and oxic zones (Conrad, 1996; Teh et al., 2005)(Conrad, 1996; Teh et al., 2005). Consequently, variations in net flux may be expected to result from changes in relative size and connectivity of anoxic versus oxic zones (Silver et al., 1999; Teh et al., 2005), or from competition for substrates among methanogens and other anaerobes using more energetically favourable metabolic pathways such as the reduction of nitrate (NO_3^-) (Chidthaisong and Conrad, 2000; von Fischer and Hedin, 2007; Teh et al., 2008)(Chidthaisong and Conrad, 2000; von Fischer and Hedin, 2007; Silver et al., 1999; Teh et al., 2008).

Well-drained tropical soils are estimated to account for approximately a third of the global atmospheric soil sink for CH_4 with nearly three-quarters of this uptake occurring within forest environments (Dutaur and Verchot, 2007)(Dutaur and Verchot, 2007). In Central and South America, tropical forests are expansive, covering ~35 % of the South American continent (Eva et al., 2004), and exhibiting considerable spatial and temporal variability in soil-atmosphere CH_4 exchange (Davidson et al., 2004; Keller et al., 1986, 2005; Steudler et al., 1996; Verchot et al., 2000)(Davidson et al., 2004; Eva et al., 2004; Keller et al., 1986, 2005; Steudler et al., 1996; Verchot et al., 2000). The majority of studies in the region have focussed on lowland forests below 600 m asbove sea-level (asl). Variations in the strength of the soils of these forests as a sink for atmospheric CH_4 are typically explained by the influence of soil texture and moisture on diffusion of CH_4 belowground (Dutaur and Verchot, 2007; Kiese et al., 2008; Veldkamp et al., 2013; Verchot et al., 2000). Whilst CH_4 emissions have been linked to the development of anoxic microsites in soils due to high levels of aerobic respiration, combined with periods of high water content (Verchot et al., 2000)(Dutaur and Verchot, 2007; Kiese et al., 2008; Verchot et al., 2000). Tropical montane forests are an spatially extensive component of the tropical forest of South America, accounting for ~8 % of continental (Eva et al., 2004) and ~25 % of Andean landcover (Tovar et al., 2013), and yet they are under-represented in atmospherien CH_4 budgets (Eva et al., 2004; Tovar et al., 2013). Currently, observations in the tropical Americas have been limited to Ecuador (Wolf et al., 2012), Brazil (Sousa Neto et al., 2011), Puerto Rico (Silver et al., 1999; Teh et al., 2005) and Panama (Veldkamp et al., 2013), making it difficult to predict the role of these environments in the regional CH_4 cycle.

Moreover, it is possible that controls on CH_4 flux from tropical montane forests may differ from their lowland forest counterparts. While the majority of tropical montane forests soils act as a net sinks for atmospheric CH_4 (Ishizuka et al., 2005b; Kiese et al., 2008; Purbopuspito et al., 2006; Sousa Neto et al., 2011; Veldkamp et al., 2013; Werner et al., 2006, 2007; Wolf et al., 2012)(Ishizuka et al., 2005b; Kiese et al., 2008; Purbopuspito et al., 2006; Sousa Neto et al., 2011; Veldkamp et al., 2013; Werner et al., 2006, 2007; Wolf et al., 2012), some ecosystems function as a net atmospheric source;s or fluctuate between source and sink activity (Delmas et al., 1992; von

Fischer and Hedin, 2007; Schuur et al., 2001; Silver et al., 1999; Teh et al., 2005)~~(Delmas et al., 1992; von Fischer and Hedin, 2007; Schuur et al., 2001; Silver et al., 1999; Teh et al., 2005)~~. Differences in behaviour among these environments may be partially explained by differences in underlying soil properties. The upper soil horizons of tropical montane forests typically accumulate more organic material than their lowland counterparts, leading to significant differences in the availability of labile carbon and nitrogen, and the evolution of very different soil structures (Nottingham et al., 2012; Teh et al., 2005; Zimmermann et al., 2009a)~~(Nottingham et al., 2012; Zimmermann et al., 2009a)~~. Similar contrasts exist between tropical montane forests where thick organic horizons develop (Purbopuspito et al., 2006; Wolf et al., 2012; Zimmermann et al., 2009a)~~(Purbopuspito et al., 2006)~~ and those where the superficial soils are organo-mineral in origin (Dubinsky et al., 2010; Silver et al., 1999)~~(Silver et al., 1999)~~. For example, in Ecuador~~,~~ net CH_4 uptake across a tropical montane forest altitudinal transect was better predicted by CO_2 flux, ammonium concentration and pH, ~~-~~than soil moisture and texture (Wolf et al., 2012)~~(Wolf et al., 2012)~~. Likewise, in analogous studies in Indonesia (Purbopuspito et al., 2006), Brazil (Sousa Neto et al., 2011) and Northern Australia (Kiese et al., 2008), variations in soil moisture content over time had little or no effect on ~~net~~ CH_4 uptake ~~(Kiese et al., 2008; Purbopuspito et al., 2006; Sousa Neto et al., 2011)~~. ~~-~~ This is significant given that soil moisture and texture are typically strong predictors of net CH_4 uptake in lowland ecosystems (Verchot et al., 2000)~~(Verchot et al., 2000),~~ and play an important role in mechanistic models of soil CH_4 uptake (Curry, 2007)~~(Curry, 2007)~~. In this context, evidence of nitrogen limitation of CH_4 uptake in both lowland and montane tropical forests (Hassler et al., 2015; Veldkamp et al., 2013; Wolf et al., 2012)~~(Veldkamp et al., 2013; Wolf et al., 2012)~~ or evidence that CH_4 production, driven by variations in soil O_2 concentration, can play a significant role in the CH_4 cycle of some tropical montane forests may help to explain these discrepancies (von Fischer and Hedin, 2007; Silver et al., 1999; Teh et al., 2005)~~(von Fischer and Hedin, 2007; Silver et al., 1999; Teh et al., 2005)~~.

Here we present a study of soil-atmosphere CH_4 exchange, for the period February 2011 to June 2013, from Andean upper montane, lower montane and premontane forests in south-eastern Peru that experience seasonal precipitation. A preliminary short-term dataset indicated that these forests act as a seasonably-variable sink for atmospheric CH_4 and that differences in net CH_4 flux across the transition from forest to high-altitude grassland is driven by decreases in soil O_2 concentration (Teh et al., 2014). ~~Here w~~We aim to: 1) provide an assessment of variations in soil-atmosphere CH_4 exchange among and within forest types across this landscape, based on a longer time series; and 2) investigate the drivers of CH_4 flux across ~~among~~ and within the forests of this landscape ~~types~~.

2 Materials and methods

2.1 Study plots~~sites~~

Nine plots were established along the Andes Biodiversity and Ecosystems Research Group altitudinal transect ~~Three sites at 1070 - 1088, 1532 - 1768 and 2811 - 2962 m above sea level (asl), in the south-eastern Peruvian department of Cusco~~(Malhi

et al., 2010; Teh et al., 2014) to study CH_4 exchange in ~~, were selected as they represent~~ montane and premontane forests typical of the eastern flank of the Andes. In this region premontane forest~~s~~ extends from 600 to 1200 m asl, lower montane cloud forest~~s~~ from 1200 to 2200 m asl and upper montane cloud forest~~s~~ from 2200 m asl to the tree line at 3400 m asl (Clark et al., 2014; Zimmermann et al., 2010a)~~(Clark et al., 2014; Zimmermann et al., 2010a)~~. Three montane forest plots were established between 2811 and 2962 m asl, three lower montane forest plots between 1532 and 1786 m asl and three premontane forest plots between 1070 and 1088 m asl. ~~The sites at 2811 - 2962 and 1532 - 1768 m asl representing upper and lower montane cloud forest, respectively, were situated close to the long term study sites of the Andes Biodiversity and Ecosystems Research Group (ABERG) altitudinal transect (Malhi et al., 2010). A new site was established in premontane forest at 1070 – 1088 because of difficult access at the original ABERG site at this elevation in 2010 - 2011.~~ Plot~~Site~~ characteristics are summarised in Table 1.

The regional climate is seasonal with decreased rainfall and slightly lower temperatures during the dry season between May and September, with this pattern becoming more pronounced at higher elevation (Fig. 1). Rainfall~~Precipitation~~ and ~~air~~ temperature are greater at lower elevations with total annual precipitations of 1700 and 2600 mm and mean annual air temperatures of 12.5 and 18.8 °C ~~annual means at the upper~~at ~ 3000 and ~~lower montane forest sites of~~1500 m asl, respectively~~, 1700 and 2600 mm for precipitation and 12.5 and 18.8 °C for temperature~~ (Girardin et al., 2010)~~(Girardin et al., 2010)~~. Total~~Mean~~ annual precipitation and mean annual air temperature ~~at the premontane forest~~at ~ 1000 m asl ~~site~~ are~~is~~ 5300 mm and 24.4 °C.

The soils of these forests vary with elevation, most notably the surface soils in the montane forests typically consist~~ed~~ of thick organic horizons, ~ 20 cm deep in the upper and ~ 10 cm deep in the lower ~~site~~, whilst~~,~~ those ~~in~~of the premontane forest are~~were~~ principally mineral in origin (Girardin et al., 2010; Zimmermann et al., 2009a)~~(Girardin et al., 2010; Zimmermann et al., 2009a)~~. This pattern is reflected in the carbon contents of these soils with typical values for the ~~upper~~superficial 10 cm ~~at~~in the upper and lower montane forest~~s sites~~ of 40 - 50 % C and < 5 % C in the~~at the~~ premontane forest ~~site~~ (Zimmermann et al., 2009a)~~(Zimmermann et al., 2009a)~~. These soils are acidic with ~~a~~ pH in the range of ~ 4~~< 4.0~~.

Soil-atmosphere CH_4 exchange for 2011 has previously been reported for these plots~~sites~~ as part of a study investigating non-CO_2 trace gas fluxes along an Andean altitudinal transect ~~(~~(Teh et al., 2014)~~Teh et al., 2014)~~. These measurements indicated that the CH_4 fluxes in the forests are small in comparison to source activity associated with wetlands in the montane grasslands found above the tree-line, with differences in CH_4 flux across this gradient best explained by a non-linear inverse relationship with O_2 concentration. In this analysis, the montane forests ~~sites~~ acted as sinks for atmospheric CH_4~~, whilst,~~ and the premontane forest had the potential to act as both a source or sink.

2.2 Sampling strategy

Each ~~forest type three~~ plot ~~s of~~ was 20 by 20 m and~~were~~ established approximately three months prior to the start of reported measurements in an attempt to minimise the effect~~s~~ of disturbances involved with installing sampling equipment (Varner et al., 2003)~~(Varner et al., 2003)~~. ~~Within forest types the distance between plots ranged from ~ 100 to 1000 m.~~ The premontane forest plots were ~~plots in the premontane forest were each~~ situated on a ridge, slope and flat at 1070, ~~slope~~ 1070 ~~and flat feature~~ and 1088 m asl, respectively. ~~between elevations of 1070 to 1088 m asl.~~ Similarly, the lower montane forest plots were established on a ridge, slope and flat at 1768, ~~slope~~, 1532 ~~and flat~~ and 1532 m asl, respectively. ~~features between elevations of 1532 to 1768 m asl.~~ ~~In the~~Two of the upper montane forest plots ~~two plots~~ were situated on slopes at 2811 and 2962 m asl and the third on a ridge at ~~elevations between 2811 to 2962~~2962 m asl. The plots all broadly fall along the same lowland to highland transition, however, they were treated as independent measurements as spatial auto-correlation of CH_4 exchange in tropical forests is small and the plots were more than 100 m apart (Ishizuka et al., 2005a; Purbopuspito et al., 2006).

Within each plot five soil collars were installed to allow for measurements of soil-atmosphere gas exchange using a static flux chamber method. Additionally, soil-gas equilibration chambers were buried at 10 cm adjacent to three collars in each plot to allow measurement of soil O_2 concentrations. From September 2011 onwards, five ion exchange resin bags were buried in the upper 10 cm of each plot, adjacent to soil collars, to allow measurement of available inorganic ammonium (NH_4^+) and nitrate (NO_3^-). ~~Despite the three plots within each forest type broadly occurring within the same forest stand they were considered independent replicates of forest type as spatial correlations between net CH_4 fluxes in tropical forests are small (Ishizuka et al., 2005a; Purbopuspito et al., 2006).~~

Plots were visited monthly to measure soil-atmosphere gas exchange at each collar, and soil moisture and temperature adjacent to each collar, together with soil O_2 concentration in each soil-gas equilibration chamber. Resin bags were also collected and replaced with new bags during these visits. These data were aggregated to produce monthly plot means of the measured variables. In the upper and lower montane forests, measurements ran from February 2011 to June 2013. In the premontane forest measurements ran from July 2011 to June 2013. No data are available for these plots ~~of this site~~ in October or December of 2011 and February, July or December of 2012 as high river levels prevented access.

2.3 Soil-atmosphere gas exchange

Net soil-atmosphere fluxes of CH_4 and CO_2, were determined using a static chamber method (Livingston and Hutchinston, 1995)~~(Livingston and Hutchinston, 1995)~~. Measurements were initiated by gently sealing cylindrical caps, using a section of

inner-tube, to pre-installed soil collars to create a chamber of ~ 0.08 m^3 over a soil surface area of ~ 0.03 m^2. Soil collars had a diameter of 20 cm and were inserted to a depth of ~ 5 cm. Each cap was equipped with a gas sampling port, a vent and a 9 V computer fan (Hutchinson and Mosier, 1981; Pumpanen et al., 2004)~~(Hutchinson and Mosier, 1981; Pumpanen et al., 2004)~~. Using a stopcock and 60 ml gas tight syringe, 20 ml gas samples were taken from the chambers at four discrete time steps over a period of ~ 30 min. Additionally, air temperature and atmospheric pressure were measured using a type K thermocouple (Omega Engineering Ltd., UK~~.~~) and a Garmin GPSmap 60CSx (Garmin Ltd.,USA). Gas samples were stored in over-pressured, pre-evacuated 12 ml Exetainers (Labco Ltd., UK) and concentrations of CH_4 and CO_2 were determined by gas chromatography. Gas chromatography was conducted using a Thermo TRACE GC Ultra (Thermo Fisher Scientific Inc., USA) with a helium carrier gas at the University of St Andrews. A flame ionization detector (FID) and methanizer-FID were used to determine CH_4 and CO_2 concentrations, respectively. Analytes were separated using a Hayesep Q 100/200 column. The gas chromatograph was equipped with a 2 ml sample loop and oven temperature was 60 °C. Detector responses were calibrated using three certified gas standards (CK Gas Products Ltd., UK: 1.8, 9.8 and 99.5 ppmv CH_4) and instrumental precision was deemed acceptable when coefficient of variances < 5 % were achieved. A custom-built auto-sampler (University of York, UK) was used to introduce gas samples directly into the sample loop.

Fluxes, in µl l^{-1} m^{-2} s^{-1}, were calculated in R (R Core Team, 2013)~~(R Core Team, 2013)~~ using the HMR package (Pedersen, 2012)~~(Pedersen, 2012)~~. Following the criteria outlined by Pedersen et al. (2010)~~(2010)~~, HMR or linear models were fitted to time-series of concentration in chamber headspaces. Significance was determined at the $p < 0.05$ level with emission and uptake indicated by positive and negative flux values, respectively. Non-significant fluxes were excluded from further analysis. Fluxes were converted from a concentration to amount basis reported in mg C m^{-2} d^{-1} of CH_4 and g C m^{-2} d^{-1} of CO_2, following the ideal gas law, using measurements of air temperature and ambient pressure.

2.4 Soil environmental conditions

Soil O_2 concentration was measured from soil gas equilibration chambers buried at 10 cm below the soil surface (Hall et al., 2013; Liptzin et al., 2011; Silver et al., 1999; Teh et al., 2005)~~(Hall et al., 2013; Liptzin et al., 2011; Silver et al., 1999; Teh et al., 2005)~~. Soil O_2 concentration was determined by withdrawing 40 ml of gas from a soil-gas equilibration chamber using a stopcock and gas tight syringe. The sample was then passed through the flow-through head of an MO-200 oxygen sensor (Apogee Instruments Inc., USA) into a second syringe. The O_2 reading was recorded at a constant volume and the gas sample re-injected into the soil-gas equilibration chamber from the second syringe. Prior to measurements the O_2 sensor was calibrated, as required, in the field with ambient air and the dead volumes of the sampling apparatus evacuated to minimise contamination of the soil gas sample by residual atmospheric air. Chambers had an internal volume of 50 ml and a surface area of 75 cm^2. Each consisted of a length of gas-permeable silicone rubber tubing (AP202/60 - 35 mm inner diameter by 1.5 mm wall, Advanced Polymers Ltd, UK) sealed at both ends with butyl rubber bungs. A suitable length of silicone tubing was passed through a hole in one of the bungs and capped with a stopcock to allow sampling at the surface. Chambers were

encased in plastic mesh to protect the membrane during installation. Typical of similar designs, soil gas equilibration chambers were capable of equilibrating with the external atmosphere in less than 24 h (Holter, 1990; Jacinthe and Dick, 1996; Kammann et al., 2001)~~(Holter, 1990; Jacinthe and Dick, 1996; Kammann et al., 2001)~~.

Soil volumetric water content was determined from triplicate measurements in the upper 6 cm of soil using a ML2x ThetaProbe (Delta-T Ltd., UK). Water-filled pore space (WFPS) was calculated from these data using estimates of porosity in the upper 10 cm based on plot averaged bulk density and forest type~~site~~ averaged particle density measurements (Table 1). Plot bulk densities were determined from the weight of volumetric soil samples after oven drying at 105 °C for 24 hours. Forest type particle density was determined from measurement of bulked plot samples using a 10 ml pyncometer (Klute and others, 1986). Soil temperature was determined from triplicate measurements at 5 cm using a type K thermocouple penetration probe (Omega Engineering Ltd., UK).

Available inorganic ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were determined from resin bags buried in the the upper 10 cm of soil ~~((~~(Giblin et al., 1994; Templer et al., 2005)~~Giblin et al., 1994; Templer et al., 2005)~~. Each resin bag consisted of 5 g of ion exchange resin (Dowex Marathon MR-3, Sigma Aldrich, UK) encased in a lycra bag. Resin bags were collected and replaced with a new bag during each plot visit. Following Templer et al. ~~((~~(Templer et al., 2005)~~2005)~~, inorganic nitrogen was extracted from collected resin bags using 2 N KCL and it's concentration determined colorimetrically using a Burkard SFA2 (Burkard Scientific Ltd., Uxbridge, UK) continuous flow analyser at the University of Aberdeen. ~~Reported a~~Available inorganic NH_4^+ and NO_3^- concentrations ~~are~~were normalised to the amount of resin from which they were extracted and their deployment period, and reported as μg NH_4^+ - N g^{-1} resin d^{-1} and μg NO_3^- - N g^{-1} resin d^{-1}.

2.5 Statistical analyses

Statistical analysis was conducted in R version 3.1.1 (R Core Team, 2013)~~(R Core Team, 2013)~~. Linear mixed effect models were used to test the influence of forest type and season on measured variables as the dataset is unbalanced, with fewer measurements in the premontane forest, and nested within sampling month across plots~~forest types and in replicate plots within forest type~~ (Pinheiro and Bates, 2000)~~(Pinheiro and Bates, 2000)~~. In this respect, random intercept linear mixed effect models computed using the NLME package were used to test the effect of forest type and season on monthly plot means of net CH_4 flux, CO_2 flux, soil O_2 concentration, WFPS, soil temperature, available NH_4^+ and available NO_3^- with forest type and season as fixed effects and sampling month and year as a random effect (Pinheiro et al., 2014)~~(Pinheiro et al., 2014)~~. Following model fits, multiple comparison of forest type~~site~~ and season was conducted in the multcomp package with Tukey contrasts (Hothorn et al., 2008)~~(Hothorn et al., 2008)~~. Time-series of monthly plot means for these variables are provided in Fig. S1 to S7 of the supplementary material. Spatial and temporal relationships between measured variables were investigated using Pearson's correlation coefficient in the Hmisc package (Harrell et al., 2015)~~(Harrell et al., 2015)~~. Spatial correlations were tested on dataset plot means whilst temporal correlations were ~~applied~~tested ~~to~~on monthly ~~site~~forest type

means calculated, in both cases, from monthly plot means. The validity of parametric tests was confirmed through visual inspection of residuals and as a result available NH_4^+ and available NO_3^+ were square root transformed in all reported statistical analyses to reduce heteroscedacity (Zuur et al., 2007)~~(Zuur et al., 2007)~~. Statistical significance is reported at $p < 0.05$ unless stated otherwise.

3 Results

3.1 Variability in gas fluxes and soil environmental conditions

Fluxes of CH_4 were ~~significantly~~ influenced by forest type with greater uptake~~larger fluxes~~ at ~~lower~~higher elevations (Table 2). All the forest types acted as a net sink for atmospheric CH_4 with mean (standard error) net CH_4 fluxes for dry and wet season of -1.6 (0.1) and -1.1 (0.1) mg CH_4 - C m^{-2} d^{-1} in the upper montane forest, -1.1 (0.1) and -1.0 (0.1) mg CH_4 - C m^{-2} d^{-1} in the lower montane forest and -0.2 (0.1) and -0.1 (0.1) mg CH_4 - C m^{-2} d^{-1} in the premontane forest. During the dry season, net CH_4 fluxes varied ~~significantly~~ among all forest types. During the wet season, ~~net~~ CH_4 uptake~~fluxes~~ was smaller in the~~from~~ premontane forest ~~were significantly larger~~ than in~~those from~~ both the upper and lower montane forests. Within forest types, no ~~significant~~ differences were identified between the dry and wet seasons when data from all time points were aggregated together. However, monthly time-series from the upper montane forest indicate seasonal variability of exchange ~~at this site~~, with a modest shift towards greater ~~more negative~~ CH_4 uptake ~~fluxes~~ with the progression of the dry season (Fig. 2 a). Uptake dominated soil-atmosphere exchange in the upper and lower montane forests with emissions accounting for only 1 and 2 % of monthly mean CH_4 fluxes, respectively. In contrast, whilst also a net sink for atmospheric CH_4 ~~uptake was also evident~~, ~~CH_4~~ emissions were more common in the premontane forest with 29 % of fluxes registering net CH_4 efflux.

Fluxes of CO_2 were ~~significantly~~ influenced by forest type with larger fluxes at lower elevations (Table 2). Fluxes of CO_2 for aggregated dry and wet season months were 2.9 (0.3) and 4.0 (0.3) g CO_2 - C m^{-2} d^{-1} in the upper montane forest, 4.3 (0.3) and 4.1 (0.3) g CO_2 - C m^{-2} d^{-1} in the lower montane forest and 5.2 (0.3) and 5.1 (0.3) g CO_2 - C m^{-2} d^{-1} in the premontane forest (Fig. 2 b). Dry season CO_2 fluxes were ~~significantly~~ smaller in the upper montane forest than both the premontane forests, whilst, during the wet season no ~~significant~~ differences were identified. Within forest types, there were no ~~significant~~ seasonal differences in CO_2 flux but some evidence of wet season increases from the upper montane forest is apparent in the monthly time-series (Fig. 2 b).

Soil O_2 concentration at 10 cm soil depth was ~~significantly~~ influenced by forest type with slightly greater concentrations at lower elevation (Table 2). Soil O_2 concentrations for aggregated dry and wet season months were 18.6 (0.3) and 18.9 (0.2) % in the upper montane forest, 19.1 (0.3) and 19.2 (0.2) % in the lower montane forest and 19.7 (0.3) and 19.8 (0.3) % in the premontane forest (Fig. 2 c). In both wet and dry season, soil O_2 concentration was ~~significantly~~ smaller in the upper montane than the premontane forest. However, these differences were marginal with a range of 1.1 %. Within forest types no

~~significant~~ differences in soil O_2 concentration between seasons were identified and little temporal variability is apparent in the monthly time-series (Fig. 2 c).

WFPS was ~~significantly~~ influenced by forest type and its interaction with season, with greater saturation at lower elevation and during the wet season (Table 2). Mean WFPS for aggregated dry and wet season months was 24.4 (2.0) and 43.7 (1.7) % in the upper montane forest, 35.4 (2.0) and 44.8 (1.7) % in the lower montane forest and 50.9 (2.1) and 53.3 (1.9) % in the premontane forest. Dry season WFPS was ~~significantly~~ different between all forest types~~; whilst d~~ During the wet season WFPS in the premontane forest was ~~significantly~~ greater than those from both the upper and lower montane forests. Within forest types, WFPS was ~~significantly~~ greater for wet than dry season for both the upper and lower montane forests as characterised by strong seasonality apparent in the monthly time-series for these forests~~sites~~ (Fig. 2 d).

Soil temperature was ~~significantly~~ influenced by forest type and its interaction with season, with greater temperatures at lower elevation and during the wet season (Table 2). Mean soil temperature for aggregated dry and wet season months was 11.0 (0.2) and 11.9 (0.1) °C in the upper montane forest, 17.3 (0.2) and 18.0 (0.1) °C in the lower montane forest and 20.4 (0.2) and 20.7 (0.2) °C in the premontane forest (Fig. 2 e). In both seasons, soil temperatures were ~~significantly~~ different between all forest types. Within forest types, soil temperatures were ~~significantly~~ greater during the wet than dry season in both the upper and lower montane forests (Fig. 2 e).

Variation in the availability of inorganic nitrogen differed between compounds~~species~~ (Fig. 3). Available NH_4^+ was not ~~significantly~~ influenced by forest type or season (Table 2). Mean aggregated dry and wet season concentrations ranged from 7.8 to 10.8 µg NH_4^+ - N g^{-1} resin d^{-1} and 14.8 to 18.6 µg NH_4^+ - N g^{-1} resin d^{-1}, respectively. In contrast, available NO_3^- was ~~significantly~~ influenced by forest type with greater availability at lower elevations (Table 2). Mean available NO_3^- for aggregated dry and wet season months was 0.4 (0.1) and 1.1 (0.0) µg NO_3^- - N g^{-1} resin d^{-1} in the upper montane forest, 6.4 (0.1) and 9.6 (0.1) 21.0 (0.1) µg NO_3^- - N g^{-1} resin d^{-1} in the lower montane forest and 21.0 (0.1) and 21.2 (0.1) µg NO_3^- - N g^{-1} resin d^{-1} in the premontane forest. Available NO_3^- was ~~significantly~~ different between all forest types with no seasonal~~significant~~ differences ~~between season~~, in part due to considerable within plot variability, within forest type.

3.2 Spatial relationships between gas fluxes and environmental conditions

Across these forest~~s types~~, plot means of net CH_4 flux were ~~significantly~~ negatively correlated with elevation (Pearson's r = -0.81, p < 0.01, n = 9) ~~and ,~~ soil porosity (Pearson's r = -0.72, p = 0.03, n = 9) and plot means of CO_2 flux (Pearson's r = -0.61, p = 0.08, n = 9 (Table 3). ~~Similarly, the p~~Plot means of net CH_4 flux w~~as~~ere ~~significantly~~ positively correlated with the plot means of WFPS (Pearson's r = 0.84, p < 0.01, n = 9), soil temperature (Pearson's r = 0.83, p < 0.01, n = 9) and soil O_2 concentration (Pearson's r = 0.73, p = 0.03, n = 9), available NH_4^+ (Pearson's r = 0.71, p = 0.03, n = 9) and available NO_3^- (Pearson's r = 0.88, p = < 0.01, n = 9), respectively. ~~There was no significant relationship between the plot mean of net CH_4~~

~~flux and the plot mean of CO_2 flux (Pearson's r = - 0.61, p = 0.08, n = 9).~~ ~~Significant~~Notable co-correlations exist between the plot means of many measured environmental variables. For example, strong correlations (i.e. $p < 0.01$) exist between plot means of net CH_4 flux and elevation, WFPS, soil temperature and available NO_3^- ~~(Fig. 4)~~. However, both WFPS (Pearson's r = -0.79, p = 0.01, n = 9) and available NO_3^- ~~soil temperature~~ (Pearson's r = -0.94, $p < 0.01$, n = 9) are significantly negatively correlated with elevation and are also significantly positively correlated with each other (Pearson's r = 0.~~8394~~, p ~~<=~~ 0.01, n ~~=<~~ 9).

3.3 Temporal relationships between gas fluxes and environmental conditions

The drivers of temporal variability in net CH_4 flux varied among~~within~~ forest types. ~~For example, I~~in the upper montane forest, monthly ~~site~~forest type mean net CH_4 flux was ~~significantly~~ positively correlated with WFPS (Pearson's r = 0.54, p < 0.01, n = 28) and soil temperature (Pearson's r = 0.52 , $p < 0.01$, n = 27). Similarly to spatial co-correlations observed across forest types, monthly ~~site~~forest type means of WFPS and soil temperature (Pearson's r = 0.60, $p < 0.01$, n = 27) were positively correlated with each other in the upper montane forest. In contrast, ~~in the lower montane forest,~~ monthly ~~site~~forest type mean net CH_4 flux was ~~significantly~~ negatively correlated with CO_2 flux (Pearson's r = -0.70, $p < 0.01$, n = 29) in the lower montane forest. Whilst~~,~~ in the premontane forest, n~~o significant~~o strong correlations between monthly ~~site~~forest type mean net CH_4 flux and other measured variables were identified (Table 4). ~~For example, the~~ Here the strongest relationship with net CH_4 flux was a positive correlation with monthly ~~site~~forest type mean WFPS (Pearson's r = 0.33, p = 0.16, n = 19).

4 Discussion

4.1 Uptake of CH_4 by Andean forest soils in southern Peru

Upper montane, lower montane and premontane forests in the southern tropical Andes of Peru principally acted as sinks for atmospheric CH_4 (Fig. 2 a). Seasonal mean net CH_4 fluxes from these soils ranged from -1.6 to -0.1 mg CH_4 - C m^{-2} d^{-1} (Table 2), indicating that soil-atmosphere CH_4 exchange in these forests ~~are~~is comparable to those previously reported ~~for these sites~~ and in similar environments elsewhere. The major difference between the exchange rates reported here and the preliminary analysis of these data by Teh et al. (2014)~~(2014)~~ is that the longer time-series indicates that these premontane forests act as a net sink rather than source of atmospheric CH_4 during the wet season. Reported mean net CH_4 fluxes for tropical forest soils above 600 m asl range from -1.6 to -0.2 mg CH_4 - C m^{-2} d^{-1} for the northern Andes in Ecuador (Wolf et al., 2012)~~(Wolf et al., 2012)~~, -0.9 to -0.2 mg CH_4 - C m^{-2} d^{-1} for central Sumatra and Sulawesi in Indonesia (Ishizuka et al., 2005b; Purbopuspito et al., 2006)~~(Ishizuka et al., 2005b; Purbopuspito et al., 2006)~~, -0.1 to 0.0 mg CH_4 - C m^{-2} d^{-1} for Mayombe highlands in the Republic of Congo (Delmas et al., 1992)~~(Delmas et al., 1992)~~, -0.7 mg CH_4 - C m^{-2} d^{-1} for a tableland in northern Australia (Kiese et al., 2008)~~(Kiese et al., 2008)~~, -1.4 mg CH_4 - C m^{-2} d^{-1} in Kenya (Werner et al., 2007)~~(Werner et al., 2007)~~, -0.5 mg CH_4 - C m^{-2} d^{-1} in China (Werner et al., 2006)~~(Werner et al., 2006)~~, -0.1 mg CH_4 - C m^{-2} d^{-1} in Panama (Veldkamp et al., 2013) ~~(Veldkamp et al., 2013)~~ and -1.2 mg CH_4 - C m^{-2} d^{-1} for Atlantic forest in Brazil (Sousa Neto et al., 2011)~~(Sousa Neto et al.,~~

2011). Similarly, mean soil-atmosphere CH_4 exchange rates for lowland tropical forests in South America have been reported in the range of -1.4 to -0.1 mg CH_4 - C m^{-2} d^{-1} (Davidson et al., 2008; Fernandes et al., 2002; Keller et al., 1986, 2005; Sousa Neto et al., 2011; Steudler et al., 1996; Verchot et al., 2000)(Davidson et al., 2004, 2008; Fernandes et al., 2002; Keller et al., 1986, 2005; Sousa Neto et al., 2011; Steudler et al., 1996; Verchot et al., 2000).

Within forest types, net CH_4 fluxes were not significantly different between wet and dry season when data were aggregated together by season, indicating that these forests show little overall seasonal variability in net CH_4 uptake (Table 2). The only exception to this was the However, the time-series of net CH_4 flux (Fig. 2 a) for the **upper** montane forest does suggest that, where we see a strengthening of net CH_4 uptake increases with the procession of the dry season; ultimately equating to a ~ 30 % differenceecrease in net CH_4 uptake between dry and wet season. Our inability to detect a statistically significant difference between seasons at this site(Table 2) may reflect interannual variability, and the fact that environmental conditions change gradually across seasonal transitions (Clark et al., 2014)(Clark et al., 2014). The aseasonality inof CH_4 exchange in the lower montane and premontane forests conforms with observations from tropical montane forests in Ecuador and Indonesia with aseasonal climates (Purbopuspito et al., 2006; Wolf et al., 2012), while the behaviour of the upper montane forests appears more similar to that of lowland tropical forests with seasonal climates (Davidson et al., 2008; Keller et al., 2005; Verchot et al., 2000)(Davidson et al., 2008; Keller et al., 2005; Purbopuspito et al., 2006; Verchot et al., 2000; Wolf et al., 2012). This may impart reflect the fact that seasonal variations in rainfall and temperature become more pronounced with elevation across this transect (Fig. 1).This contrast between the upper montane forest on one hand, and lower montane and premontane forest on the other, may reflect a threshold associated with edaphic conditions and decreases in total precipitation and temperature with elevation across our transect.

We did not observe notable spatial or temporal hotspots of CH_4 emission in these forests, contrasting with observations from regions such as the Caribbean and Hawaii (Schuur et al., 2001; Silver et al., 1999; Teh et al., 2005)(Schuur et al., 2001; Silver et al., 1999; Teh et al., 2005). For example, Silver et al. (1999)(1999) report mean net CH_4 fluxes of 0.2 to 73.2 mg CH_4 - C m^{-2} d^{-1} from montane ecosystems in Puerto Rico. Indeed, emissions represented only 1 – 2 % of fluxes souree activity in the upper and lower montane forests of this study represented only 1 - 2 % of fluxes. Emissions were more prevalent in the premontane forest, accounting for 29 % of fluxes, suggesting that emission hotspots are possible in these soils but may not have been captured by our sampling strategy (Delmas et al., 1992; Silver et al., 1999)(Davidson et al., 2004; Delmas et al., 1992; Silver et al., 1999). Assessing and studying the potential for emissions from these ecosystems is likely to require higher resolution observations to capture spatial and temporal variability (Liptzin et al., 2011; Silver et al., 1999) combined with experimental manipulations (Hall et al., 2013) and a better understanding of below-ground CH_4 cycling (von Fischer and Hedin, 2007; Teh et al., 2005).

4.2 Environmental controls on net CH_4 fluxes in tropical Andean forests of southern Peru

The increase ~~decrease~~ in ~~net~~ CH_4 uptake~~flux~~ with elevation across the transect was~~is~~ strongly related to decreases in available NO_3^-, WFPS and soil temperature (Fig. 4). As there is considerable covariance between these environmental conditions (Table 3) a number of plausible, but confounded, mechanisms may explain why CH_4 uptake was~~is~~ greatest in the upper montane forest and smallest in the premontane forest ~~(Table 3)~~. The predominance of CH_4 uptake and the lack of evidence for widespread anoxia, with soil O_2 measurements typically in excess of 15 % (Fig. 2 c), indicates that net CH_4 exchange was~~is~~ dominated by the activity of high affinity methanotrophs which are unlikely to be sensitive to O_2 availability (Bender and Conrad, 1992; Teh et al., 2006)~~(Bender and Conrad, 1992; Teh et al., 2006)~~. Indeed, unlike studies where landscapes exhibiting net source activity are considered we di~~d~~e not find evidence that decreases in O_2 concentration were~~are~~ driving ~~net~~ CH_4 exchange (Silver et al., 1999; Teh et al., 2014)~~(Silver et al., 1999; Teh et al., 2014)~~. The positive relationship between available NO_3^+ and net CH_4 flux (Fig. 4 b) may suggest that CH_4 uptake was~~is~~ inhibited by NO_3^-. This observation supports previous, albeit poorly understood, observations that CH_4 oxidation is more sensitive to the presence of NO_3^- rather than NH_4^+ (Mochizuki et al., 2012; Reay and Nedwell, 2004)~~(Mochizuki et al., 2012; Reay and Nedwell, 2004)~~. Interestingly, this negative relationship between CH_4 uptake and NO_3^- is the reverse of that observed across a similar transect in the Ecuadorian Andes (Wolf et al., 2012)~~(Wolf et al., 2012)~~. The positive relationship between net CH_4 flux and WFPS (Fig. 4 d) across forest ~~type~~plots conforms to the expectation that high-affinity methanotrophs are limited by CH_4 supply in response to diffusional constraints imposed by soil structure and water content (Curry, 2007; von Fischer et al., 2009; Smith et al., 2003) ~~(Curry, 2007; von Fischer et al., 2009; Smith et al., 2003)~~. Notably, this relationship appears to ~~be underpinned~~be driven by decreased ~~dissimilarities~~ ~~in~~ WFPS and increased ~~net~~ CH_4 uptake ~~flux~~ in the ~~across the~~ upper ~~and lower~~ montane forest plot~~s~~ during the dry season. The importance of such spatial relationships between soil-atmosphere CH_4 exchange and WFPS have previously been highlighted for lowland tropical soils (Verchot et al., 2000) and across the plots~~sites~~ considered here (Teh et al., 2014) but not in studies across other montane forests, where gravimetric water contents rather than WFPS have been reported (Purbopuspito et al., 2006; Wolf et al., 2012)~~(Purbopuspito et al., 2006; Teh et al., 2014; Verchot et al., 2000; Wolf et al., 2012)~~. A positive relationship between net CH_4 flux and soil temperature (Fig. 4 c) was also identified. Given that we would expect metabolic rates to increase rather than decrease in response to increased temperature, we suggest that this relationship results from covariance between soil temperature (Table 3) and available NO_3^- or WFPS with elevation (Sousa Neto et al., 2011)~~(Sousa Neto et al., 2011)~~. ~~-~~Alternatively~~,~~ if methanogenic activity, despite limited evidence for anoxia, was~~is~~ playing a sizeable role in determining net CH_4 flux across these forests this relationship could reflect the greater temperature sensitivity of methanogenesis relative to methanotrophy, leading to increased production at lower elevations (Segers, 1998)~~(Segers, 1998)~~. Similarly, in this situation~~,~~ the positive relationship between WFPS and net CH_4 flux could reflect the promotion of anoxic microsites, not captured by our O_2 measurements, by greater diffusional constraints (Verchot et al., 2000)~~(Verchot et al., 2000)~~. However, ~~counter to our observations~~ we may also have expected increases in available NO_3^- to competitively suppress methanogenic activity (Chidthaisong and Conrad, 2000)~~(Chidthaisong and Conrad, 2000)~~.

This is counter to the observation that net CH_4 flux is positively correlated to available NO_3^- and that emissions are most prevalent in the premontane forest. Greater below-ground productivity at lower elevations (Girardin et al., 2010), potentially driven by greater nutrient availability and temperature, may also stimulate CH_4 production in the rhizosphere through the supply of labile substrates to methanogenic communities or maintenance of anaerobic microsites through the O_2 demand of aerobic respiration (Bodelier, 2011). Such a mechanism, not observed in this data, might be supported by a positive relationship between net CH_4 and CO_2 fluxes (Verchot et al., 2000).

The controls on temporal variations in net CH_4 flux differed among~~within~~ forests ~~types in net CH_4 flux differed among forests~~. As with the comparison across these forests ~~types~~, we found~~ind~~ little evidence to suggest that ~~support for~~ soil O_2 concentration was ~~as~~ an important factor in determining variability in soil-atmosphere~~net~~ CH_4 exchange~~fluxes~~. In the upper montane forest, net CH_4 fluxes were best explained by a positive correlation with WFPS (Table 4), indicating that wet season increases in soil moisture act to limit the diffusion of CH_4 to methanotrophic communities ~~(Table 4)~~. Similar~~ly~~ to spatial relationships observed across these forests, a strong positive relationship between temporal variations in net CH_4 flux and soil temperature was also observed ~~for this site,~~ presumably because of covariance, with wetter and~~,~~ warmer conditions from October to April (Fig. 1), between WFPS and soil temperature. Interestingly, the positive correlation between net CO_2 flux and WFPS (Table 4) ~~at this site~~ suggests that soil respiration, but not CH_4 uptake, may be water limited during the dry season. Given the importance of the contribution of root and litter respiration to total soil respiration in these~~is~~ forests this may reflect differences in the sensitivity of the communities involved; for example, microbial communities in the litter may experience greater water limitations than those in the soil (Zimmermann et al., 2009b, 2010b)~~(Zimmermann et al., 2009b, 2010b)~~. In the lower montane forest, increased~~increases in net~~ CH_4 ~~flux~~uptake was~~were~~ related to increased~~decreases in~~ CO_2 flux (Table 4) indicating that conditions favourable for methanotrophy may be similar to those for general soil respiration (Purbopuspito et al., 2006; Wolf et al., 2012)~~(Purbopuspito et al., 2006; Wolf et al., 2012)~~. Significant differences in WFPS between the wet and dry season (Table 2) were not reflected in net CH_4 fluxes from these soils suggesting these variations were not great enough to sufficiently limit diffusion of CH_4 as to constrain uptake rates. In the premontane forest no strong drivers of net CH_4 flux were identified~~able~~ potentially reflecting fewer observations ~~from this site~~, the greater apparent role of production within microsites and the ~~apparent~~ lack of seasonality in any of the measured parameters ~~(~~(Purbopuspito et al., 2006; Sousa Neto et al., 2011; Wolf et al., 2012)~~Purbopuspito et al., 2006; Sousa Neto et al., 2011; Wolf et al., 2012)~~.

4.3 Altitudinal trends in soil CH_4 cycling across tropical montane forests

With the exception of strong source activity in some island settings, rates of CH_4 uptake by tropical montane forest soils are broadly comparable across tropical montane and lowland locations globally. However~~, within montane regions,~~ the relationship between soil-atmosphere CH_4 exchange and elevation is poorly understood within montane regions~~constrained (Table 5)~~. For example, differing patterns in soil-atmosphere CH_4 exchange are reported here compared to that of altitudinal transects in Ecuador (Wolf et al., 2012)~~(Wolf et al., 2012)~~ or Indonesia (Purbopuspito et al., 2006)~~(Purbopuspito et al., 2006)~~.

The relationship between elevation and edaphic conditions is broadly similar for these studies (Table 5) with upper montane, lower montane and premontane forests occurring acrosswithin similar similar elevation bandsranges (Foster, 2001)(Foster, 2001). In this respect, The soils of the montane and premontane forests in these three soils in these studies are differentiated from those of the premontane forests by the presence of thick organic horizons at the surface. Despite this similarity, differing relationships between net CH_4 flux and elevation are apparent for the soils of Peru and Ecuador, with the former showing greatest uptake in the upper montane soils, while the latter shows greatest uptake in premontane soils (Wolf et al., 2012)(Wolf et al., 2012). Furthermore, uptake peaked in the lower montane soils in Indonesia (Purbopuspito et al., 2006) (Purbopuspito et al., 2006). From these contrasts, it is possible to suggest that relationships with temperature identified here, as discussed with reference to spatial correlations across the Peruvian transect in the previous section, and in Ecuador (Wolf et al., 2012), as previously discussed, result from covariance with some other drivers like soil moisture or nutrient availability rather than as a result of the temperature sensitivity of CH_4 uptake (Wolf et al., 2012). Similarly, differing relationships between net CH_4 fluxes and the availability of inorganic nitrogen do not allow for simple generalisations to be drawn across these ecosystems. For example, In this study, a positive relationship between net CH_4 flux and available NO_3^- suggests inhibition of uptake,; whilste in Ecuador, a negative relationship between these parameters led Wolf (2012)(2012) to hypothesize that uptake in Ecuador wasis nitrogen limited. In contrast to both of these Andean studies, no relationship was identified in Indonesia (Purbopuspito et al., 2006)(Purbopuspito et al., 2006). We speculate that the inverse altitudinal patterns in soil-atmosphere CH_4 exchange in Peru and Ecuador may be driven byreflect differences in their precipitation regimes and the influence of soil structure and water content on diffusion. Increased WFPS, a function of decreasing soil porosity and increasing precipitation across the transition from upper montane to premontane forests, appears to limit CH_4 uptake in Peru through diffusional constraints on the supply of CH_4 to methanotrophic communities. Whilst a similar pattern in soil porosity with elevation can be inferred from the presence organic horizons in montane forests studied in Ecuador (Wolf et al., 2012), the alignment between increasing precipitation and decreasing CH_4 uptake across this transect might suggest that diffusional constraints, in response to changes in soil moisture, might provide a generalised explanation for the patterns observed. Indeed, Veldkamp et al. (2013) invoke gas diffusional control to explain positive correlation between net annual CH_4 fluxes and rainfall in a meta-analysis of 7 tropical forests above 800 m elevation. Such a mechanism is supported by the positive relationship between net CH_4 flux and WFPS in this study. The fact that no relationship between net CH_4 flux and water content werewas identified in either Ecuador (Wolf et al., 2012) or Indonesia (Purbopuspito et al., 2006) may reflect the fact that both of these studies reportmeasured gravimetric water content rather than WFPSwater-filled pore space, where the former moisture index does not always adequately characterise the influence of soil structure on diffusion (Verchot et al., 2000) (Purbopuspito et al., 2006; Verchot et al., 2000; Wolf et al., 2012). Wolf et al. (2012)(2012) highlight that organic horizons of these montane forests are active zones of methanotrophy. It seems likely that a better understanding of the edaphic controls, relating soil structure and precipitation, on methanotrophy in such soils is required to reconcile differences in soil atmosphere CH_4 exchange across such landscapes.

5 Conclusion

The findings of this study suggest that the upper montane, lower montane and premontane forests of south-eastern Peru principally act as sinks for atmospheric CH_4. Uptake rates in these soils are comparable to activity observed globally for both montane and lowland tropical forests. Uptake rates were greatest in the upper montane forest and lowest in the premontane forest. We find that across the landscape, these soils are predominantly oxic and soil CH_4 cycling is likely dominated by the activity of high affinity methanotrophs. In this regard, strong positive relationships between net CH_4 flux and both available NO_3^- and WFPS were identified suggesting that variations in CH_4 uptake across the landscape may be driven by NO_3^- inhibition and/or constraints on the diffusional ingress of CH_4 from the atmosphere. Despite distinct wet and dry seasons in this region, evidence for seasonality in net CH_4 fluxes were only identified in the upper montane forest soils. The increase in CH_4 uptake with elevation differs with that previously reported for similar environments in Ecuador and Indonesia, suggesting that an improved understanding of the controls on methanotrophy in the organic horizons of tropical montane forest soils are required.

Data Availability

The reported datasets (doi: X, X & X) have been deposited with the Centre for Enviromental Data Analysis, UK Natural Environmental Research Council (www.ceda.ac.uk).

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References

Bender, M. and Conrad, R.: Kinetics of methane oxidation in oxic soils exposed to ambient air or high methane mixing ratios, FEMS Microbiology Letters, 101(4), 261–269, 1992.

Bergamaschi, P., Frankenberg, C., Meirink, J. F., Krol, M., Villani, M. G., Houweling, S., Dentener, F., Dlugokencky, E. J., Miller, J. B., Gatti, L. V. and others: Inverse modeling of global and regional methane emissions using SCIAMACHY satellite retrievals, Journal of Geophysical Research: Atmospheres (1984–2012), 114(D22), doi:10.1029/2009JD012287, 2009.

Bloom, A. A., Palmer, P. I., Fraser, A., Reay, D. S. and Frankenberg, C.: Large-scale controls of methanogenesis inferred from methane and gravity spaceborne data, Science, 327(5963), 322–325, 2010.

Burgin, A. J., Yang, W. H., Hamilton, S. K. and Silver, W. L.: Beyond carbon and nitrogen: how the microbial energy economy couples elemental cycles in diverse ecosystems, Frontiers in Ecology and the Environment, 9(1), 44–52, 2011.

Chidthaisong, A. and Conrad, R.: Turnover of glucose and acetate coupled to reduction of nitrate, ferric iron and sulfate and to methanogenesis in anoxic rice field soil, FEMS Microbiology Ecology, 31(1), 73–86, 2000.

Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., Jones, C., Le Quéré, C., Myneni, R. B., Piao, S. and Thornton, P.: Carbon and Other Biogeochemical Cycles, in Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, edited by T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, pp. 465–570, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. [online] Available from: www.climatechange2013.org, 2013.

Cicerone, R. J. and Oremland, R. S.: Biogeochemical aspects of atmospheric methane, Global Biogeochemical Cycles, 2(4), 299–327, 1988.

Clark, K. E., Torres, M. A., West, A. J., Hilton, R. G., New, M., Horwath, A. B., Fisher, J. B., Rapp, J. M., Robles Caceres, A. and Malhi, Y.: The hydrological regime of a forested tropical Andean catchment, Hydrology and Earth System Sciences, 18(12), 5377–5397, doi:10.5194/hess-18-5377-2014, 2014.

Conrad, R.: Soil microorganisms as controllers of atmospheric trace gases (hydrogen, carbon monoxide, methane, carbonyl sulfide, nitrous oxide, and nitric oxide)., Microbiological Reviews, 60(4), 609–640, 1996.

Curry, C. L.: Modeling the soil consumption of atmospheric methane at the global scale, Global Biogeochemical Cycles, 21(4), doi:10.1029/2006GB002818, 2007.

Davidson, E. A., Ishida, F. Y. and Nepstad, D. C.: Effects of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest, Global Change Biology, 10(5), 718–730, 2004.

Davidson, E. A., Nepstad, D. C., Ishida, F. Y. and Brando, P. M.: Effects of an experimental drought and recovery on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest, Global Change Biology, 14(11), 2582–2590, 2008.

Delmas, R. A., Servant, J., Tathy, J. P., Cros, B. and Labat, M.: Sources and sinks of methane and carbon dioxide exchanges in mountain forest in equatorial Africa, Journal of Geophysical Research: Atmospheres (1984–2012), 97(D6), 6169–6179, 1992.

Dubinsky, E. A., Silver, W. L. and Firestone, M. K.: Tropical forest soil microbial communities couple iron and carbon biogeochemistry, Ecology, 91(9), 2604–2612, 2010.

Dutaur, L. and Verchot, L. V.: A global inventory of the soil methane sink, Global Biogeochemical Cycles, 21(4), doi:10.1029/2006GB002734, 2007.

Eva, H. D., Belward, A. S., Miranda, E. E. D., Bella, C. M. D., Gond, V., Huber, O., Jones, S., Sgrenzaroli, M. and Fritz, S.: A land cover map of South America, Global Change Biology, 10(5), 731–744, 2004.

Fernandes, S. A. P., Bernoux, M., Cerri, C. C., Feigl, B. J. and Piccolo, M. C.: Seasonal variation of soil chemical properties and carbon dioxide and methane fluxes in unfertilized and P-fertilized pastures in an Ultisol of the Brazilian Amazon, Geoderma, 107(3), 227–241, 2002.

von Fischer, J. C. and Hedin, L. O.: Controls on soil methane fluxes: Tests of biophysical mechanisms using stable isotope tracers, Global Biogeochemical Cycles, 21(2), n/a–n/a, doi:10.1029/2006GB002687, 2007.

von Fischer, J. C., Butters, G., Duchateau, P. C., Thelwell, R. J. and Siller, R.: In situ measures of methanotroph activity in upland soils: A reaction-diffusion model and field observation of water stress, Journal of Geophysical Research: Biogeosciences, 114(G1), n/a–n/a, doi:10.1029/2008JG000731, 2009.

Foster, P.: The potential negative impacts of global climate change on tropical montane cloud forests, Earth-Science Reviews, 55(1), 73–106, 2001.

Frankenberg, C., Meirink, J. F., Weele, M. V., Platt, U. and Wagner, T.: Assessing methane emissions from global space-borne observations, Science, 308(5724), 1010–1014, 2005.

Giblin, A. E., Laundre, J. A., Nadelhoffer, K. J. and Shaver, G. R.: Measuring Nutrient Availability in Arctic Soils Using Ion Exchange Resins: A Field Test, Soil Science Society of America Journal, 58(4), 1154–1162, doi:10.2136/sssaj1994.03615995005800040021x, 1994.

Girardin, C. A. J., Malhi, Y., Aragao, L., Mamani, M., Huasco, W. H., Durand, L., Feeley, K. J., Rapp, J., SILVA-ESPEJO, J., Silman, M. and others: Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes, Global Change Biology, 16(12), 3176–3192, 2010.

Hall, S. J., McDowell, W. H. and Silver, W. L.: When wet gets wetter: decoupling of moisture, redox biogeochemistry, and greenhouse gas fluxes in a humid tropical forest soil, Ecosystems, 16(4), 576–589, 2013.

Harrell, F. E., Dupont, C. and others: Hmisc: Harrell Miscellaneous. [online] Available from: http://CRAN.R-project.org/package=Hmisc, 2015.

Hassler, E., Corre, M. D., Tjoa, A., Damris, M., Utami, S. R. and Veldkamp, E.: Soil fertility controls soil–atmosphere carbon dioxide and methane fluxes in a tropical landscape converted from lowland forest to rubber and oil palm plantations, Biogeosciences, 12(19), 5831–5852, doi:10.5194/bg-12-5831-2015, 2015.

Holter, P.: Sampling air from dung pats by silicone rubber diffusion chambers, Soil Biology and Biochemistry, 22(7), 995–997, 1990.

Hothorn, T., Bretz, F. and Westfall, P.: Simultaneous Inference in General Parametric Models, Biometrical Journal, 50(3), 346–363, 2008.

Hutchinson, G. L. and Mosier, A. R.: Improved Soil Cover Method for Field Measurement of Nitrous Oxide Fluxes, Soil Science Society of America Journal, 45(2), 311–316, doi:10.2136/sssaj1981.03615995004500020017x, 1981.

Ishizuka, S., Iswandi, A., Nakajima, Y., Yonemura, S., Sudo, S., Tsuruta, H. and Muriyarso, D.: Spatial patterns of greenhouse gas emission in a tropical rainforest in Indonesia, Nutrient Cycling in Agroecosystems, 71(1), 55–62, 2005a.

Ishizuka, S., Iswandi, A., Nakajima, Y., Yonemura, S., Sudo, S., Tsuruta, H. and Murdiyarso, D.: The variation of greenhouse gas emissions from soils of various land-use/cover types in Jambi province, Indonesia, Nutrient Cycling in Agroecosystems, 71(1), 17–32, 2005b.

Jacinthe, P. A. and Dick, W. A.: Use of silicone tubing to sample nitrous oxide in the soil atmosphere, Soil Biology and Biochemistry, 28(6), 721–726, 1996.

Kammann, C., Grünhage, L. and Jäger, H. J.: A new sampling technique to monitor concentrations of methane, nitrous oxide and carbon dioxide in air at well-defined depths in soils with varied water potential, European Journal of Soil Science, 52(2), 297–303, 2001.

Keller, M., Kaplan, W. A. and Wofsy, S. C.: Emissions of nitrous oxide, methane and carbon dioxide from tropical forest soils, Journal of Geophysical Research: Atmospheres (1984–2012), 91(D11), 11791–11802, 1986.

Keller, M., Varner, R., Dias, J. D., Silva, H., Crill, P., Asner, G. P. and others: Soil–Atmosphere Exchange of Nitrous Oxide, Nitric Oxide, Methane, and Carbon Dioxide in Logged and Undisturbed Forest in the Tapajos National Forest, Brazil, Earth Interactions, 9(1), 1–21, 2005.

Kiese, R., Wochele, S. and Butterbach-Bahl, K.: Site specific and regional estimates of methane uptake by tropical rainforest soils in north eastern Australia, Plant and soil, 309(1–2), 211–226, 2008.

Klute, A. and others: Methods of soil analysis. Part 1. Physical and mineralogical methods., American Society of Agronomy, Inc., 1986.

Le Mer, J. and Roger, P.: Production, oxidation, emission and consumption of methane by soils: a review, European Journal of Soil Biology, 37(1), 25–50, 2001.

Liptzin, D., Silver, W. L. and Detto, M.: Temporal dynamics in soil oxygen and greenhouse gases in two humid tropical forests, Ecosystems, 14(2), 171–182, 2011.

Livingston, G. and Hutchinston, G.: Chapter 2: Enclosure-based measurement of trace gas exchange: applications and sources of error. In: Matson, P., Harriss, RC (ed.) Biogenic Trace Gases: Measuring Emissions from Soil and Water, Blackwell Scientific Ltd., 1995.

Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P. and Saatchi, S.: Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research, Global Change Biology, 16(12), 3171–3175, 2010.

Mochizuki, Y., Koba, K. and Yoh, M.: Strong inhibitory effect of nitrate on atmospheric methane oxidation in forest soils, Soil Biology and Biochemistry, 50, 164–166, 2012.

Myhre, G., Shindell, D., Bréon, F.-M., Collins, W., Fuglestvedt, J., Huang, J., Koch, D., Lamarque, J.-F., Lee, D., Mendoza, B., Nakajima, T., Robock, A., Stephens, G., Takemura, T. and Zhang, H.: Anthropogenic and Natural Radiative Forcing, in Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, edited by T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, pp. 659–740, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. [online] Available from: www.climatechange2013.org, 2013.

Nottingham, A. T., Ccahuana, A. J. and Meir, P.: Soil properties in tropical montane cloud forests influence estimates of soil carbon dioxide efflux, Agricultural and Forest Meteorology, 166, 215–220, 2012.

Pedersen, A. R.: HMR: Flux estimation with static chamber data. [online] Available from: http://cran.r-project.org/package=HMR, 2012.

Pedersen, A. R., Petersen, S. O. and Schelde, K.: A comprehensive approach to soil-atmosphere trace-gas flux estimation with static chambers, European Journal of Soil Science, 61(6), 888–902, 2010.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and R Core Team: nlme: Linear and Nonlinear Mixed Effects Models. [online] Available from: http://CRAN.R-project.org/package=nlme, 2014.

Pinheiro, J. C. and Bates, D. M.: Mixed-effects models in S and S-PLUS, Springer., 2000.

Pumpanen, J., Kolari, P., Ilvesniemi, H., Minkkinen, K., Vesala, T., Niinistö, S., Lohila, A., Larmola, T., Morero, M., Pihlatie, M. and others: Comparison of different chamber techniques for measuring soil carbon dioxide efflux, Agricultural and Forest Meteorology, 123(3), 159–176, 2004.

Purbopuspito, J., Veldkamp, E., Brumme, R. and Murdiyarso, D.: Trace gas fluxes and nitrogen cycling along an elevation sequence of tropical montane forests in Central Sulawesi, Indonesia, Global Biogeochemical Cycles, 20(3), doi:10.1029/2005GB002516, 2006.

R Core Team: R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria. [online] Available from: http://www.r-project.org, 2013.

Reay, D. S. and Nedwell, D. B.: Methane oxidation in temperate soils: effects of inorganic N, Soil Biology and Biochemistry, 36(12), 2059–2065, 2004.

Schuur, E. A., Chadwick, O. A. and Matson, P. A.: Carbon cycling and soil carbon storage in mesic to wet Hawaiian montane forests, Ecology, 82(11), 3182–3196, 2001.

Segers, R.: Methane production and methane consumption: a review of processes underlying wetland methane fluxes, Biogeochemistry, 41(1), 23–51, 1998.

Sexstone, A. J., Revsbech, N. P., Parkin, T. B. and Tiedje, J. M.: Direct measurement of oxygen profiles and denitrification rates in soil aggregates, Soil Science Society of America Journal, 49(3), 645–651, 1985.

Silver, W. L., Lugo, A. E. and Keller, M.: Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils, Biogeochemistry, 44(3), 301–328, 1999.

Smith, K. A., Ball, T., Conen, F., Dobbie, K. E., Massheder, J. and Rey, A.: Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes, European Journal of Soil Science, 54(4), 779–791, 2003.

Sousa Neto, E., Carmo, J. B., Keller, M., Martins, S. C., Alves, L. F., Vieira, S. A., Piccolo, M. C., Camargo, P., Couto, H. T. Z., Joly, C. A. and Martinelli, L. A.: Soil-atmosphere exchange of nitrous oxide, methane and carbon dioxide in a gradient of elevation in the coastal Brazilian Atlantic forest, Biogeosciences, 8(3), 733–742, doi:10.5194/bg-8-733-2011, 2011.

Spahni, R., Wania, R., Neef, L., Weele, M. V., Pison, I., Bousquet, P., Frankenberg, C., Foster, P. N., Joos, F., Prentice, I. C. and others: Constraining global methane emissions and uptake by ecosystems., Biogeosciences Discussions, 8(1), doi:10.5194/bg-8-1643-2011, 2011.

Steudler, P. A., Bowden, R. D., Melillo, J. M. and Aber, J. D.: Influence of nitrogen fertilization on methane uptake in temperate forest soils, Nature, 341(6240), 314–316, doi:10.1038/341314a0, 1989.

Steudler, P. A., Melillo, J. M., Feigl, B. J., Neill, C., Piccolo, M. C. and Cerri, C. C.: Consequence of forest-to-pasture conversion on methane fluxes in the Brazilian Amazon Basin, Journal of Geophysical Research: Atmospheres (1984–2012), 101(D13), 18547–18554, 1996.

Teh, Y. A., Silver, W. L. and Conrad, M. E.: Oxygen effects on methane production and oxidation in humid tropical forest soils, Global Change Biology, 11(8), 1283–1297, 2005.

Teh, Y. A., Silver, W. L., Conrad, M. E., Borglin, S. E. and Carlson, C. M.: Carbon isotope fractionation by methane-oxidizing bacteria in tropical rain forest soils, Journal of Geophysical Research: Biogeosciences (2005–2012), 111(G2), doi:10.1029/2005JG000053, 2006.

Teh, Y. A., Dubinsky, E. A., Silver, W. L. and Carlson, C. M.: Suppression of methanogenesis by dissimilatory iron (III)-reducing bacteria in tropical rain forest soils: Implications for ecosystem methane flux, Global Change Biology, 14(2), 413–422, 2008.

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

Templer, P., Lovett, G., Weathers, K., Findlay, S. and Dawson, T. E.: Influence of Tree Species on Forest Nitrogen Retention in the Catskill Mountains, New York, USA, Ecosystems, 8(1), 1–16, doi:10.1007/s10021-004-0230-8, 2005.

Tovar, C., Arnillas, C. A., Cuesta, F. and Buytaert, W.: Diverging responses of tropical Andean biomes under future climate conditions, PloS One, 8(5), e63634, doi:10.1371/journal.pone.0063634, 2013.

Varner, R. K., Keller, M., Robertson, J. R., Dias, J. D., Silva, H., Crill, P. M., McGroddy, M. and Silver, W. L.: Experimentally induced root mortality increased nitrous oxide emission from tropical forest soils, Geophysical Research Letters, 30(3), 1144, doi:10.1029/2002GL016164, 2003.

Veldkamp, E., Koehler, B. and Corre, M. D.: Indications of nitrogen-limited methane uptake in tropical forest soils, Biogeosciences, 10(8), 5367–5379, doi:10.5194/bg-10-5367-2013, 2013.

Verchot, L. V., Davidson, E. A., Cattânio, J. H. and Ackerman, I. L.: Land-use change and biogeochemical controls of methane fluxes in soils of eastern Amazonia, Ecosystems, 3(1), 41–56, 2000.

Werner, C., Zheng, X., Tang, J., Xie, B., Liu, C., Kiese, R. and Butterbach-Bahl, K.: Nitrous oxide, methane and carbon dioxide emissions from seasonal tropical rainforests and a rubber plantation in Southwest China, Plant and Soil, 289(1–2), 335–353, 2006.

Werner, C., Kiese, R. and Butterbach-Bahl, K.: Soil-atmosphere exchange of N2O, CH4, and CO2 and controlling environmental factors for tropical rain forest sites in western Kenya, Journal of Geophysical Research: Atmospheres, 112(D3), doi:10.1029/2006JD007388, 2007.

Wolf, K., Flessa, H. and Veldkamp, E.: Atmospheric methane uptake by tropical montane forest soils and the contribution of organic layers, Biogeochemistry, 111(1–3), 469–483, 2012.

Zimmermann, M., Meir, P., Bird, M. I., Malhi, Y. and Ccahuana, A. J. Q.: Climate dependence of heterotrophic soil respiration from a soil-translocation experiment along a 3000 m tropical forest altitudinal gradient, European Journal of Soil Science, 60(6), 895–906, 2009a.

Zimmermann, M., Meir, P., Bird, M., Malhi, Y. and Ccahuana, A.: Litter contribution to diurnal and annual soil respiration in a tropical montane cloud forest, Soil Biology and Biochemistry, 41(6), 1338–1340, doi:http://dx.doi.org/10.1016/j.soilbio.2009.02.023, 2009b.

Zimmermann, M., Meir, P., Silman, M. R., Fedders, A., Gibbon, A., Malhi, Y., Urrego, D. H., Bush, M. B., Feeley, K. J., Garcia, K. C. and others: No differences in soil carbon stocks across the tree line in the Peruvian Andes, Ecosystems, 13(1), 62–74, 2010a.

Zimmermann, M., Meir, P., Bird, M. I., Malhi, Y. and Ccahuana, A. J.: Temporal variation and climate dependence of soil respiration and its components along a 3000 m altitudinal tropical forest gradient, Global Biogeochemical Cycles, 24(4), doi:10.1029/2010GB003787, 2010b.

Zuur, A. F., Ieno, E. N. and Smith, G. M.: Analysing ecological data, Springer New York., 2007.

Bender, M. and Conrad, R.: Kinetics of methane oxidation in oxic soils exposed to ambient air or high methane mixing ratios, FEMS Microbiology Letters, 101(4), 261–269, 1992.

Bergamaschi, P., Frankenberg, C., Meirink, J. F., Krol, M., Villani, M. G., Houweling, S., Dentener, F., Dlugokencky, E. J., Miller, J. B., Gatti, L. V. and others: Inverse modeling of global and regional methane emissions using SCIAMACHY satellite retrievals, Journal of Geophysical Research: Atmospheres (1984–2012), 114(D22), doi:10.1029/2009JD012287, 2009.

Bloom, A. A., Palmer, P. I., Fraser, A., Reay, D. S. and Frankenberg, C.: Large-scale controls of methanogenesis inferred from methane and gravity spaceborne data, Science, 327(5963), 322–325, 2010.

Burgin, A. J., Yang, W. H., Hamilton, S. K. and Silver, W. L.: Beyond carbon and nitrogen: how the microbial energy economy couples elemental cycles in diverse ecosystems, Frontiers in Ecology and the Environment, 9(1), 44–52, 2011.

Chidthaisong, A. and Conrad, R.: Turnover of glucose and acetate coupled to reduction of nitrate, ferric iron and sulfate and to methanogenesis in anoxic rice field soil, FEMS Microbiology Ecology, 31(1), 73–86, 2000.

Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., Jones, C., Le Quéré, C., Myneni, R. B., Piao, S. and Thornton, P.: Carbon and Other Biogeochemical Cycles, in Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, edited by T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, pp. 465–570, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. [online] Available from: www.climatechange2013.org, 2013.

Cicerone, R. J. and Oremland, R. S.: Biogeochemical aspects of atmospheric methane, Global Biogeochemical Cycles, 2(4), 299–327, 1988.

Clark, K. E., Torres, M. A., West, A. J., Hilton, R. G., New, M., Horwath, A. B., Fisher, J. B., Rapp, J. M., Robles Caceres, A. and Malhi, Y.: The hydrological regime of a forested tropical Andean catchment, Hydrology and Earth System Sciences, 18(12), 5377–5397, doi:10.5194/hess-18-5377-2014, 2014.

Conrad, R.: Soil microorganisms as controllers of atmospheric trace gases (hydrogen, carbon monoxide, methane, carbonyl sulfide, nitrous oxide, and nitric oxide)., Microbiological Reviews, 60(4), 609–640, 1996.

Curry, C. L.: Modeling the soil consumption of atmospheric methane at the global scale, Global Biogeochemical Cycles, 21(4), doi:10.1029/2006GB002818, 2007.

Davidson, E. A., Ishida, F. Y. and Nepstad, D. C.: Effects of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest, Global Change Biology, 10(5), 718–730, 2004.

Davidson, E. A., Nepstad, D. C., Ishida, F. Y. and Brando, P. M.: Effects of an experimental drought and recovery on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest, Global Change Biology, 14(11), 2582–2590, 2008.

Delmas, R. A., Servant, J., Tathy, J. P., Cros, B. and Labat, M.: Sources and sinks of methane and carbon dioxide exchanges in mountain forest in equatorial Africa, Journal of Geophysical Research: Atmospheres (1984–2012), 97(D6), 6169–6179, 1992.

Dutaur, L. and Verchot, L. V.: A global inventory of the soil methane sink, Global Biogeochemical Cycles, 21(4), doi:10.1029/2006GB002734, 2007.

Eva, H. D., Belward, A. S., Miranda, E. E. D., Bella, C. M. D., Gond, V., Huber, O., Jones, S., Sgrenzaroli, M. and Fritz, S.: A land cover map of South America, Global Change Biology, 10(5), 731–744, 2004.

Fernandes, S. A. P., Bernoux, M., Cerri, C. C., Feigl, B. J. and Piccolo, M. C.: Seasonal variation of soil chemical properties and carbon dioxide and methane fluxes in unfertilized and P-fertilized pastures in an Ultisol of the Brazilian Amazon, Geoderma, 107(3), 227–241, 2002.

von Fischer, J. C. and Hedin, L. O.: Controls on soil methane fluxes: Tests of biophysical mechanisms using stable isotope tracers, Global Biogeochemical Cycles, 21(2), n/a–n/a, doi:10.1029/2006GB002687, 2007.

von Fischer, J. C., Butters, G., Duchateau, P. C., Thelwell, R. J. and Siller, R.: In situ measures of methanotroph activity in upland soils: A reaction-diffusion model and field observation of water stress, Journal of Geophysical Research: Biogeosciences, 114(G1), n/a–n/a, doi:10.1029/2008JG000731, 2009.

Foster, P.: The potential negative impacts of global climate change on tropical montane cloud forests, Earth-Science Reviews, 55(1), 73–106, 2001.

Frankenberg, C., Meirink, J. F., Weele, M. V., Platt, U. and Wagner, T.: Assessing methane emissions from global space-borne observations, Science, 308(5724), 1010–1014, 2005.

Giblin, A. E., Laundre, J. A., Nadelhoffer, K. J. and Shaver, G. R.: Measuring Nutrient Availability in Arctic Soils Using Ion Exchange Resins: A Field Test, Soil Science Society of America Journal, 58(4), 1154–1162, doi:10.2136/sssaj1994.03615995005800040021x, 1994.

Girardin, C. A. J., Malhi, Y., Aragao, L., Mamani, M., Huasco, W. H., Durand, L., Feeley, K. J., Rapp, J., SILVA-ESPEJO, J., Silman, M. and others: Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes, Global Change Biology, 16(12), 3176–3192, 2010.

Hall, S. J., McDowell, W. H. and Silver, W. L.: When wet gets wetter: decoupling of moisture, redox biogeochemistry, and greenhouse gas fluxes in a humid tropical forest soil, Ecosystems, 16(4), 576–589, 2013.

Harrell, F. E., Dupont, C. and others: Hmisc: Harrell Miscellaneous. [online] Available from: http://CRAN.R-project.org/package=Hmisc, 2015.

Holter, P.: Sampling air from dung pats by silicone rubber diffusion chambers, Soil Biology and Biochemistry, 22(7), 995–997, 1990.

Hothorn, T., Bretz, F. and Westfall, P.: Simultaneous Inference in General Parametric Models, Biometrical Journal, 50(3), 346–363, 2008.

Hutchinson, G. L. and Mosier, A. R.: Improved Soil Cover Method for Field Measurement of Nitrous Oxide Fluxes, Soil Science Society of America Journal, 45(2), 311–316, doi:10.2136/sssaj1981.03615995004500020017x, 1981.

Ishizuka, S., Iswandi, A., Nakajima, Y., Yonemura, S., Sudo, S., Tsuruta, H. and Muriyarso, D.: Spatial patterns of greenhouse gas emission in a tropical rainforest in Indonesia, Nutrient Cycling in Agroecosystems, 71(1), 55–62, 2005a.

Ishizuka, S., Iswandi, A., Nakajima, Y., Yonemura, S., Sudo, S., Tsuruta, H. and Murdiyarso, D.: The variation of greenhouse gas emissions from soils of various land-use/cover types in Jambi province, Indonesia, Nutrient Cycling in Agroecosystems, 71(1), 17–32, 2005b.

Jacinthe, P. A. and Dick, W. A.: Use of silicone tubing to sample nitrous oxide in the soil atmosphere, Soil Biology and Biochemistry, 28(6), 721–726, 1996.

Kammann, C., Grünhage, L. and Jäger, H. J.: A new sampling technique to monitor concentrations of methane, nitrous oxide and carbon dioxide in air at well-defined depths in soils with varied water potential, European Journal of Soil Science, 52(2), 297–303, 2001.

Keller, M., Kaplan, W. A. and Wofsy, S. C.: Emissions of nitrous oxide, methane and carbon dioxide from tropical forest soils, Journal of Geophysical Research: Atmospheres (1984–2012), 91(D11), 11791–11802, 1986.

Keller, M., Varner, R., Dias, J. D., Silva, H., Crill, P., Asner, G. P. and others: Soil–Atmosphere Exchange of Nitrous Oxide, Nitric Oxide, Methane, and Carbon Dioxide in Logged and Undisturbed Forest in the Tapajos National Forest, Brazil, Earth Interactions, 9(1), 1–21, 2005.

Kiese, R., Wochele, S. and Butterbach-Bahl, K.: Site specific and regional estimates of methane uptake by tropical rainforest soils in north eastern Australia, Plant and soil, 309(1-2), 211–226, 2008.

Le Mer, J. and Roger, P.: Production, oxidation, emission and consumption of methane by soils: a review, European Journal of Soil Biology, 37(1), 25–50, 2001.

Liptzin, D., Silver, W. L. and Detto, M.: Temporal dynamics in soil oxygen and greenhouse gases in two humid tropical forests, Ecosystems, 14(2), 171–182, 2011.

Livingston, G. and Hutchinston, G.: Chapter 2: Enclosure-based measurement of trace gas exchange: applications and sources of error. In: Matson, P., Harriss, RC (ed.) Biogenic Trace Gases: Measuring Emissions from Soil and Water, Blackwell Scientific Ltd., 1995.

Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P. and Saatchi, S.: Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research, Global Change Biology, 16(12), 3171–3175, 2010.

Mochizuki, Y., Koba, K. and Yoh, M.: Strong inhibitory effect of nitrate on atmospheric methane oxidation in forest soils, Soil Biology and Biochemistry, 50, 164–166, 2012.

Myhre, G., Shindell, D., Bréon, F.-M., Collins, W., Fuglestvedt, J., Huang, J., Koch, D., Lamarque, J.-F., Lee, D., Mendoza, B., Nakajima, T., Robock, A., Stephens, G., Takemura, T. and Zhang, H.: Anthropogenic and Natural Radiative Forcing, in Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, edited by T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, pp. 659–740, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. [online] Available from: www.climatechange2013.org, 2013.

Nottingham, A. T., Ccahuana, A. J. Q. and Meir, P.: Soil properties in tropical montane cloud forests influence estimates of soil CO2 efflux, Agricultural and Forest Meteorology, 166–167, 215–220, doi:http://dx.doi.org/10.1016/j.agrformet.2012.08.008, 2012.

Pedersen, A. R.: HMR: Flux estimation with static chamber data. [online] Available from: http://cran.r-project.org/package=HMR, 2012.

Pedersen, A. R., Petersen, S. O. and Schelde, K.: A comprehensive approach to soil-atmosphere trace-gas flux estimation with static chambers, European Journal of Soil Science, 61(6), 888–902, 2010.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and R Core Team: nlme: Linear and Nonlinear Mixed Effects Models. [online] Available from: http://CRAN.R-project.org/package=nlme, 2014.

Pinheiro, J. C. and Bates, D. M.: Mixed-effects models in S and S-PLUS, Springer., 2000.

Pumpanen, J., Kolari, P., Ilvesniemi, H., Minkkinen, K., Vesala, T., Niinistö, S., Lohila, A., Larmola, T., Morero, M., Pihlatie, M. and others: Comparison of different chamber techniques for measuring soil carbon dioxide efflux, Agricultural and Forest Meteorology, 123(3), 159–176, 2004.

Purbopuspito, J., Veldkamp, E., Brumme, R. and Murdiyarso, D.: Trace gas fluxes and nitrogen cycling along an elevation sequence of tropical montane forests in Central Sulawesi, Indonesia, Global Biogeochemical Cycles, 20(3), doi:10.1029/2005GB002516, 2006.

R Core Team: R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria. [online] Available from: http://www.r-project.org, 2013.

Reay, D. S. and Nedwell, D. B.: Methane oxidation in temperate soils: effects of inorganic N, Soil Biology and Biochemistry, 36(12), 2059–2065, 2004.

Schuur, E. A., Chadwick, O. A. and Matson, P. A.: Carbon cycling and soil carbon storage in mesic to wet Hawaiian montane forests, Ecology, 82(11), 3182–3196, 2001.

Segers, R.: Methane production and methane consumption: a review of processes underlying wetland methane fluxes, Biogeochemistry, 41(1), 23–51, 1998.

Sexstone, A. J., Revsbech, N. P., Parkin, T. B. and Tiedje, J. M.: Direct measurement of oxygen profiles and denitrification rates in soil aggregates, Soil Science Society of America Journal, 49(3), 645–651, 1985.

Silver, W. L., Lugo, A. E. and Keller, M.: Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils, Biogeochemistry, 44(3), 301–328, 1999.

Smith, K. A., Ball, T., Conen, F., Dobbie, K. E., Massheder, J. and Rey, A.: Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes, European Journal of Soil Science, 54(4), 779–791, 2003.

Sousa Neto, E., Carmo, J. B., Keller, M., Martins, S. C., Alves, L. F., Vieira, S. A., Piccolo, M. C., Camargo, P., Couto, H. T. Z., Joly, C. A. and Martinelli, L. A.: Soil-atmosphere exchange of nitrous oxide, methane and carbon dioxide in a gradient of elevation in the coastal Brazilian Atlantic forest, Biogeosciences, 8(3), 733–742, doi:10.5194/bg-8-733-2011, 2011.

Spahni, R., Wania, R., Neef, L., Weele, M. V., Pison, I., Bousquet, P., Frankenberg, C., Foster, P. N., Joos, F., Prentice, I. C. and others: Constraining global methane emissions and uptake by ecosystems., Biogeosciences Discussions, 8(1), doi:10.5194/bg-8-1643-2011, 2011.

Steudler, P. A., Bowden, R. D., Melillo, J. M. and Aber, J. D.: Influence of nitrogen fertilization on methane uptake in temperate forest soils, Nature, 341(6240), 314–316, doi:10.1038/341314a0, 1989.

Steudler, P. A., Melillo, J. M., Feigl, B. J., Neill, C., Piccolo, M. C. and Cerri, C. C.: Consequence of forest-to-pasture conversion on methane fluxes in the Brazilian Amazon Basin, Journal of Geophysical Research: Atmospheres (1984–2012), 101(D13), 18547–18554, 1996.

Teh, Y. A., Silver, W. L. and Conrad, M. E.: Oxygen effects on methane production and oxidation in humid tropical forest soils, Global Change Biology, 11(8), 1283–1297, 2005.

Teh, Y. A., Silver, W. L., Conrad, M. E., Borglin, S. E. and Carlson, C. M.: Carbon isotope fractionation by methane-oxidizing bacteria in tropical rain forest soils, Journal of Geophysical Research: Biogeosciences (2005–2012), 111(G2), doi:10.1029/2005JG000053, 2006.

Teh, Y. A., Dubinsky, E. A., Silver, W. L. and Carlson, C. M.: Suppression of methanogenesis by dissimilatory iron (III)-reducing bacteria in tropical rain forest soils: Implications for ecosystem methane flux, Global Change Biology, 14(2), 413–422, 2008.

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

Templer, P., Lovett, G., Weathers, K., Findlay, S. and Dawson, T. E.: Influence of Tree Species on Forest Nitrogen Retention in the Catskill Mountains, New York, USA, Ecosystems, 8(1), 1–16, doi:10.1007/s10021-004-0230-8, 2005.

Tovar, C., Arnillas, C. A., Cuesta, F. and Buytaert, W.: Diverging responses of tropical Andean biomes under future climate conditions, PloS One, 8(5), e63634, doi:10.1371/journal.pone.0063634, 2013.

Varner, R. K., Keller, M., Robertson, J. R., Dias, J. D., Silva, H., Crill, P. M., McGroddy, M. and Silver, W. L.: Experimentally induced root mortality increased nitrous oxide emission from tropical forest soils, Geophysical Research Letters, 30(3), 1144, doi:10.1029/2002GL016164, 2003.

Veldkamp, E., Koehler, B. and Corre, M. D.: Indications of nitrogen-limited methane uptake in tropical forest soils, Biogeosciences, 10(8), 5367–5379, doi:10.5194/bg-10-5367-2013, 2013.

Verchot, L. V., Davidson, E. A., Cattânio, J. H. and Ackerman, I. L.: Land-use change and biogeochemical controls of methane fluxes in soils of eastern Amazonia, Ecosystems, 3(1), 41–56, 2000.

Werner, C., Zheng, X., Tang, J., Xie, B., Liu, C., Kiese, R. and Butterbach-Bahl, K.: Nitrous oxide, methane and carbon dioxide emissions from seasonal tropical rainforests and a rubber plantation in Southwest China, Plant and Soil, 289(1-2), 335–353, 2006.

Werner, C., Kiese, R. and Butterbach-Bahl, K.: Soil-atmosphere exchange of N2O, CH4, and CO2 and controlling environmental factors for tropical rain forest sites in western Kenya, Journal of Geophysical Research: Atmospheres, 112(D3), doi:10.1029/2006JD007388, 2007.

Wolf, K., Flessa, H. and Veldkamp, E.: Atmospheric methane uptake by tropical montane forest soils and the contribution of organic layers, Biogeochemistry, 111(1-3), 469–483, 2012.

Zimmermann, M., Meir, P., Bird, M. I., Malhi, Y. and Ccahuana, A. J. Q.: Climate dependence of heterotrophic soil respiration from a soil-translocation experiment along a 3000 m tropical forest altitudinal gradient, European Journal of Soil Science, 60(6), 895–906, 2009a.

Zimmermann, M., Meir, P., Bird, M., Malhi, Y. and Ccahuana, A.: Litter contribution to diurnal and annual soil respiration in a tropical montane cloud forest, Soil Biology and Biochemistry, 41(6), 1338 – 1340, doi:http://dx.doi.org/10.1016/j.soilbio.2009.02.023, 2009b.

Zimmermann, M., Meir, P., Silman, M. R., Fedders, A., Gibbon, A., Malhi, Y., Urrego, D. H., Bush, M. B., Feeley, K. J., Garcia, K. C. and others: No differences in soil carbon stocks across the tree line in the Peruvian Andes, Ecosystems, 13(1), 62–74, 2010a.

Zimmermann, M., Meir, P., Bird, M. I., Malhi, Y. and Ccahuana, A. J.: Temporal variation and climate dependence of soil respiration and its components along a 3000 m altitudinal tropical forest gradient, Global Biogeochemical Cycles, 24(4), doi:10.1029/2010GB003787, 2010b.

Zuur, A. F., Ieno, E. N. and Smith, G. M.: Analysing ecological data, Springer New York., 2007.

Table 1 Study area~~Study site~~ and plot characteristics.

Study area~~Study sites~~		Study plots								
Field station	Forest type	Longitude (°S)	Latitude (°W)	MAT[a] (°C)	MAP[a] (mm)	Elevation (m asl)	Topography	Bulk density[b] (g cm^{-2})	Particle density[b] (g cm^{-2})	Porosity[b]
Villa Carmen	Pre-montane	12°53'43"	71°24'04"	23.4	5300	1070 to 1088	ridge, slope & flat	0.27 to 0.31	2.2	0.86 to 0.88
San Pedro	Lower montane	13°02'56"	71°32'13"	18.8	2600	1532 to 1768	ridge, slope & flat	0.09 to 0.22	1.7	0.87 to 0.95
Wayqecha	Upper montane	13°11'24"	71°35'13"	12.5	1700	2811 to 2962	ridge & slopes	0.08 to 0.11	1.4	0.92 to 0.94

[a]mean annual air temperature and mean annual precipitation & [b]soil properties in the upper 10 cm.

Table 2 Forest type means and standard errors for aggregated dry (May - September) and wet (October - April) season months. Capital letters indicate significant differences ($p < 0.05$) among forest types within season and lower case letters indicate significant differences between season within forest types.

Forest type	Net CH_4 flux ($mg\ C\ m^{-2}\ d^{-1}$)		Net CO_2 flux ($g\ C\ m^{-2}\ d^{-1}$)		O_2 concentration (%)		WFPS (%)		Soil temperature (°C)		Available NH_4^+ ($\mu g\ N\ g^{-1}$ res. d^{-1})		Available NO_3^- ($\mu g\ N\ g^{-1}$ res. d^{-1})	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Pre-montane	-0.2 (0.1)^{A}	-0.1 (0.1)^{A}	5.2 (0.3)^{A}	5.1 (0.3)^{A}	19.7 (0.3)^{A}	19.8 (0.3)^{A}	50.9 (2.1)^{A}	53.3 (1.9)^{A}	20.4 (0.2)^{A}	20.7 (0.2)^{A}	10.0 (0.6)	17.9 (0.05)	21.0 (0.1)^{A}	21.2 (0.1)^{A}
Lower montane	-1.1 (0.1)^{B}	-1.0 (0.1)^{B}	4.3 (0.3)^{AB}	4.1 (0.3)^{A}	19.1 (0.3)^{AB}	19.2 (0.2)^{AB}	35.4 (2.0)^{Ba}	44.8 (1.7)^{Bb}	17.3 (0.2)^{Ba}	18.0 (0.1)^{Bb}	7.8 (0.6)	14.8 (0.5)	6.4 (0.1)^{B}	9.6 (0.1)^{B}
Upper montane	-1.6 (0.1)^{C}	-1.1 (0.1)^{B}	2.9 (0.3)^{B}	4.0 (0.3)^{A}	18.6 (0.3)^{B}	18.9 (0.2)^{B}	24.4 (2.0)^{Ca}	43.7 (1.7)^{Bb}	11.0 (0.2)^{Ca}	11.9 (0.1)^{Cb}	10.8 (0.6)	18.6 (0.5)	0.4 (0.1)^{C}	1.1 (0.0)^{C}

Table 3 Pearson's correlation coefficient matrix for dataset plot means of measured variables among forest types. ** $p < 0.01$, * $p < 0.05$.

Variable pairs	Net CH_4 flux	Net CO_2 flux	O_2 concentration	WFPS	Soil temperature	√Available NH_4^+	√Available NO_3^-
Net CO_2 flux	0.61	-	-	-	-	-	-
O_2 concentration	0.73*	0.55	-	-	-	-	-
WFPS	0.84**	0.43	0.51	-	-	-	-
Soil temperature	0.83**	0.66	0.77*	0.79*	-	-	-
√Available NH_4^+	0.71*	0.36	0.31	0.41	0.25	-	-
√Available NO_3^-	0.88**	0.67*	0.72*	0.83**	-0.94**	0.42	-
Elevation	-0.81**	-0.66	-0.76*	-0.79*	-1.00**	-0.22	-0.94**
Porosity	-0.72*	-0.75*	-0.59	-0.68*	-0.80*	-0.23	-0.86**

Table 4 Pearson's correlation coefficient matrix for monthly forest type~~site~~ means of measured variables within forest types. ** $p < 0.01$, * $p < 0.05$.

Forest type	Variable pairs	Net CH_4 flux	Net CO_2 flux	O_2 concentration	WFPS	Soil temperature	√Available NH_4^+
Premontane	Net CO_2 flux	-0.21	-	-	-	-	-
	O_2 concentration	0.05	0.33	-	-	-	-
	WFPS	0.33	-0.34	-0.44	-	-	-
	Soil temperature	-0.16	0.13	-0.44	-0.49*	-	-
	√Available NH_4^+	-0.05	0.00	0.47	-0.38	0.11	-
	√Available NO_3^-	-0.25	0.20	0.46	-0.46	0.03	0.93**
Lower montane	Net CO_2 flux	-0.70**	-	-	-	-	-
	O_2 concentration	-0.20	0.08	-	-	-	-
	WFPS	0.16	0.15	-0.23	-	-	-
	Soil temperature	0.08	-0.08	-0.29	0.12	-	-
	√Available NH_4^+	0.04	-0.20	0.37	-0.11	0.40	-
	√Available NO_3^-	-0.14	0.06	0.53	0.22	0.35	0.24
Upper montane	Net CO_2 flux	-0.20	-	-	-	-	-
	O_2 concentration	0.04	0.09	-	-	-	-
	WFPS	0.54**	0.49**	0.09	-	-	-
	Soil temperature	0.52**	0.29	-0.21	0.60**	-	-
	√Available NH_4^+	0.19	0.11	0.03	-0.10	0.11	-
	√Available NO_3^-	-0.02	0.46	-0.32	0.53*	0.54*	0.39

Table 5 Characteristics and annual mean ~~(standard error)~~ net CH_4 fluxes reported for montane forests in Peru (this study), Ecuador (Wolf et al., 2012) and Indonesia (Purbopuspito et al., 2006).

Country	Forest type	Elevation (m asl)	Organic horizon thickness (cm)	MAT[a] (°C)	MAP[a] (mm)	Net CH_4 flux (mg ~~CH_4 -~~ C m^{-2} d^{-1})
Ecuador	Premontane	900 to 1200	2.5 to 6.5	19.4	2230	-1.5
	Lower montane	1800 to 2100	4.0 to 24.0	15.7	1950	-0.9
	Upper montane	2800 to 3000	6.6 to 22.2	9.4	4500	-0.3
Peru	Premontane	1070 to 1088	< 5	23.4	5300	-0.2
	Lower montane	1532 to 1768	~ 10	18.8	2600	-1.1
	Upper montane	2811 to 2962	~ 20	12.5	1700	-1.3
Indonesia	Premontane	1190	0	22.5	1500	-0.7
	Lower montane	1800	15 to 25	18.3	-	-0.9
	Upper montane	2470	10 to 20	14.6	-	-0.4

[a]mean annual air temperature and mean annual precipitation

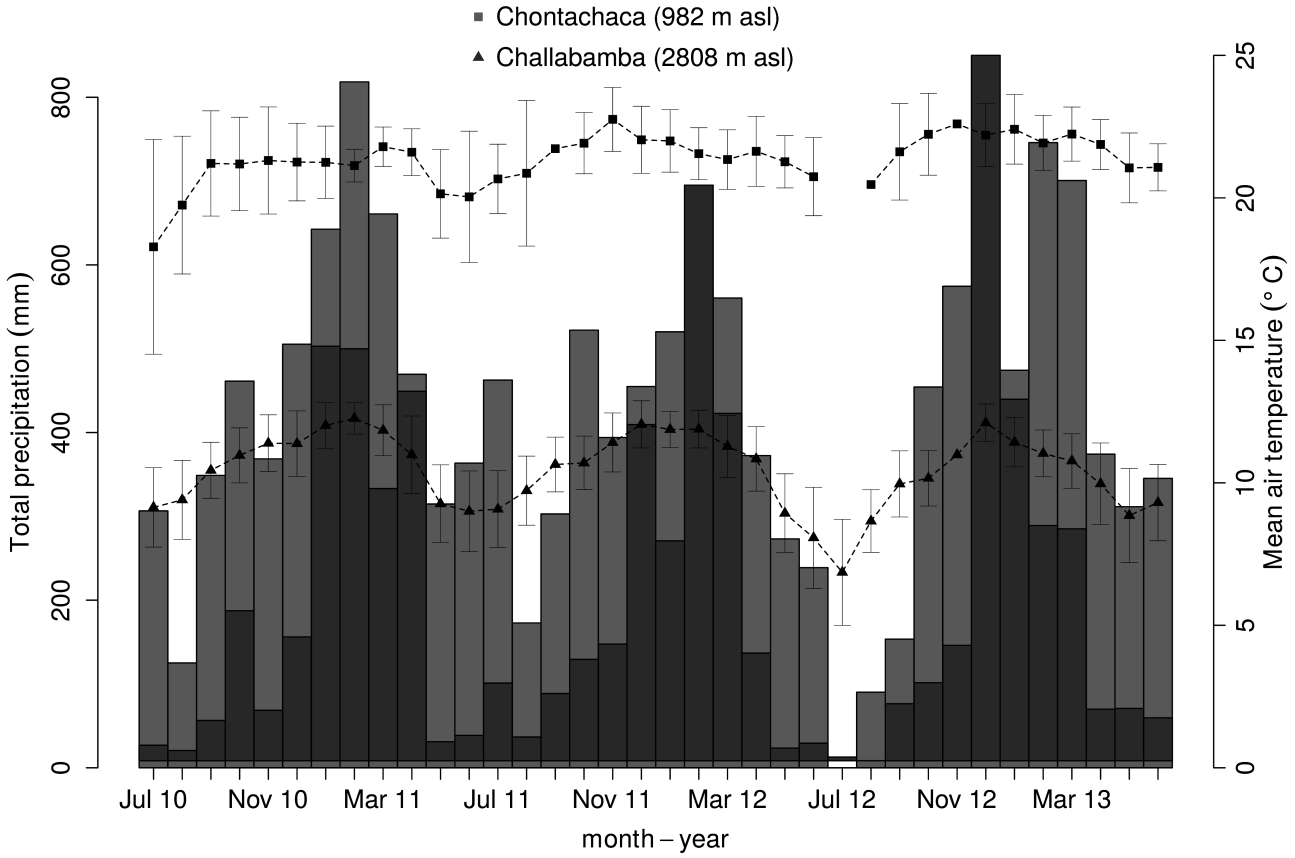

Figure 1 Total monthly precipitation and monthly mean diurnal~~day time~~ temperature between July 2010 and June 2013 at 982 m asl (Chontachaca weather station: 13°01 ′ 26 ″ S 71°28 ′ 04 ″ W) and 2808 m asl (Challabamba weather station: 13°13 ′ 03 ″ S 71°38 ′ 50 ″ W). Temperature error bars are standard errors. No data was available for July 2012 at Contachaca. Plotted data was retrieved from the Servicio Nacional De Meteorogia e Hidrologia Del Peru (http://www.senamhi.gob.pe).

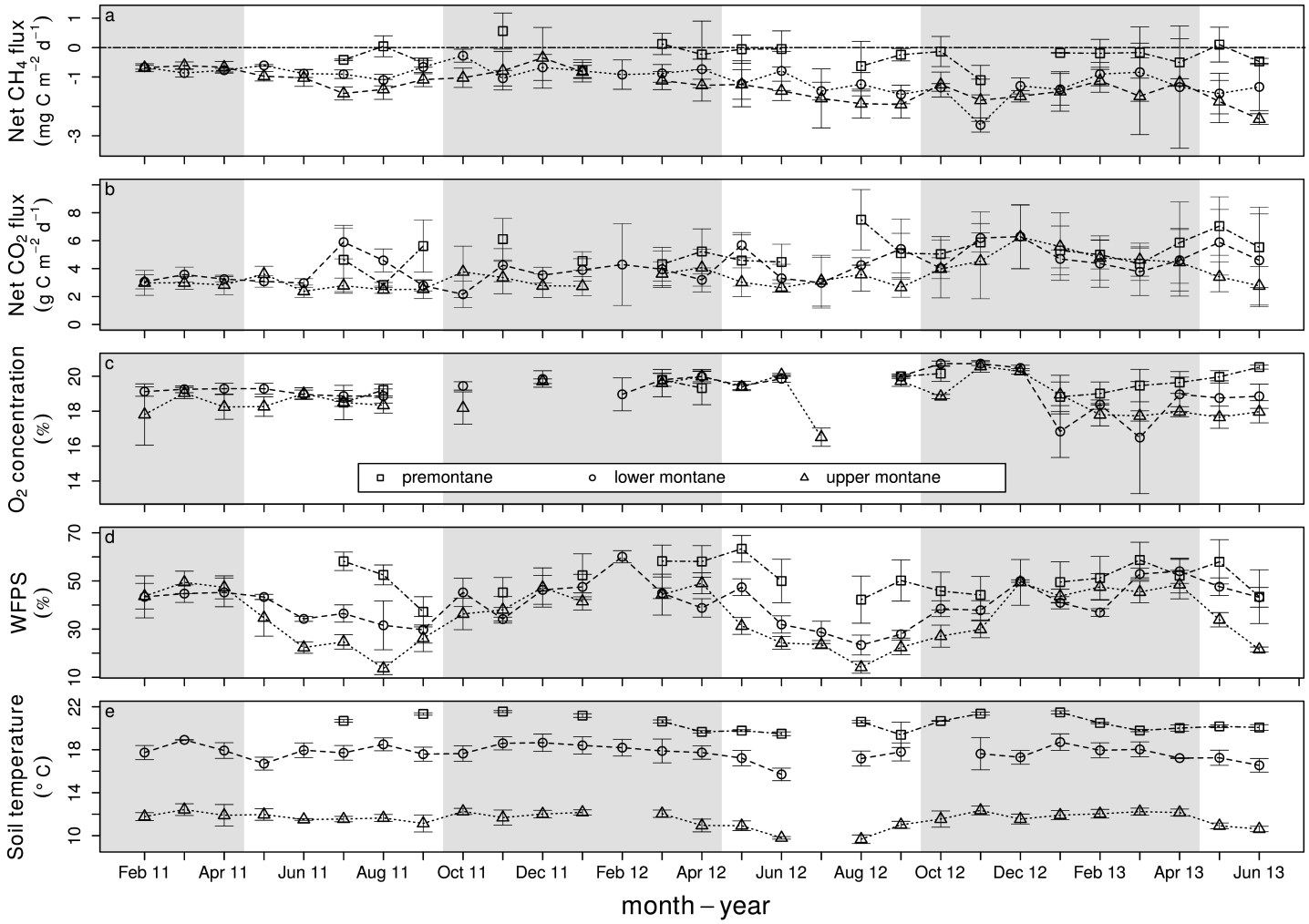

Figure 2 Monthly ~~site~~forest type means and standard deviation of a) net CH_4 flux, b) net CO_2 flux, c) soil O_2 concentration, d) WFPS and e) soil temperature. Shading indicates the wet season of October – April.

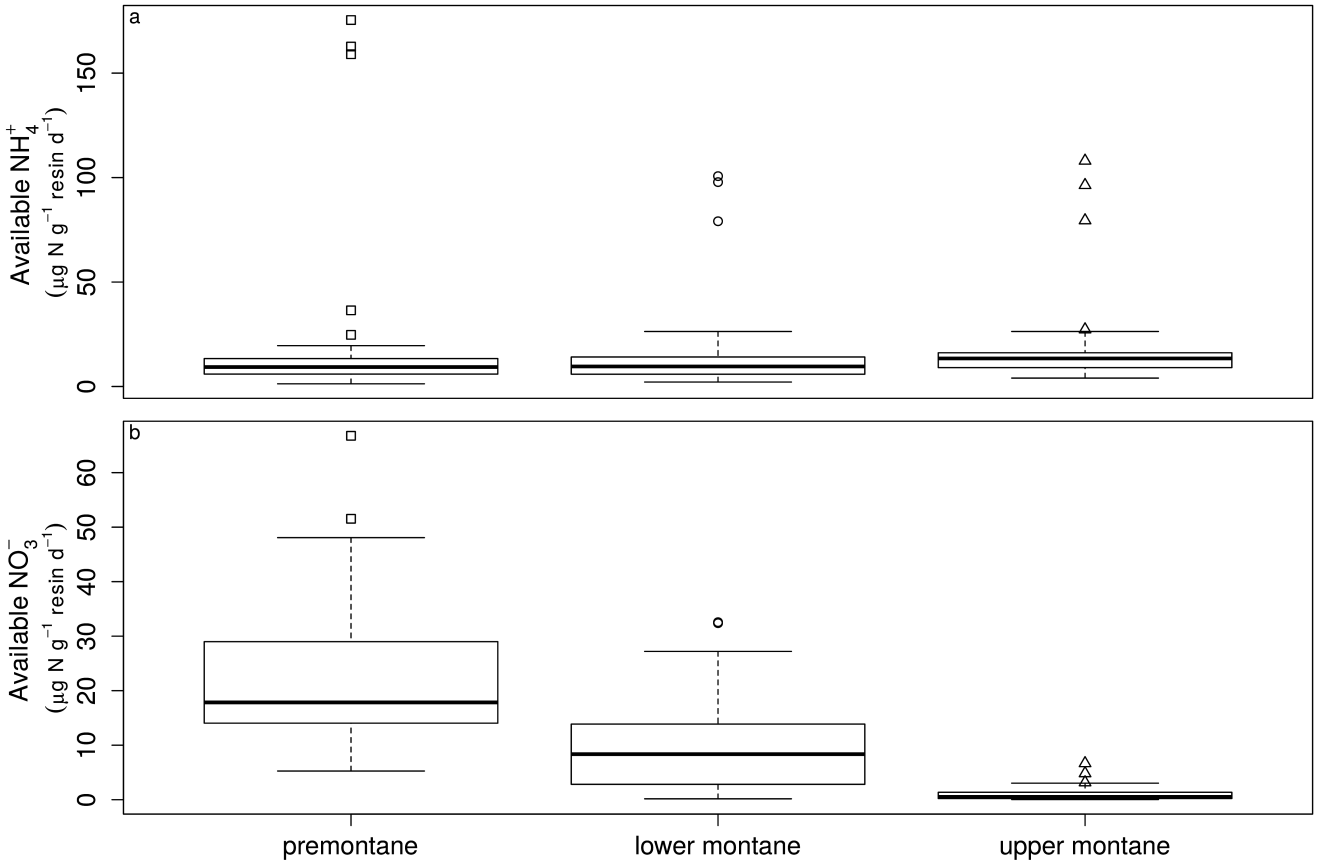

Figure 3 Boxplots of monthly mean inorganic nitrogen availability a) available NH_4^+ and b) available NO_3^-.

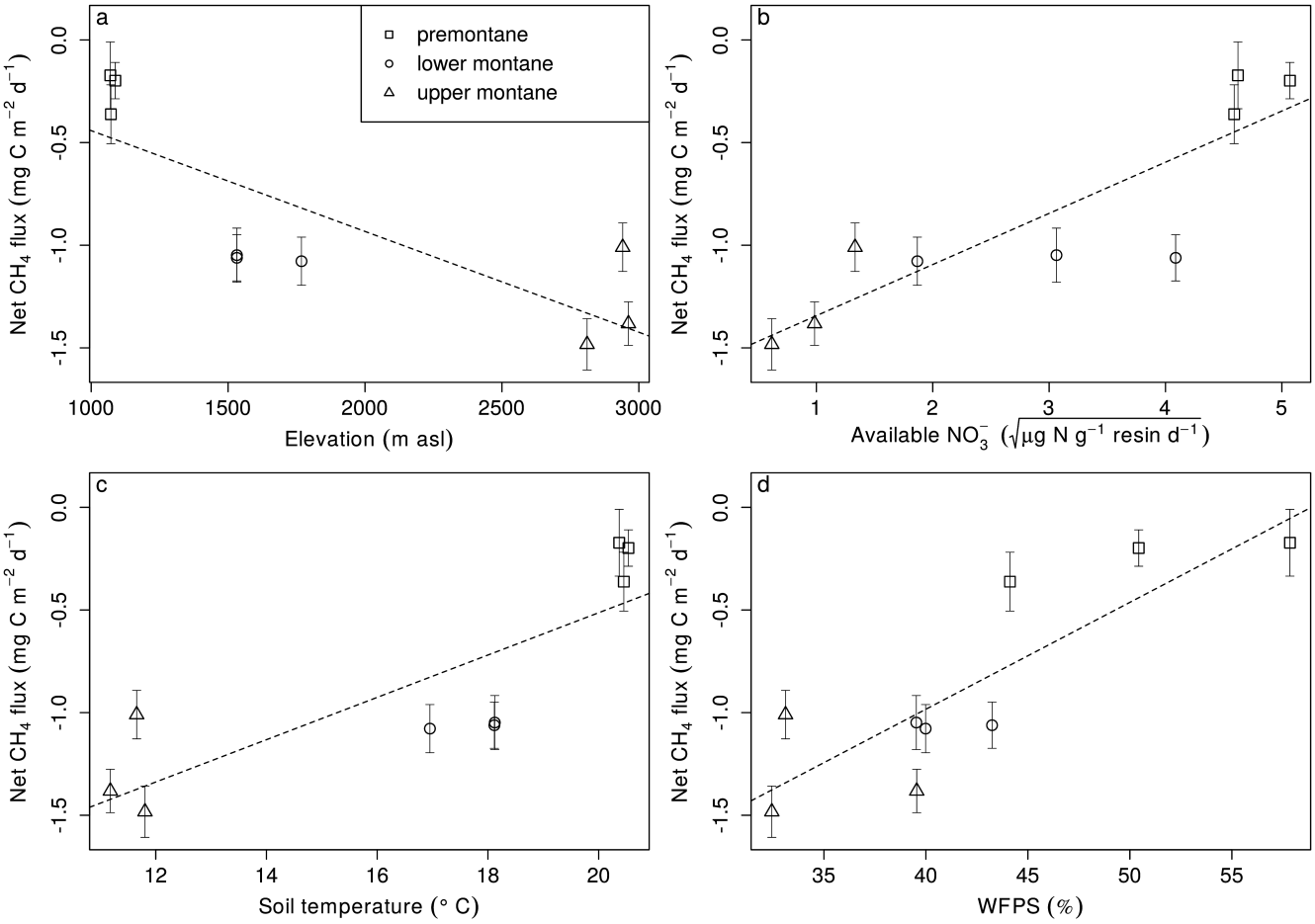

Figure 4 Relationships between dataset plot means of net CH_4 flux and a) elevation, b) square-root transformed available NO_3^-, c) soil temperature and d) WFPS across forest types. Error bars indicate standard error. Dashed lines indicate linear regressions between plotted variables: a) Net CH_4 flux = 0.49×10^{-3} * elevation – 0.05 ($r^2 = 0.61$), b) Net CH_4 flux = 0.25 * √available NO_3^- – 1.59 ($r^2 = 0.74$), c) Net CH_4 flux = 0.10 * soil temperature – 2.58 ($r^2 = 0.64$) and d) Net CH_4 flux = 0.05 * WFPS – 3.07 ($r^2 = 0.67$).