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. 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. Seasonality in CH_4 exchange varied among forest types with increased dry season CH_4 uptake 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). 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). This likely reflects 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 biological sink (Ciais et al., 2013). As soils are capable of acting as both globally significant sources or sinks for atmospheric CH_4 they are of particular interest in refining our understanding of CH_4 exchange across tropical landscapes (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 (Conrad, 1996; Le Mer and Roger, 2001). Well-drained soils are typically thought to act as 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). 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). 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). 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). 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). These anoxic 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 occluded microsites (Burgin et al., 2011; Sexstone et al., 1985). Where biological O_2 demand outstrips diffusional supply, these gradients can result in localised anoxia within such microsites (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). 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). 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).

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). In Central and

South America tropical forests are expansive, covering ~35 % of the South American continent (Eva et al., 2004), and exhibit 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). The majority of studies in the region have focussed on lowland forests below 600 m above 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). Tropical montane forests are an 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 CH_4 budgets. 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 forest soils act as 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), some ecosystems function as net atmospheric sources 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). 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). Similar contrasts exist between tropical montane forests where thick organic horizons develop (Purbopuspito et al., 2006; Wolf et al., 2012; Zimmermann et al., 2009a) and those where the superficial soils are organo-mineral in origin (Dubinsky et al., 2010; 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). 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 CH_4 uptake. 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) and play an important role in mechanistic models of soil CH_4 uptake (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) 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).

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). 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 and within the forests of this landscape.

2 Materials and methods

2.1 Study plots

Nine plots were established along the Andes Biodiversity and Ecosystems Research Group altitudinal transect (Malhi et al., 2010; Teh et al., 2014) to study CH_4 exchange in montane and premontane forests typical of the eastern flank of the Andes. In this region premontane forest extends from 600 to 1200 m asl, lower montane cloud forest from 1200 to 2200 m asl and upper montane cloud forest from 2200 m asl to the tree line at 3400 m asl (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. Plot 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 and 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 at ~ 3000 and 1500 m asl, respectively (Girardin et al., 2010). Total annual precipitation and mean annual air temperature at ~ 1000 m asl are 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 of thick organic horizons, ~ 20 cm deep in the upper and ~ 10 cm deep in the lower, whilst those of the premontane forest are principally mineral in origin (Girardin et al., 2010; Zimmermann et al., 2009a). This pattern is reflected in the carbon contents of these soils with typical values for the superficial 10 cm in the upper and lower montane forests of 40 - 50 % C and < 5 % C in the premontane forest (Zimmermann et al., 2009a). These soils are acidic with pH in the range of ~ 4.

Soil-atmosphere CH_4 exchange for 2011 has previously been reported for these plots as part of a study investigating non-CO_2 trace gas fluxes along an Andean altitudinal transect (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 acted as sinks for atmospheric CH_4 and the premontane forest had the potential to act as both a source or sink.

2.2 Sampling strategy

Each plot was 20 by 20 m and established approximately three months prior to the start of reported measurements in an attempt to minimise the effect of disturbances involved with installing sampling equipment (Varner et al., 2003). The premontane forest plots were situated on a ridge, slope and flat at 1070, 1070 and 1088 m asl, respectively. Similarly, the lower montane forest plots were established on a ridge, slope and flat at 1768, 1532 and 1532 m asl, respectively. Two of the upper montane forest plots were situated on slopes at 2811 and 2962 m asl and the third on a ridge at 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^-).

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 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). 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). 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 $\mu l\ l^{-1}\ m^{-2}\ s^{-1}$, were calculated in R (R Core Team, 2013) using the HMR package (Pedersen, 2012). Following the criteria outlined by Pedersen et al. (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). 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).

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 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). 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), 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. Available inorganic NH_4^+ and NO_3^- concentrations 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). 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 (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). Following model fits, multiple comparison of forest type and season was conducted in the multcomp package with Tukey contrasts (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). Spatial correlations were tested on dataset plot means whilst temporal correlations were tested on monthly 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). 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 influenced by forest type with greater uptake at 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 among all forest types. During the wet season, CH_4 uptake was smaller in the premontane forest than in both the upper and lower montane forests. Within forest types, no 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, with a modest shift towards greater CH_4 uptake 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, emissions were more common in the premontane forest with 29 % of fluxes registering net CH_4 efflux.

Fluxes of CO_2 were 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 smaller in the upper montane forest than both the premontane forests, whilst, during the wet season no differences were identified. Within forest types, there were no 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 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 smaller in the upper montane than the premontane forest. However, these differences were marginal with a range of 1.1 %. Within forest types no 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 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 different between all forest types. During the wet season WFPS in the premontane forest was

greater than those from both the upper and lower montane forests. Within forest types, WFPS was 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 (Fig. 2 d).

Soil temperature was 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 different between all forest types. Within forest types, soil temperatures were 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 (Fig. 3). Available NH_4^+ was not 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 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 different between all forest types with no seasonal differences, in part due to considerable within plot variability, within forest type.

3.2 Spatial relationships between gas fluxes and environmental conditions

Across these forests, plot means of net CH_4 flux were negatively correlated with elevation (Pearson's $r = -0.81$, $p < 0.01$, $n = 9$), 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). Plot means of net CH_4 flux were 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. 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^-. However, both WFPS (Pearson's $r = -0.79$, $p = 0.01$, $n = 9$) and available NO_3^- (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 $r = 0.83$, $p < 0.01$, $n = 9$).

3.3 Temporal relationships between gas fluxes and environmental conditions

The drivers of temporal variability in net CH_4 flux varied among forest types. In the upper montane forest, monthly forest type mean net CH_4 flux was 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 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, monthly forest type mean net CH_4 flux was 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, no strong correlations between monthly forest type mean net CH_4 flux and other measured variables were identified (Table 4). Here the strongest relationship with net CH_4 flux was a positive correlation with monthly 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 is comparable to those previously reported 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) 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), -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), -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), -0.7 mg CH_4 - C m^{-2} d^{-1} for a tableland in northern Australia (Kiese et al., 2008), -1.4 mg CH_4 - C m^{-2} d^{-1} in Kenya (Werner et al., 2007), -0.5 mg CH_4 - C m^{-2} d^{-1} in China (Werner et al., 2006), -0.1 mg CH_4 - C m^{-2} d^{-1} in Panama (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). 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).

Within forest types, net CH_4 fluxes were not significantly different between wet and dry season, indicating that these forests show little overall seasonal variability in net CH_4 uptake (Table 2). 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 (Table 2) may reflect interannual variability, and the fact that environmental conditions change gradually across seasonal transitions (Clark et al., 2014). The aseasonality of 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). This may impart reflect the fact that seasonal variations in rainfall and temperature become more pronounced with elevation across this transect (Fig. 1).

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). For example, Silver et al. (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 in the upper and lower montane forests of this study. 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).

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

The increase in CH_4 uptake with elevation across the transect was 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 greatest in the upper montane forest and smallest in the premontane forest. 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 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). Indeed, unlike studies where landscapes exhibiting net source activity are considered we did not find evidence that decreases in O_2 concentration were driving CH_4 exchange (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 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). 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). The positive relationship between net CH_4 flux and WFPS (Fig. 4 d) across forest 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). 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. 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 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). 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). Alternatively if methanogenic activity, despite limited evidence for anoxia, was 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). 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). 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 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 forests. As with the comparison across these forests, we found little evidence to suggest that soil O_2 concentration was an important factor in determining variability in soil-atmosphere CH_4 exchange. 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. Similar 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 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) 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 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). In the lower montane forest, increased CH_4 uptake was related to increased 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). 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 potentially reflecting fewer observations, the greater apparent role of production within microsites and the lack of seasonality in any of the measured parameters (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 the relationship between soil-atmosphere CH_4 exchange and elevation is poorly understood within montane regions. 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) or Indonesia (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 across similar elevation ranges (Foster, 2001). 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. 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). Furthermore, uptake peaked in the lower montane soils in Indonesia (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) 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. 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. In this study, a positive relationship between net CH_4 flux and available NO_3^- suggests inhibition of uptake, whilst a negative relationship between these parameters led Wolf (2012) to hypothesize that uptake in Ecuador was nitrogen limited. In contrast to both of these Andean studies, no relationship was identified in Indonesia (Purbopuspito et al., 2006). We speculate that the inverse altitudinal patterns in soil-atmosphere CH_4 exchange in Peru and Ecuador may be driven by 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. The fact that no relationship between net CH_4 flux and water content was identified in either Ecuador (Wolf et al.,

2012) or Indonesia (Purbopuspito et al., 2006) may reflect the fact that both of these studies report gravimetric water content rather than WFPS, where the former moisture index does not always adequately characterise the influence of soil structure on diffusion (Verchot et al., 2000). Wolf et al. (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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Table 1 Study area and plot characteristics.

Study area						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^+ (µg N g^{-1} res. d^{-1})		Available NO_3^- (µg 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 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 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 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

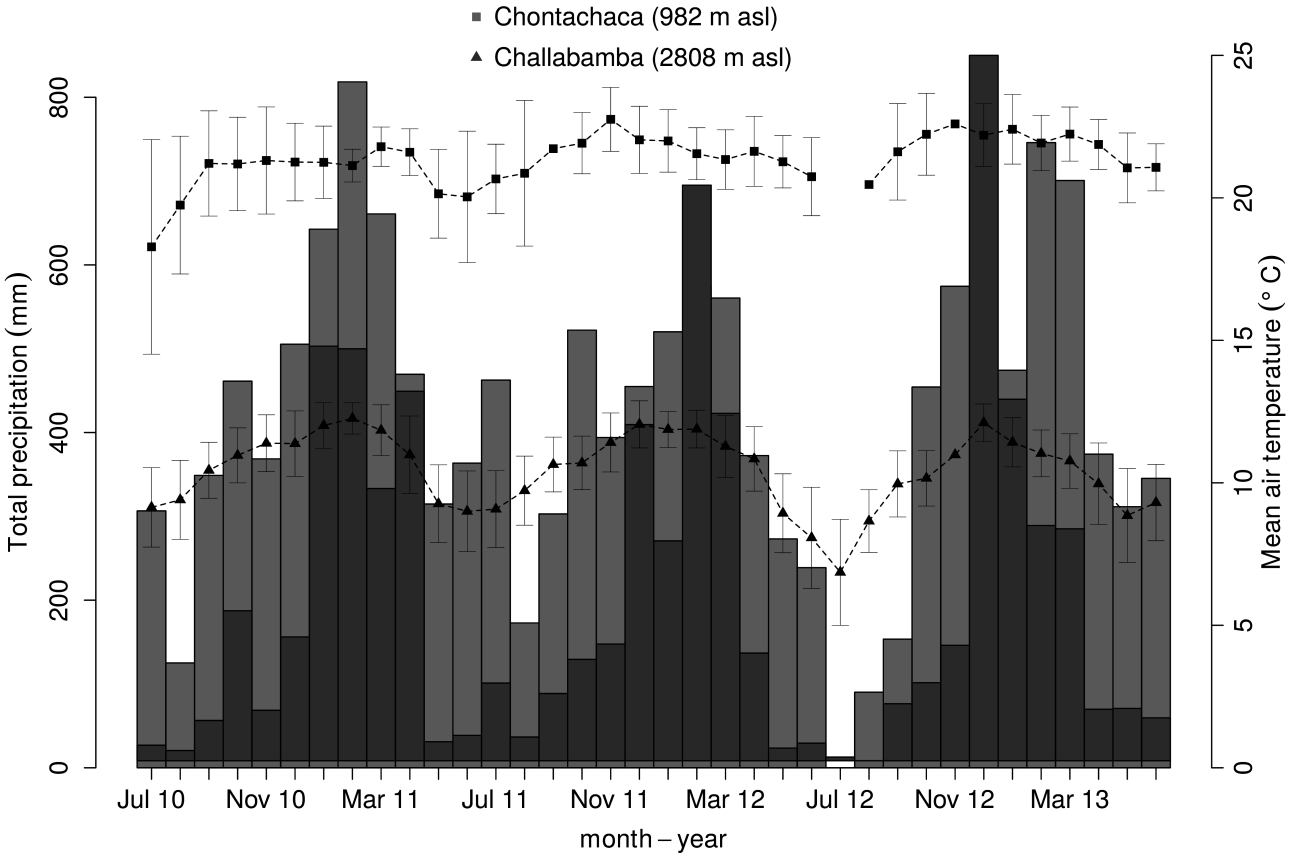

Figure 1 Total monthly precipitation and monthly mean diurnal temperature between July 2010 and June 2013 at 982 m asl (Chontachaca weather station: 13°01 ′ 26 ″ S 71°28 ′ 04 ″ W) and 2808 m asl (Challabamba weather station: 13°13 ′ 03 ″ S 71°38 ′ 50 ″ W). Temperature error bars are standard errors. 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).

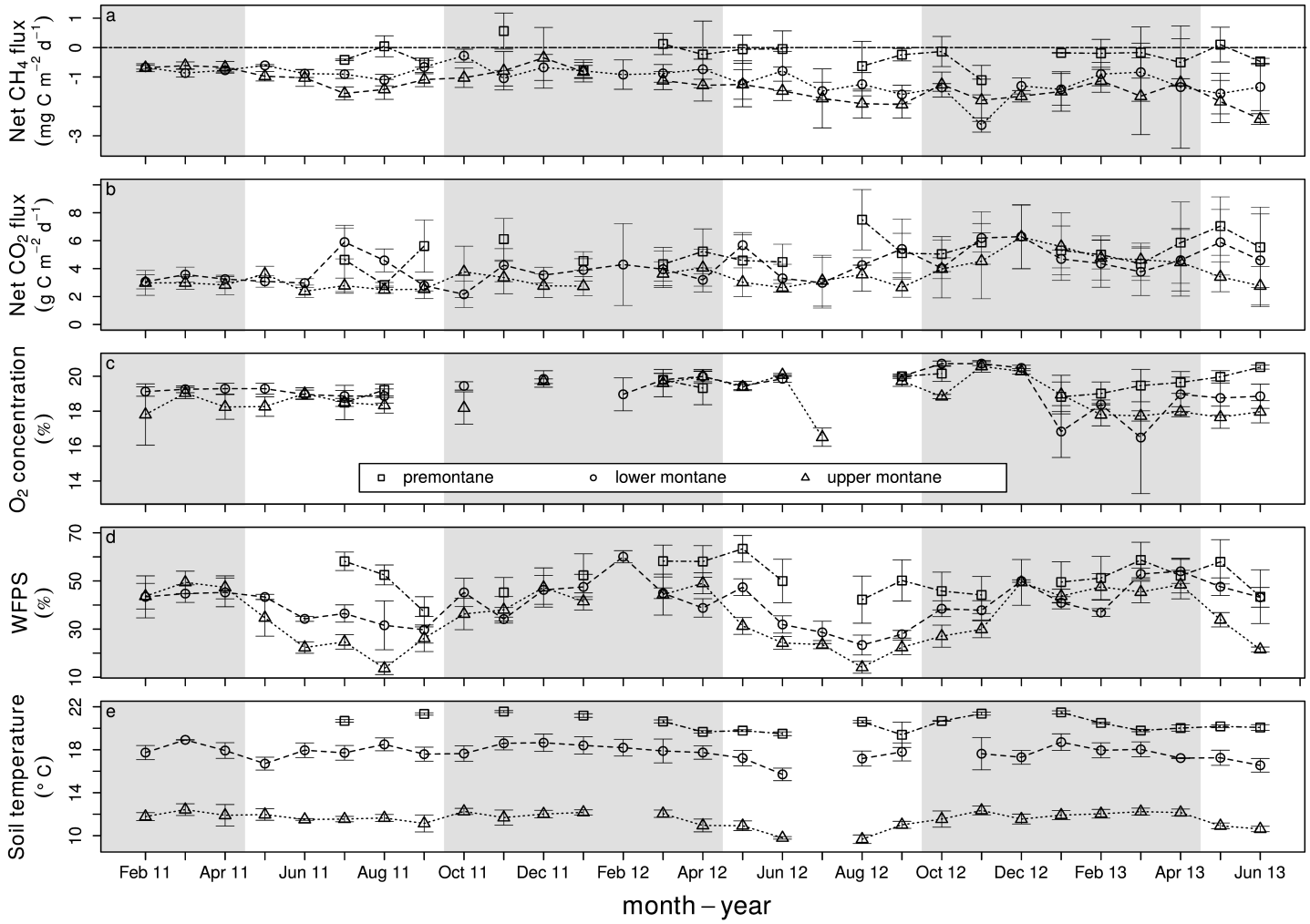

Figure 2 Monthly forest type means and standard deviation of a) net CH_4 flux, b) net CO_2 flux, c) soil O_2 concentration, d) WFPS and e) soil temperature. Shading indicates the wet season of October – April.

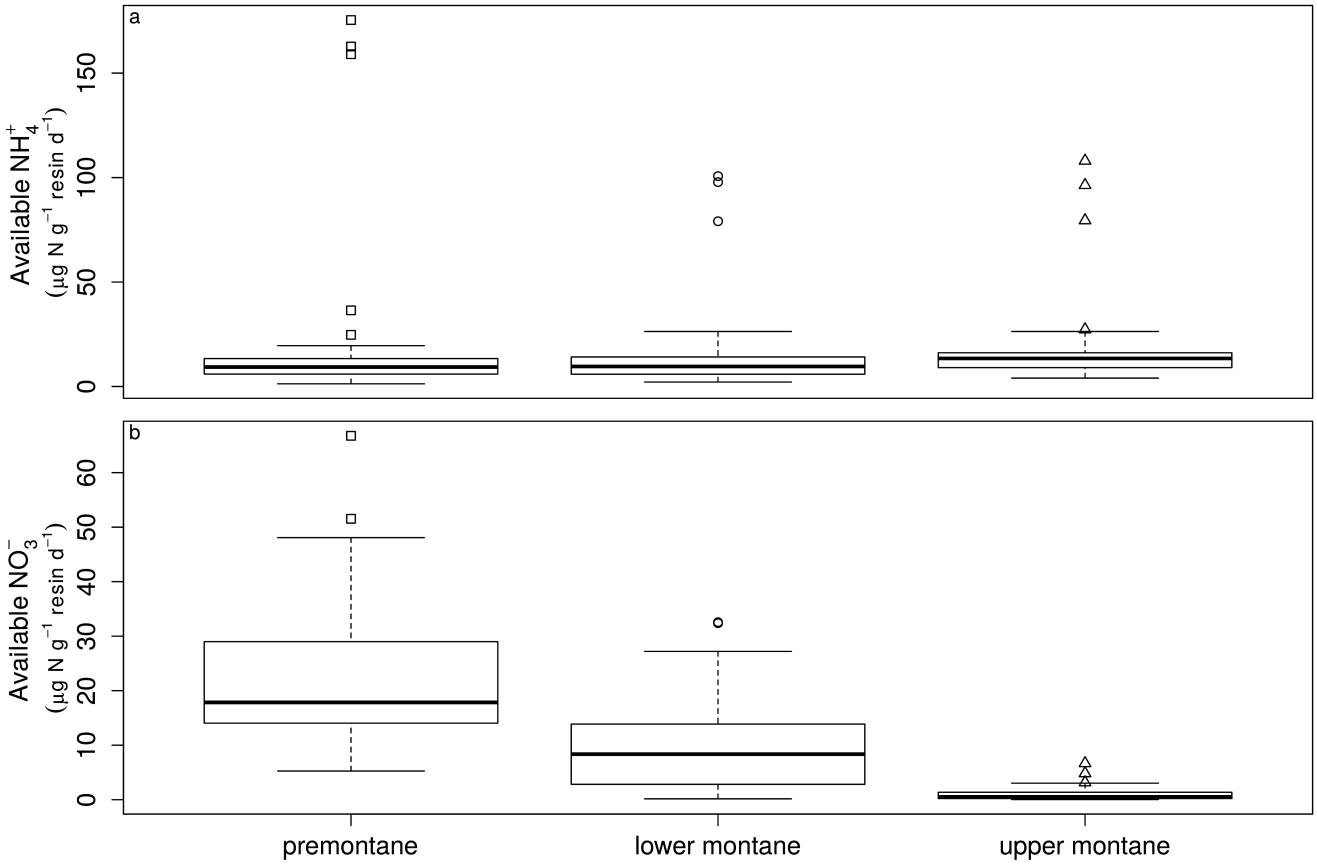

Figure 3 Boxplots of monthly mean inorganic nitrogen availability a) available NH_4^+ and b) available NO_3^-.

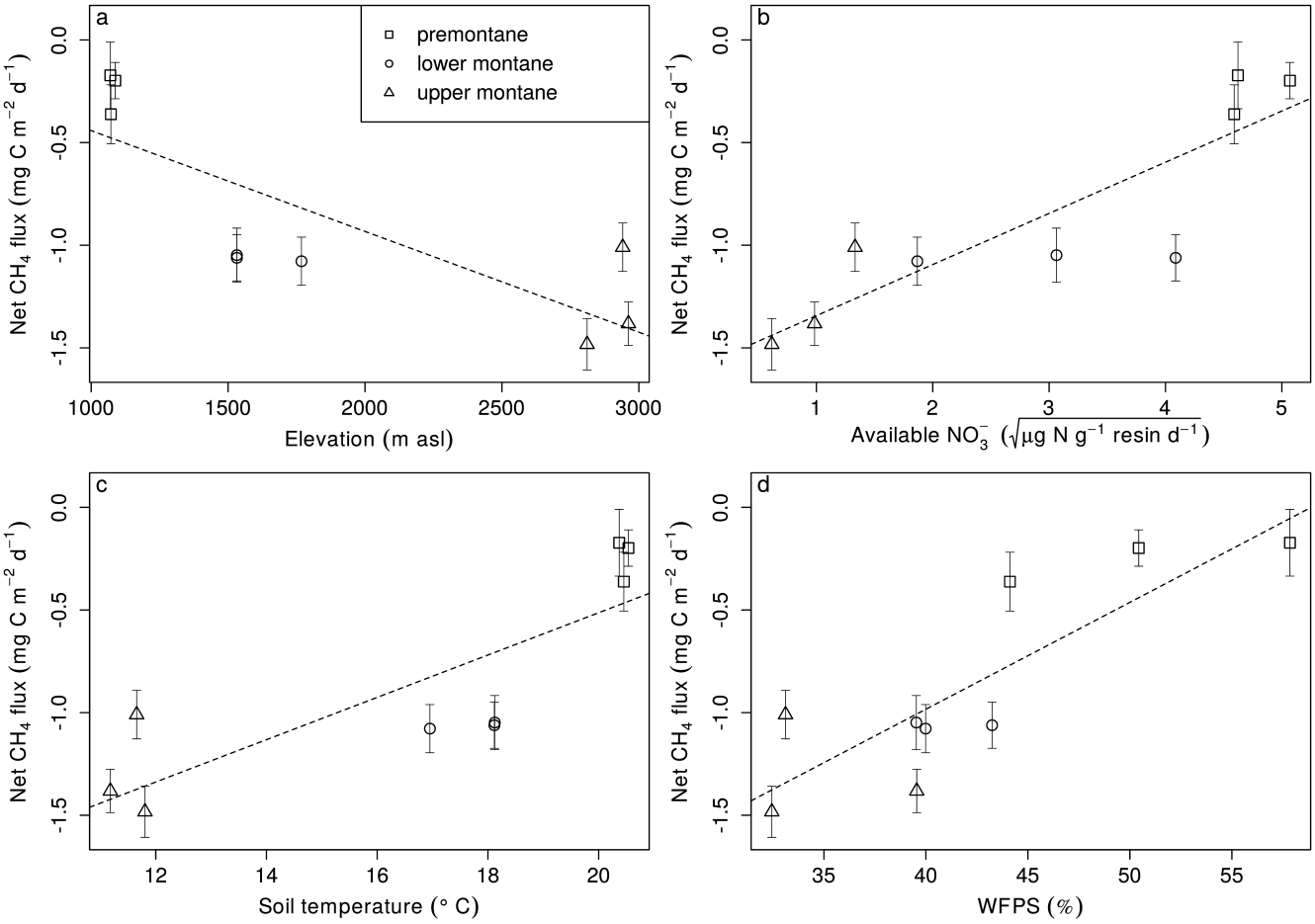

Figure 4 Relationships between dataset plot means of net CH_4 flux and a) elevation, b) square-root transformed available NO_3^-, c) soil temperature and d) WFPS across forest types. Error bars indicate standard error. Dashed lines indicate linear regressions between plotted variables: a) Net CH_4 flux = 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 ($r^2 = 0.67$).