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Soil trace gas fluxes along orthogonal precipitation and soil fertility gradients in tropical lowland forests of Panama

Amanda L. Matson[*1], Marife D. Corre[*1], Kerstin Langs[1] and Edzo Veldkamp[1]

[*]These authors contributed equally to this work

[1]Buesgen Institute, Soil Science of Tropical and Subtropical Ecosystems, Georg-August University, Buesgenweg 2, 37077, Goettingen, Germany

Correspondence to: Amanda L. Matson (amatson@gwdg.de)

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Abstract

Tropical lowland forest soils are significant sources and sinks of trace gases. In order to model soil trace gas flux for future climate scenarios, it is necessary to be able to predict changes in soil trace gas fluxes along natural gradients of soil fertility and climatic characteristics. We quantified trace gas fluxes in lowland forest soils at five locations in Panama, which encompassed orthogonal precipitation and soil fertility gradients. Soil trace gas fluxes were measured monthly for one (NO) or two (CO_2, CH_4, N_2O) years (2010-2012), using vented dynamic (for NO only) or static chambers with permanent bases. Across the five sites, annual fluxes ranged from: 8.0 to 10.2 Mg CO_2-C ha^{-1} yr^{-1}, -2.0 to -0.3 kg CH_4-C ha^{-1} yr^{-1}, 0.4 to 1.3 kg N_2O-N ha^{-1} yr^{-1} and -0.82 to -0.03 kg NO-N ha^{-1} yr^{-1}. Soil CO_2 emissions did not differ across sites, but did exhibit clear seasonal differences and a parabolic pattern with soil moisture across sites. All sites were CH_4 sinks; within-site fluxes were largely controlled by soil moisture whereas fluxes across sites were positively correlated with an integrated index of soil fertility. Soil N_2O fluxes were low throughout the measurement years, but highest emissions occurred at a mid-precipitation site with high soil N availability. NO uptake in the soil occurred at all sites, with the highest uptake at the low-precipitation site closest to Panama City; NO uptake was likely due to high ambient NO concentrations from anthropogenic sources. Our study highlights the dual importance of short-term (climatic) and long-term (soil/site characteristics) factors in predicting soil trace gas fluxes.

Keywords: greenhouse gases, carbon dioxide, methane, nitric oxide, nitrous oxide, tropical forest

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1 Introduction

Soils can be both sources and sinks of carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O) and nitric oxide (NO). Tropical forest soils, specifically, are the largest natural source of soil CO_2 (Raich and Schlesinger, 1992) and N_2O (Bouwman et al., 1993; Prather et al., 1995) and can be significant sinks of CH_4 (Steudler et al., 1996; Keller et al., 2005; Sousa Neto et al., 2011). Although soil NO fluxes in tropical forests are often low (Keller and Reiners, 1994; Koehler et al., 2009b), and the canopy can act as a sink for a large proportion of soil-emitted NO (Rummel et al., 2002), even low emissions may be important in regulating atmospheric oxidant production (Keller et al., 1991; Chameides et al., 1992). Studies from Central and South American (CSA) tropical lowland forests have measured a large range of annual soil trace gas fluxes; in one case, N_2O emissions varied by one order of magnitude within a single study (1.23 to 11.39 kg N ha^{-1} yr^{-1}; Silver et al., 2005). Such disparity in measurements, caused by the temporal and spatial variability found in tropical forests (Townsend et al., 2008), makes it challenging to model soil trace gas fluxes from these areas and to predict how they might be affected by climate change.

Temporal variations in soil trace gas fluxes are primarily correlated with temperature and moisture. Temperature is often more important where there are annual extremes in temperature - such as in temperate and boreal regions - whereas precipitation and soil moisture are more important in tropical regions, where air temperature does not vary much throughout the year (Saikawa et al., 2013). Soil temperature in CSA tropical forests can be positively correlated with soil CO_2 emissions (Chambers et al., 2004; Schwendenmann and Veldkamp, 2006; Sotta et al., 2006, Koehler et al., 2009a) and NO flux (Gut et al., 2002), and negatively correlated with soil N_2O emissions (Keller et al., 2005), though the latter may be due to a co-correlation of soil

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temperature with soil moisture (see below). For soil CH_4 fluxes, given that the activity of both methanotrophs (CH_4 consumers) and methanogens (CH_4 producers) can increase with temperature (Conrad, 1996; Chin et al., 1999; Mohanty et al., 2007), net changes of soil CH_4 fluxes in response to temperature may be driven by other site conditions, such as soil moisture.

Soil moisture affects microbial activity, which leads to trace gas production or consumption, both directly through water availability and indirectly through its influence on the soil oxygen status and gas diffusivity (Davidson and Schimel, 1995). Soil CO_2 emissions from CSA tropical forest soils generally exhibit positive relationships with soil moisture (Davidson et al., 2000), which may be parabolic, with emissions increasing until the threshold at which anaerobic conditions start to inhibit soil CO_2 production and/or gas diffusion and then decreasing (Schwendenmann et al., 2003; Sotta et al., 2006; Kohler et al., 2009a). Soil CH_4 fluxes (positive values for net emissions and negative values for net consumption) in CSA tropical lowland forests also tend to exhibit positive correlations with soil moisture (Keller and Reiners, 1994; Verchot et al., 2000; Davidson et al., 2004; Veldkamp et al., 2013) since high soil moisture conditions favor CH_4 production, while CH_4 consumption is reduced due to inhibited diffusion of CH_4 from the atmosphere to the soil (Le Mer and Roger, 2001; Koehler et al., 2012; Veldkamp et al., 2013). In general, soil NO production through nitrification dominates in aerobic conditions whereas soil N_2O production through denitrification dominates in anaerobic conditions (Conrad, 2002). Therefore, as shown in several CSA tropical forest studies (Keller and Reiners, 1994; Verchot et al., 1999; Davidson et al., 2004; Keller et al., 2005; Koehler et al., 2009b), with increases in soil moisture, soil NO fluxes generally decrease (though Gut et al., 2002 show that this relationship is complex) while soil N_2O fluxes increase.

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Spatial variations in soil trace gas fluxes are largely controlled by soil physical and biochemical characteristics. Soil texture strongly influences soil water retention and gas diffusivity (Koehler et al. 2010; Hassler et al. 2015) as well as soil fertility, plant productivity, decomposition and ultimately soil N availability (Silver et al., 2000; Sotta et al., 2008; Allen et al., 2015). In CSA tropical forests, both Silver et al. (2005) and Sotta et al. (2006) observed higher soil CO_2 emissions from sandy than clayey Ferralsol soils, which were attributed to respiration from the higher fine root biomass in the sandy soils. Soil N-oxide fluxes may also be affected by soil texture; soil N_2O emissions can be stimulated by the higher soil N availability and greater proportion of anaerobic microsites in clayey soils (Keller et al., 2005; Silver et al., 2005; Sotta et al., 2008) whereas soil NO fluxes can be facilitated by the higher diffusivity in sandy soils (Silver et al., 2005). Although they have less often been the focus of trace gas studies, soil biochemical characteristics (i.e. soil fertility status) also play an important role in soil trace gas fluxes. Schwendenmann et al. (2003) observed a positive relationship between soil CO_2 flux and spatial differences in soil organic C and total N, and a negative relationship with soil total P (possibly due to lower fine root biomass in areas of high P). Veldkamp et al. (2013) reported that increases in soil N availability stimulate CH_4 uptake and/or reduce CH_4 production in soil, and Hassler et al. (2015) also showed that soil fertility (i.e. increased soil N availability and decreased soil exchangeable Al) enhances soil CH_4 uptake. Finally, as an essential substrate for nitrification and denitrification, N availability in the soil is the primary controlling factor of soil N-oxide fluxes (Koehler et al., 2009b; Corre et al., 2014).

Climate scenarios suggest that tropical regions may experience large changes in precipitation regimes in the future, with moist tropical regions likely experiencing both higher annual precipitation and more extreme precipitation events (Stocker et al., 2013). Such changes

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could significantly alter current soil trace gas fluxes, since soil moisture – as described above – plays an important role in both the temporal and spatial variability of soil trace gas fluxes. One approach to studying how changes in precipitation may alter soil trace gas fluxes is to investigate these fluxes along a natural gradient of climate (e.g. precipitation) in a localized region. This approach was used by Holtgrieve et al. (2006) on the Kula volcanic series lava flow in Hawaii, to show that soil N cycling and N-oxide fluxes were strongly affected by mean annual precipitation. However, as suggested by Santiago et al. (2005), precipitation gradients in continental tropical forests, where there are variations in species composition and soil parent material, may exhibit different patterns than those from Hawaii. Additionally, precipitation (or climate) is itself a soil forming factor (Jenny, 1945), and continental tropical lowland soils are considerably older than the relatively young volcanic soils (i.e. Santiago et al., 2005). Therefore, soils of continental precipitation gradients will reflect both the long-term effects of the precipitation regime (i.e. on differences in soil physical and biochemical characteristics) in addition to short-term effects (i.e. on soil moisture).

In this study, we quantified soil trace gas fluxes in tropical lowland forests of the Panama Canal Watershed, spanning a precipitation gradient of 1700-3400 mm yr^{-1} (Figure S1). Soil fertility (based on an aggregate index that included clay content, ^{15}N natural abundance, effective cation exchange capacity (ECEC), organic C:N ratio, and exchangeable Al; see 2.4) varied orthogonally with this precipitation gradient (Figure S2). The objectives of our study were to: (1) determine how soil fluxes of CO_2, CH_4, N_2O and NO vary along orthogonal gradients of precipitation and soil fertility, and (2) assess and compare the spatial and temporal controls of soil trace gas fluxes in lowland tropical forests. By using orthogonal gradients of precipitation and soil fertility, we were able to examine the relative importance of climatic factors vs. soil

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biochemical characteristics for soil trace gas fluxes. We hypothesized that the temporal and spatial patterns of soil trace gas fluxes across sites would follow the pattern of the most important controlling soil factors: soil CO_2 fluxes would be parabolic in relation to increasing soil moisture along the precipitation gradient; soil CH_4 fluxes would increase (or CH_4 consumption would decrease) with increasing soil moisture and decreasing soil fertility along the precipitation gradient; and soil NO fluxes would decrease whereas soil N_2O fluxes would increase with increasing soil moisture along the precipitation gradient.

2 Methods

2.1 Study sites

Soil trace gas fluxes were measured in five study sites of the Center for Tropical Forest Science (CTFS) located in the Panama Canal Watershed, central Panama (Table 1; Figure S1). Mean annual air temperature is 27 °C (Windsor, 1990); the soil temperature across all sites fluctuated between 22.5 and 27.5 °C during our study years (Fig. 1a). The five sites span a gradient of annual precipitation from 1700 mm yr^{-1} in Metropolitan National Park (Met) on the Pacific side to 3400 mm yr^{-1} in P32 on the Atlantic side; the dry season generally lasts from January through April (Corre et al., 2014). The sites were located in either old growth (P8 and P32) or mature secondary (Met, P27, and P19) lowland forests, with tree densities (≥10 cm diameter at breast height, DBH) of: 322 stems ha^{-1} in Met, 395 stems ha^{-1} in P27, 560 stems ha^{-1} in P8, 520 stems ha^{-1} in P19, and 537 stems ha^{-1} in P32 (Pyke et al., 2001). Since precipitation and parent materials vary across these sites, soil types also vary from Cambisols (Met and P27) on the Pacific side to Ferralsols (P8, P19, and P32) on the Atlantic side (Table 1). Floristic composition in these sites has been shown to be correlated with both regional precipitation and geology/soil

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147 attributes (Pyke et al., 2001). The amounts and forms of soil organic P are strongly controlled by
148 soil properties whereas the proportion of soil organic P to total P is insensitive to the variation in
149 rainfall and soil properties (Turner and Engelbrecht, 2011).
150
151 **2.2 Soil trace gas flux measurement**
152 Soil CO_2, CH_4 and N_2O fluxes were measured every 2-4 weeks from June 2010 through
153 February 2012 (28-31 sampling dates) using static vented chambers. Within each of the five
154 sites, a 20 m grid was placed over a 1 ha area and we randomly chose four 20 m x 20 m replicate
155 plots with a minimum distance of 20 m between plots. In each replicate plot, four permanent
156 chamber bases were installed (0.04 m^2 area and 0.25 m height after inserting 2 cm into the soil)
157 at the ends of two perpendicular 20 m transects that crossed in the plot's center. The total volume
158 of the chamber (with cover) was 11 L. To measure soil trace gas fluxes, chamber covers were
159 placed on the bases and gas samples (100 mL) were taken 2, 12, 22 and 32 min later. Samples
160 were stored in pre-evacuated glass containers with Teflon-coated stopcocks. At the Gamboa field
161 laboratory, gas samples were then analyzed for CO_2, CH_4 and N_2O concentrations using a gas
162 chromatograph (Shimadzu GC-14B, Columbia, MD, USA) equipped with a flame ionization
163 detector (FID), an electron capture detector (ECD) and an autosampler, the same instrument that
164 was used in our earlier studies (Koehler et al. 2009a, 2009b, 2010, 2012; Veldkamp et al., 2013;
165 Corre et al. 2014). Gas concentrations were determined by comparing integration peaks with
166 those of three or four standard gases containing increasing concentrations of CO_2, CH_4 and N_2O
167 (Deuste Steininger GmbH, Mühlhausen, Germany).
168 Soil NO fluxes were measured every 2-4 weeks from June 2010 through June 2011 (18-
169 21 sampling dates) using open dynamic chambers (11 L volume) placed for 5-7 minutes on the

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same permanent bases described above. The air from the chamber was sampled by a pump with a flow rate of 0.5-0.6 L min^{-1}, passed through a CrO_3 catalyst that oxidizes NO to NO_2, and flowed across a fabric wick that is saturated with a luminol solution. The luminol then oxidizes and produces chemiluminescence, which is proportional to the concentration of NO_2, and is measured with a Scintrex LMA-3 chemiluminescence detector (ScintrexUnisearch, Ontario, Canada). To minimize deposition losses within the sampling system, all parts in contact with the sample gas are made of Teflon (PTFE). To prevent contamination of tubing and analyzers, particulate matter is removed from the sampled air by PTFE particulate filters (pore size: 5 µm). In order to minimize potential changes in catalyst efficiency caused by variations of air humidity, a known flux of ambient air dried by silica gel was mixed to the sampled air to maintain a humidity of ~50 %; the detector was also calibrated in-situ prior to and following chamber measurements, using a standard gas (3000 ppb NO; DeusteSteininger GmbH, Mühlhausen, Germany).

Soil trace gas fluxes were calculated as the linear change in concentration over time, and were adjusted for air temperature and atmospheric pressure measured during or directly after sampling; zero fluxes were included in the data statistical analysis. Annual soil NO fluxes were calculated using the June 2010-May 2011 measurements and annual soil CO_2 and N_2O fluxes were calculated using the January to December 2011 measurements; annual fluxes were calculated using the trapezoid rule between days with measured fluxes (Koehler et al. 2009a, 2009b, 2010; Veldkamp et al., 2013; Corre et al. 2014).

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191 **2.3 Soil biochemical characteristics**

192 In each replicate plot after each soil trace gas flux measurement, samples of the top 5 cm of soil
193 were taken about 1 m from each of the 4 chamber bases, pooled and mixed thoroughly in the
194 field to measure soil extractable NH_4^+ and NO_3^- concentrations and gravimetric water content. In
195 the field, soil samples were placed into prepared extraction bottles containing 150 mL of 0.5M
196 K_2SO_4 and shaken thoroughly. Back at the field station (≤ 6 h after samples were taken), the
197 extraction bottles were again shaken (~ 1 h) and then the extracts were filtered and frozen
198 immediately. The remaining soil was oven-dried at 105 °C for 1 day in order to ascertain
199 gravimetric water content; this was then used to calculate the dry mass of the soil that had been
200 extracted for mineral N. The frozen extracts were sent by air to the University of Göttingen,
201 Germany for analysis by continuous flow injection colorimetry (Cenco/Skalar Instruments,
202 Breda, Netherlands). The Berthelot reaction method was used to determine NH_4^+ (Skalar Method
203 155-000) and the copper-cadmium reduction method was used to determine NO_3^- (NH_4Cl buffer
204 without ethylenediaminetetraacetic acid; Skalar Method 461-000).

205 Soil pits were dug in the center of each of the four replicate plots per site and soil samples
206 were taken for the depth intervals of 0-5, 5-10, 10-25 and 25-50 cm. Soil samples were air-dried
207 and sieved through a 2-mm sieve. Natural abundance ^{15}N signatures were determined from the
208 ground soil samples using isotope ratio mass spectrometry (IRMS; Delta Plus, Finnigan MAT,
209 Bremen, Germany). We calculated the $\delta^{15}N$enrichment factor (ε) using the Rayleigh equation
210 (Mariotti et al., 1981): $\varepsilon = d_s - d_{so} / \ln f$, where d_s is the $\delta^{15}N$ natural abundance at different depths
211 in the soil profile, d_{so} is the $\delta^{15}N$ natural abundance of the reference depth (top 5 cm), and f is the
212 fraction of total N remaining (i.e. the total N concentration at a given depth divided by the total
213 N concentration in the top 5 cm). The ε value was used as an integrative indicator of soil N

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214 availability, as this correlates with internal soil-N cycling rates (Sotta et al., 2008; Baldos et al.,
215 2015). Total organic C and N were measured from the ground soil samples by dry combustion
216 using a CN analyzer (ElementarVario EL; Elementar Analysis Systems GmbH, Hanau,
217 Germany). ECEC was determined from the sieved soil samples by percolating with unbuffered
218 1M NH_4Cl and measuring the exchangeable element concentrations (Ca, Mg, K, Mn, Na, Fe and
219 Al) in the percolates using an inductively coupled plasma-atomic emission spectrometer (ICP-
220 AES; Spectroflame, Spectro Analytical Instruments, Kleve, Germany). Base saturation was
221 calculated as the ratio of exchangeable base cations to the ECEC. Soil pH (H_2O) was analyzed
222 from a 1:4 soil-to-water ratio. Particle size distribution of the mineral soil was determined using
223 the pipette method with pyrophosphate as a dispersing agent (König and Fortmann, 1996).
224
225 **2.4. Soil fertility index**
226 The variation in soil types along our rainfall gradient (Table 1) was paralleled with variations in
227 soil biochemical characteristics (Table 2; see 3.1). Thus, we developed a soil fertility index using
228 principal component analysis (PCA), similar to the approach employed by Swaine (1996); for
229 each site, the index was based on five soil physical and biochemical properties: 1) clay content,
230 which reflects water- and nutrient-holding capacity, 2) ε that signifies long-term soil N status, 3)
231 ECEC and soil C:N ratio, which indicate bioavailability of rock-derived nutrients and soil
232 organic matter, and 4) exchangeable Al, which implies soil chemical suitability. We used the
233 depth-weighted average of these soil parameters (Table 2), measured at various depth intervals in
234 the top 50 cm depth (except for ε that is calculated for the whole depth; see above). The first
235 component factor of this PCA analysis explained 42 % of the variation in these soil
236 characteristics among sites (Figure S2) and the factor scores were used as the quantitative index

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of soil fertility for each of the four replicate plots per site. This analysis showed that soil fertility of the five lowland forests varied orthogonally with the precipitation gradient (Figure S2).

2.4 Statistical analyses

We note that our statistical tests are based on the four replicate plots in each of the five 1-ha forest sites along these orthogonal gradients of precipitation and soil fertility, and that the sites themselves were not replicated along the gradients. Consequently, our interpretations and conclusions are limited only to these studied sites.

Soil trace gas fluxes (based on the average of the four chambers per replicate plot on each sampling day) and the accompanying soil explanatory variables (soil temperature, gravimetric moisture, NH_4^+ concentration and NO_3^- concentration) were tested for normality using Shapiro-Wilk's test; variables with non-normal distributions were square root or log transformed. We then used linear mixed effects models (LMEs) to assess the differences in these repeatedly-measured variables along the orthogonal precipitation and soil fertility gradients, with site and/or season as the fixed effect(s) and sampling days and replicate plots as random effects. If the Akaike information criterion showed an improvement in the LME models, we included a first-order temporal autoregressive function to account for the decreasing correlation of measurements with increasing time (Zuur et al., 2009) and/or a variance function (varIdent) to account for heteroscedasticity of fixed-factor variances (Crawley, 2012). To assess the relationships between soil trace gas fluxes and soil explanatory variables, we used the mean values of the four replicate plots on each sampling date, and conducted Pearson correlation tests over the entire sampling period across the five sites and for each site.

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For the soil biochemical characteristics measured only once (Table 2), differences in depth-weighted values (for the top 50 cm) among sites were evaluated using one-way analysis of variance followed by a Tukey HSD test. Their relationships with soil trace gas fluxes across the five sites (using annual values and average seasonal values) were tested using Spearman rank correlations. In all statistical tests, differences among sites or between seasons and correlation coefficients were considered significant at $P \leq 0.05$. Data analyses were conducted using the R open source software (R Core Team, 2013).

3 Results

3.1 Soil biochemical characteristics

The soil $\delta^{15}N$ natural abundance signatures and ε, which are proxies of the long-term soil N status (i.e. the higher the values, the higher the soil N availability), were lower at the low-rainfall sites (Met and P27) than at one of the mid-rainfall sites (P19) ($P \leq 0.05$; Table 2). Soil organic C was lower at one of the lower-rainfall sites (P27) than at the high-rainfall site (P32) whereas the differences in total soil N among sites paralleled the increase in annual precipitation ($P \leq 0.05$; Table 2). Soil pH, ECEC and exchangeable bases generally showed the opposite trend to that of total soil N – higher values at the low-rainfall sites (with less-weathered soils) than at the mid- and high-rainfall sites (with highly weathered soils) (all $P \leq 0.05$; Tables 1 and 2). Soil exchangeable Al showed the converse pattern to that of exchangeable bases ($P \leq 0.02$; Table 2).

Of the four soil controlling factors that were monitored over time (temperature, moisture, extractable NH_4^+ and extractable NO_3^-; Fig. 1a-d), only moisture and extractable NO_3^- differed strongly between seasons ($P < 0.01$; Fig. 1b-c; Table 3); soil moisture contents were higher in the wet season than the dry season at all sites, while extractable soil NO_3^- concentrations were lower

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282 in the wet season that the dry season at all sites but P19. Within each season, all four soil
283 controlling factors differed along the precipitation gradient (all $P < 0.01$ except $P = 0.04$ for
284 extractable NH_4^+ in the wet season; Table 3). Soil temperatures in both seasons were lower at
285 P32 (3400 mm) than at all other sites (not significant at P27 in the dry season), and also lower at
286 P27 (2030 mm) than Met (1700 mm). Soil moisture contents, in contrast, were higher in both
287 seasons at P32 than at the other four sites. Extractable soil NO_3^- concentrations in both seasons
288 were higher at Met and P8 (2360 mm) than at P27, P19 (2690 mm) and P32, and in the wet
289 season, also higher at Met than P8. Extractable soil NH_4^+ concentrations were higher at P32 than
290 Met in both seasons. Across sites, over the 21-month measurement period, soil moisture was
291 inversely correlated with temperature ($r = -0.28$, $P < 0.01$, $n = 145$) and extractable soil NO_3^- ($r =$
292 -0.51, $P < 0.01$, $n = 145$) and directly correlated with extractable soil NH_4^+ ($r = 0.46$, $P < 0.01$, n
293 $= 145$).
294
295 **3.2 CO_2 fluxes**
296 Although soil CO_2 emissions did not differ among the five sites over the 21-month measurement
297 period ($P = 0.40$; Fig. 2a; Table 3), emissions exhibited a parabolic relationship with soil
298 moisture across sites (Fig. 3) and were higher in the wet season than the dry season at each site
299 ($P \leq 0.05$; Table 3). Over the 21-month sampling period, average daily soil CO_2 emissions from
300 the five sites were correlated with soil temperature ($r = 0.46$, $P < 0.01$, $n = 145$), soil moisture (r
301 $= 0.35$, $P < 0.01$, $n = 145$; Fig. 3), extractable soil NH_4^+ ($r = 0.32$, $P < 0.01$, $n = 145$) and
302 extractable soil NO_3^- ($r = -0.21$, $P = 0.01$, $n = 145$). Within individual sites, average daily soil
303 CO_2 emissions also exhibited negative correlations with extractable soil NO_3^- at Met ($r = -0.48$, P
304 $= 0.01$, $n = 27$), P8 ($r = -0.39$, $P = 0.03$, $n = 30$), and P32 ($r = -0.54$, $P < 0.01$, $n = 30$).

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Similar to the relationship observed for average daily fluxes (Fig. 3), the annual soil CO_2 emissions (Table 4) also exhibited a parabolic pattern across the five sites of the precipitation gradient: high at the mid-rainfall sites (P8 and P19) and low at both ends of the precipitation gradient (Met and P32). There were no significant correlations between soil CO_2 emissions (neither for annual CO_2 fluxes nor for wet- and dry-season averages) and the soil biochemical characteristics (Table 5; Table S1).

3.3 CH_4 fluxes

On average, despite occasional emissions in the wet season (Fig. 2b), the soils in the five sites acted as CH_4 sinks (Tables 3 and 4). Comparing between seasons, soil CH_4 uptake was higher in the dry season than the wet season at all sites ($P \leq 0.05$; Table 3). Differences among sites were the same in both seasons; soil CH_4 uptake at P19 (2690 mm) was higher than at Met (1700 mm), P27 (2030 mm) and P32 (3400 mm), and higher at P8 (2360 mm) than at Met ($P \leq 0.05$; Table 3). Over the 21-month sampling period, average daily soil CH_4 fluxes from the five sites were positively correlated (i.e. soil CH_4 uptake decreased) with soil moisture (r = 0.44, $P < 0.01$, n = 145; Fig. 4a). Within individual sites, average daily soil CH_4 fluxes at P8 (r = -0.63, $P < 0.01$, n = 30), P19 (r = -0.48, $P < 0.01$, n = 28) and P32 (r = -0.48, $P < 0.01$, n = 30) also exhibited negative correlations with extractable soil NO_3^- (i.e. soil CH_4 uptake increased as extractable soil NO_3^- increased).

The annual soil CH_4 fluxes (Table 4) were positively correlated (Spearman *rho* = 0.84, $P < 0.01$, n = 20; Fig. 4b) with the soil fertility index (Figure S2) and negatively correlated with annual precipitation (*rho* = -0.63, $P < 0.01$, n = 20; Fig. 4c). Of the soil biochemical properties measured once, annual soil CH_4 fluxes were negatively correlated with soil ^{15}N natural

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abundance and exchangeable Al, and positively correlated with ECEC, base saturation and pH (Table 5). Average seasonal soil CH_4 fluxes exhibited similar correlations (Table S1); it is notable that when correlation analysis was separated by season, correlations with soil ^{15}N natural abundance were stronger in the dry season than the wet season.

3.4 N_2O fluxes

Soil N_2O fluxes differed among sites only in the wet season and not in the dry season (Table 3; Fig. 2c); soil N_2O emissions in the wet season were higher at P8 (2360 mm) than all other sites ($P < 0.01$). Within individual sites, soil N_2O emissions were higher in the wet season than the dry season at P8 and P19 (2690 mm) ($P < 0.01$; Table 3). These two sites were also the only two to exhibit correlations with soil controlling factors; soil N_2O emissions increased with increases in soil moisture at P8 ($r = 0.69$, $P < 0.01$, $n = 30$) and P19 ($r = 0.60$, $P < 0.01$, $n = 28$), and decreased with increases in soil NO_3^- concentration at P8 ($r = -0.57$, $P < 0.01$, $n = 30$) and P19 ($r = -0.38$, $P = 0.05$, $n = 28$). Annual soil N_2O emissions (Table 4) were negatively correlated with clay content (Table 5). Seasonal average soil N_2O emissions were positively correlated with soil ^{15}N natural abundance in the wet season but not in the dry season (Table S1).

3.5 NO fluxes

In all five sites, net uptake of NO was measured more often than net NO emissions from the soil (Fig. 2d) and NO uptake was consistently higher ($P \leq 0.05$) in the wet than dry season, except at P19 (2690 mm) where there was no difference between seasons (Table 3). Wet-season soil NO uptake at Met (1700 mm) was larger than all other sites ($P < 0.01$; Table 3), while in the dry season soil NO uptake at P19 was larger than at P8 (2360 mm) and P32 (3400 mm) ($P < 0.01$;

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Table 3). Over the 13-month measurement period, soil NO fluxes were negatively correlated (i.e. net NO uptake increased) with ambient NO concentration (r = -0.34, P < 0.01, n = 103; Fig. 5). Within individual site, only soil NO fluxes at P8 showed a negative correlation with soil moisture (r = -0.67, P < 0.01; n = 21) and positive correlation (i.e. net NO uptake decreased) with extractable soil NO_3^- (r = 0.65, P < 0.01; n = 21). There were no correlations with average seasonal soil NO fluxes in the wet season, but in the dry season average seasonal soil NO fluxes were negatively correlated with clay content across sites (Table S1).

4 Discussion

4.1 CO_2 fluxes

Soil CO_2 emissions from CSA tropical lowland forests, including Brazil (Davidson et al., 2000, Chambers et al., 2004, Silver et al., 2005, Sotta et al., 2006), Puerto Rico (Raich and Schlesinger, 1992), Panama (Kursar 1989, Koehler et al., 2009a; Nottingham et al., 2010) and Costa Rica (Schwendenmann and Veldkamp, 2006), range from 10.8 Mg C ha^{-1} yr^{-1} (Silver et al., 2005) to 39.7 Mg C ha^{-1} yr^{-1} (Sotta et al., 2006). Our annual soil CO_2 emissions (Table 4) were on the lower end of this range. When compared with other studies in lowland forests of Panama, our values were also at the lower end of those reported for Barro Colorado Island (BCI) (estimated at 14.5 Mg C ha^{-1} yr^{-1} in 1986; Kursar 1989) and Gigante (ranging from 13.59 ± 1.34 to 17.12 ± 1.59 Mg C ha^{-1} yr^{-1} between 2006 and 2008; Koehler et al., 2009a), which can, in part, be attributed to inter-annual variation. Soil CO_2 fluxes at Gigante varied by more than 3 Mg C ha^{-1} yr^{-1} between 2006 and 2008 (Koehler et al., 2009a), and fine litterfall, one of the substrates of heterotrophic respiration, also varied by about 2 Mg ha^{-1} yr^{-1} from 1998 to 2008 (with annual averages of 7.7-9.7 Mg ha^{-1} yr^{-1}; Wright et al., 2011). Moreover, our values were comparable

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374 with that of a mature secondary forest (P15 site, 7-18 Mg C ha^{-1} yr^{-1} in 2007/2008; Notthingham
375 et al., 2010) close to our P8 and P19 sites (Figure S1). Finally, three of our sites (Met, P27 and
376 P19) were mature secondary forests, with tree densities (particularly at Met and P27; see 2.1)
377 lower than the old growth forests on BCI (Pyke et al., 2001) and Gigante (Koehler et al., 2009a).
378 This may have additionally influenced soil CO_2 fluxes since up to 35 % of CO_2 emissions can be
379 contributed by root respiration (Silver et al., 2005).

380 Soil CO_2 emissions responded to changes in climatic factors on a seasonal scale (i.e.
381 higher soil CO_2 fluxes in the wet than dry season at all sites; Table 3) and to daily fluctuations in
382 soil temperature and moisture across the five sites (see 3.2). The higher CO_2 emissions in the wet
383 season were likely due to the alleviation of water competition between decomposers and
384 vegetation; in seasonal tropical forests, litter tends to fall in the dry season, but low soil moisture
385 limits decomposition until the start of the wet season (Yavitt et al., 2004). Other studies from
386 CSA lowland forests have also reported a positive relationship between soil CO_2 emissions and
387 soil temperature (Chambers et al., 2004; Schwendenmann and Veldkamp, 2006; Sotta et al.,
388 2006, Koehler et al., 2009a), and parabolic relationships (Fig. 3) between soil CO_2 emissions and
389 soil moisture (Schwendenmann et al., 2003; Sotta et al., 2006; Kohler et al., 2009). Additionally,
390 soil CO_2 emissions responded to changes in soil mineral N both on the plot level and across sites
391 (see 3.2). Relationships between soil CO_2 emissions and soil mineral N concentrations have not
392 been reported in other studies, although Schwendenmann et al. (2003) observed that spatial
393 differences in soil total N were positively correlated with soil CO_2 fluxes, and Koehler et al.
394 (2009a) found that chronic N addition decreased soil CO_2 fluxes in a montane tropical forest
395 (although not in a lowland forest). However, the correlations between CO_2 emissions and both

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396 NH_4^+ (positive correlation) and NO_3^- (negative correlation) may also simply be reflecting a co-
397 correlation between extractable mineral N and soil moisture (see 3.2).

398 In support of our hypothesis, we observed that annual soil CO_2 fluxes exhibited a
399 parabolic pattern along the precipitation gradient (Table 4) similar to the relationship seen with
400 the daily emissions and soil moisture (Fig. 3). However, soil CO_2 efflux did not differ among the
401 five forest sites of this precipitation gradient (Table 3). This lack of differences between sites
402 could be due to similarity of a soil-controlling factor that results in comparably low soil CO_2
403 emissions at all sites. For example, although organic C and total N differed between sites, the
404 soil C:N ratios were comparable along these orthogonal gradients of annual precipitation and soil
405 fertility (Table 2), suggesting that the bioavailability of soil organic matter for heterotrophic
406 respiration may be similar across sites. Additionally, the microbial communities that contribute
407 to heterotrophic respiration may have adapted to the existing differences in substrate quantity
408 (e.g. soil organic C), soil and climatic characteristics between the sites (Tables 2 and 3) and
409 therefore exhibited an overall similar soil CO_2 efflux.

410

411 **4.2 CH_4 fluxes**

412 Our annual soil CH_4 uptake (Table 4) was within the range of other reported values from Brazil
413 and Panama (Verchot et al., 2000; Davidson et al., 2004; Keller et al., 2005; Silver et al., 2005;
414 Veldkamp et al., 2013) although studies have also measured stronger uptake in CSA lowland
415 forests (up to 4.90 kg C ha^{-1} yr^{-1}; Keller and Reiners, 1994; Steudler et al., 1996; Keller et al.,
416 2005; Sousa Neto et al., 2011). Studies that measured higher uptake may have had soils with
417 higher gas diffusivity due to lower soil water content and/or lower clay content (see Veldkamp et

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418 al., 2013); in our five sites, the two sites with the highest sand content (P8 and P19; Table 1)
419 exhibited the highest soil CH_4 uptake (Tables 3 and 4).

420 As shown in several CSA tropical forest studies (Keller and Reiners, 1994; Verchot et al.,
421 2000; Davidson et al., 2004; Veldkamp et al., 2013), soil CH_4 fluxes are strongly regulated by
422 soil moisture content. Soil CH_4 fluxes from our sites exhibited this expected pattern, with
423 regards to less uptake during periods of high water content (i.e. wet vs. dry season; Table 3) as
424 well as a positive correlation of soil CH_4 fluxes with water content (Fig. 4a). This we attributed
425 to limited gas diffusivity from the atmosphere into the soil and/or methanogenic activity during
426 periods of high moisture. Another soil factor controlling the temporal soil CH_4 uptake in our sites
427 may have been soil NO_3^-, as we observed increased CH_4 uptake as NO_3^- concentrations increased
428 in P8, P19 and P32 (see 3.3). Although this could be a co-correlation between soil NO_3^-
429 concentration and soil moisture (see 3.1), increasing CH_4 uptake in the soil with increasing
430 mineral N has been observed in tropical forest soils of Australia (Kiese et al., 2003), Panama
431 (Veldkamp et al., 2013) and Indonesia (Hassler et al., 2013). Additionally, our soils exhibited a
432 correlation between annual soil CH_4 fluxes and soil ^{15}N natural abundance signatures (Table 5),
433 the latter being an indicator of soil N availability (Sotta et al. 2008; Arnold et al. 2009; Baldos et
434 al. 2015). When separated by season, the correlation between soil CH_4 fluxes and soil ^{15}N natural
435 abundance was stronger in the dry season than the wet season (Table S1), supporting our claim
436 that soil N availability enhanced CH_4 uptake in soils when gas diffusion was favorable (dry
437 season).

438 The negative correlation between annual soil CH_4 uptake and annual precipitation (Fig.
439 4c; see 3.3) seemed at first to conflict with the mechanism we explained above for the positive
440 correlation with soil moisture content (Fig. 4a). However, we attribute this to the fact that annual

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441 precipitation was not the underlying factor controlling the annual soil CH_4 fluxes across these
442 sites. Instead, the best indicator for annual soil CH_4 flux across the five sites was soil fertility
443 (Fig. 4b), which showed an opposite pattern to that of annual precipitation (Figure S2). This soil
444 fertility control was supported by the strong correlations of both annual (Table 5) and seasonal
445 (Table S1) soil CH_4 fluxes with ECEC and exchangeable Al, both included in the soil fertility
446 index (Figure S2; see 2.4). The negative correlation of soil CH_4 fluxes with exchangeable Al,
447 which was clearly observed in the wet season (Table S1), could suggest an inhibition of
448 methanogens by water-soluble Al (as opposed to inhibiting methanotrophs, as seen by Tamai et
449 al., 2003). The correlations between soil CH_4 fluxes and fertility indicators reflected the site
450 differences in soil biochemical characteristics (Table 2). Specifically, as shown by the strong
451 inverse correlation between soil $\delta^{15}N$ natural abundance signatures and exchangeable cations
452 (Table 5), the positive correlation between soil CH_4 flux and fertility (Fig. 4b) likely reflected the
453 long-term effects of soil development (Tables 1 and 2) - more CH_4 uptake occurred in highly
454 weathered soils with less rock-derived nutrients but high soil N availability (i.e. high $\delta^{15}N$
455 natural abundance signatures) (Tables 4 and 5). This supports our hypothesis that soil CH_4
456 uptake reflected the control of soil moisture and N availability across sites along this
457 precipitation gradient. Our results also highlight the importance of considering soil properties - in
458 particular the degree of soil development - rather than simply climatic factors, when
459 predicting/modeling soil CH_4 fluxes on a large scale.
460
461 **4.3 N_2O fluxes**
462 Our annual soil N_2O fluxes (Table 4) were within the lower end of the range (1.23 - 11.4 kg N
463 ha^{-1} yr^{-1}) reported from other CSA forest studies (Keller and Reiners 1994, Verchot et al., 1999,

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464 Keller et al., 2005, Silver et al., 2005). In comparison with other studies from Panama, our N_2O
465 fluxes were similar to those measured from Gigante during dry years (0.5 ± 0.2 kg N ha^{-1} yr^{-1} in
466 2008–2009 with annual precipitation 5–26 % lower than the 12-year average; Corre et al. 2014)
467 but slightly lower than those measured from the same site during wet years (1.0 - 1.4 kg N ha^{-1}
468 yr^{-1} in 2006–2007 with annual precipitation 5–17 % higher than the 12-year average; Koehler et
469 al., 2009b). The low soil N_2O fluxes at our sites were likely caused by the generally lower soil N
470 availability compared to the Gigante site; the five sites in our present study had an average gross
471 N mineralization rate of 4 ± 1 mg N kg^{-1} d^{-1} in the 2010 wet season (Corre et al. unpublished
472 data), which was significantly lower than those from Gigante (29 ± 6 mg N kg^{-1} d^{-1} in the 2006
473 wet season; Corre et al. 2010). In addition, inter-annual variation in rainfall and hence soil
474 moisture can strongly affect soil N_2O emissions (Corre et al., 2014). Our measured soil N_2O
475 emissions exhibited a tendency to be higher in the wet season than the dry season (P8 and P19;
476 Table 3), highest at the mid-rainfall site of P8 (which could mean that at the high-rainfall sites
477 N_2O could have been further denitrified to N_2), and were only correlated with the soil ^{15}N natural
478 abundance signatures (as an indicator of soil N availability) in the wet season (Table S1). At the
479 sites (P8 and P19), where N_2O emissions were higher in the wet than dry season and soil NO_3^-
480 levels were lower in the wet than dry season (Table 3), the inverse correlation between daily soil
481 N_2O emissions with NO_3^- concentrations over the 21-month measurement period suggests that
482 during the wet season N_2O production could have been high but might have been further
483 denitrified to N_2, and hence resulted in low soil NO_3^- concentrations. This argument is supported
484 by our earlier study in Gigante, where nitrification and denitrification contributed equally to soil
485 N_2O emissions during the dry season but denitrification was the main process contributing to soil
486 N_2O emission in the wet season (Koehler et al., 2012; Corre et al. 2014). Our results partly

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487 supported our hypothesis in that soil N_2O emissions were highest at the mid-precipitation site
488 (with the highest soil N availability as indicated by ^{15}N natural abundance; Table 2) due to
489 possible reduction of N_2O to N_2 at the high precipitation site.
490
491 **4.4 NO fluxes**
492 Our annual soil NO uptake (Table 4) was considerably lower than other reported NO fluxes,
493 which are usually small net emissions rather than net uptake. Soil NO emissions from Panama,
494 Costa Rica and Brazil range from 0.26 to 7.88 kg N $ha^{-1}yr^{-1}$ (Keller and Reiners 1994, Verchot et
495 al., 1999, Gut et al., 2002, Keller et al., 2005, Silver et al., 2005, Koehler et al., 2009b; Corre et
496 al. 2014). However, the net uptake that we measured may be reflecting unusually high ambient
497 air NO concentrations in our forest sites as compared to forests from other studies. Although all
498 of our sites were located in mature-secondary or old-growth forests, the forests were located
499 within the Panama Canal watershed, where there is heavy, year-round marine traffic (~13,000
500 cargo ships in 2011; Hricko, 2012). Furthermore, the highest levels of soil NO uptake that we
501 measured were in the Met site (Table 4); in addition to being in the vicinity of the Panama Canal,
502 the park is located within the city limits of Panama City, which has a population of
503 approximately 1.6 million people (The World Factbook, 2015). Therefore, elevated ambient air
504 NO concentrations from anthropogenic emissions may be driving the NO uptake that we
505 measured. Our instrument cannot measure O_3 concentration, which could be high in these sites
506 influenced by anthropogenic emissions. Thus, the NO uptake that we saw may have been driven
507 by both chemical (Pape et al. 2009) and microbiological reactions (as NO is an intermediate
508 product of nitrification and denitrification; Davidson et al. 2000). The dominance of a chemical
509 reaction of NO uptake at our sites was supported by the fact that we observed a negative

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correlation of soil NO fluxes with ambient air NO concentrations (i.e. net NO uptake increased as ambient air NO concentration increased; Fig. 5). The reaction of NO with O_3, which is then subsequently removed from the enclosed chamber air and deposited onto the soil, is driven by the ambient air NO concentrations (Pape et al. 2009). This can occur in under a minute (which we observed on days with low ambient air NO concentrations when we measured net soil NO emissions; e.g. at P8 during the dry season, Fig. 2b) or can take up to the same order of magnitude as the turnover time of the chamber air (which we observed on days with high ambient air NO concentrations when we measured net NO uptake; e.g. at the Met site on most of the sampling days, Fig. 2b). It is notable, that an earlier study in Gigante, which is also part of the Panama Canal watershed, did not show net NO uptake but instead small net NO emissions (Koehler et al., 2009b; Corre et al. 2014). However, as mentioned above, the Gigante site had higher soil N-cycling rates (Corre et al. 2010) and lower ambient air NO concentrations than our sites, such that NO production in the soil overrides the chemical reaction of NO uptake and thus resulted in net soil NO emissions.

The general trend across sites did not support our hypothesis regarding soil NO emission, since local conditions of high ambient NO concentrations in the atmosphere had an overriding effect resulting in net NO uptake in soils (Fig. 2d). However, our results indicated that our soils could also be a net source of NO when soil conditions were favourable and/or ambient air NO concentrations were not elevated. We observed that net NO uptake was consistently higher in the wet season than the dry season (Table 3); in the dry season, when aerobic soil conditions prevailed due to low soil moisture contents (Table 3), NO production in the soil may have been more favoured (Conrad, 2002), partly counteracting the chemical reaction of NO removal from the atmosphere and its deposition onto the soil. This is also supported by the negative correlation

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533 between dry-season soil NO fluxes and clay contents of the sites (Table S1), suggesting that soil
534 NO fluxes were responding to conditions favourable for NO production. Favourable soil
535 conditions were most visible at P8, which had the highest soil NO emissions (with low ambient
536 air NO concentrations) in the dry season (Table 3; Fig. 2d); soil NO fluxes at this site increased
537 when aerobic soil conditions prevailed (i.e. negative correlation with soil moisture; see 3.5) and
538 increased with substrate availability (i.e. positive correlation with soil NO_3^-; see 3.5).
539
540 **4.5 Implications for climate change**
541 It is notable that, although all four trace gases were strongly correlated with the temporal
542 variation in soil moisture and had clear differences between seasons (Table 3), there were no
543 correlations between the soil trace gases when looking at the annual fluxes (Table 5) or seasonal
544 averages (Table S1). This lack of correlation is presumably rooted in the interaction of other soil
545 and/or climatic factors with known drivers of soil trace gas production and consumption. We
546 have shown that in the short term, soil trace gas fluxes were largely controlled by soil moisture,
547 with the additional influences of soil temperature and mineral N concentration. However, in the
548 long term and/or over large spatial scales, the degree of soil development and related soil fertility
549 had a strong influence. Additionally, we have shown that even in presently undisturbed forests,
550 gas fluxes can be affected by 'upstream' anthropogenic activities. Therefore, in order to
551 understand and be able to predict soil trace gas fluxes under future climate scenarios, research
552 needs to focus on identifying and predicting interacting effects of soil and site, as well as
553 climatic characteristics, on soil-atmosphere trace gas exchange.
554

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739 **Table 1** Description of location, rainfall and geology of one hectare forest inventory plots located in the Panama Canal watershed,
740 central Panama.

Plot code [a]	Longitude, latitude	Elevation (m above sea level)	Forest age classification [a]	Soil taxonomic order [b]	Soil texture (% sand/ silt/clay) [c]	Precipitation (mm yr^{-1}) [b]	Geology [b]
Metropolitan	79º 33' W, 8º 59' N	30	mature secondary	Inceptisol (Cambisol)	3/35/62	1700	Aglomerate of andesitic tuff, Early-Late Oligocene
P27	79º 38' W, 9º 4' N	160	mature secondary	Inceptisol (Cambisol)	2/38/60	2030	Aglomerate of siltstone, tuff and limestone, Early Miocene
P8	79º 44' W, 9º 10' N	50	old growth	Oxisol (Ferralsol)	12/39/48	2360	Basaltic and andesitic lavas and tuff, pre-Tertiary
P19	79º 46' W, 9º 11' N	160	mature secondary	Oxisol (Ferralsol)	10/27/63	2690	Basaltic and andesitic lavas and tuff, pre-Tertiary
P32	79º 43' W, 9º 21' N	340	old growth	Oxisol (Ferralsol)	1/39/60	3400	Basaltic and andesitic lavas and tuff, pre-Tertiary

741 [a] Plot codes and forest age classification are from Pyke et al. (2001).

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[b] Turner and Engelbrecht (2011) reported the tentative soil order (based on US Soil Taxonomy with equivalent FAO classification in brackets), mean annual precipitation (estimated from location and elevation data as described by Engelbrecht et al. 2007), and the geological information (taken from Stewart et al. 1980).

[c] Textural analyses are the weighted average of the sampling depth intervals: 0-5, 5-10, 10-25 and 25-50 cm.

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Table 2 Soil biochemical characteristics in the top 50 cm of lowland forest soils along orthogonal gradients of annual precipitation (shown in brackets below each site) and soil fertility in the Panama Canal watershed, central Panama.

Soil characteristics [a]	Metropolitan (1700 mm)	P27 (2030 mm)	P8 (2360 mm)	P19 (2690 mm)	P32 (3400 mm)
$\delta^{15}N$ enrichment factor, ε [b]	-1.95 ± 0.52 [b]	-0.37 ± 1.69 [b]	-2.76 ± 0.54 [ab]	-4.70 ± 0.44 [a]	-2.65 ± 0.30 [ab]
$\delta^{15}N$ natural abundance (‰)	5.9 ± 0.8 [c]	6.3 ± 0.4 [bc]	12.0 ± 1.0 [a]	9.2 ± 0.9 [a]	7.0 ± 0.3 [b]
Organic C (mg C g^{-1})	12.8 ± 1.7 [ab]	10.8 ± 3.3 [b]	15.1 ± 0.2 [ab]	15.0 ± 1.3 [ab]	19.6 ± 2.1 [a]
Total N (mg C g^{-1})	1.08 ± 0.15 [b]	1.05 ± 0.25 [b]	1.49 ± 0.02 [ab]	1.44 ± 0.11 [ab]	1.85 ± 0.17 [a]
C:N ratio	10.9 ± 4.1 [a]	9.07 ± 1.8 [a]	9.76 ± 1.0 [a]	9.88 ± 1.0 [a]	10.1 ± 1.2 [a]
pH (1:4 H_2O)	6.20 ± 0.46 [a]	5.82 ± 0.72 [a]	5.05 ± 0.17 [b]	4.88 ± 0.30 [b]	5.14 ± 0.22 [b]
ECEC [c] ($mmol_c$ kg^{-1})	199 ± 72 [ab]	267 ± 11 [a]	56 ± 2 [c]	51 ± 6 [c]	118 ± 12 [bc]
Exch. bases [c] ($mmol_c$ kg^{-1})	198 ± 72 [a]	264 ± 10 [a]	37 ± 6 [c]	21 ± 8 [c]	90 ± 11 [b]
Exchangeable Al ($mmol_c$ kg^{-1})	0.22 ± 0.13 [b]	1.96 ± 0.51 [b]	12.2 ± 4.7 [ab]	22.6 ± 7.3 [a]	22.2 ± 3.2 [a]

[a] Means (±SE, n = 4) followed by different letters indicate significant differences between sites (one-way ANOVA with Tukey HSD at $P \leq 0.05$). Values for each replicate plot are weighted average of the sampling depth intervals of 0-5, 5-10, 10-25 and 25-50 cm.

[b] Calculated using Rayleigh equation (Mariotti et al. 1981): $\varepsilon = d_s - d_{so} / \ln f$; d_s- $\delta^{15}N$ natural abundance signatures at various depths in the soil profile, d_{so}- $\delta^{15}N$ natural abundance of the reference depth (top 5cm) and f is the remaining fraction of total N (i.e. total N concentration at a given depth divided by the total N concentration in the top 5 cm).

[c] ECEC – Effective cation exchange capacity; Exch. bases – sum of exchangeable Ca, Mg, K, Na

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Table 3 Soil factors (measured in the top 5 cm of soil) and trace gas fluxes from lowland forest soils along orthogonal gradients of annual precipitation (mm per year; shown in brackets below each site) and soil fertility in the Panama Canal watershed, central Panama.

Site / season [a]	Soil temperature (° C)	Soil moisture ($g\ g^{-1}$)	Soil NH_4^+ ($mg\ N\ kg^{-1}$)	Soil NO_3^- ($mg\ N\ kg^{-1}$)	CO_2 flux ($mg\ C\ m^{-2}\ h^{-1}$)	CH_4 flux ($\mu g\ C\ m^{-2}\ h^{-1}$)	N_2O flux ($\mu g\ N\ m^{-2}\ h^{-1}$)	NO flux ($\mu g\ N\ m^{-2}\ h^{-1}$)
Wet season								
Metropolitan (1700)	25.8 (0.4)^{a}	0.64 (0.04)^{Ac}	5.94 (1.52)^{b}	1.95 (0.71)^{Ba}	126 (26)^{A}	1.47 (3.66)^{Aa}	5.78 (2.69)^{b}	-11.6 (7.08)^{Bb}
P27 (2030)	25.2 (0.4)^{b}	0.72 (0.06)^{Ab}	6.39 (1.35)^{Aab}	0.51 (0.17)^{Bc}	124 (18)^{A}	-3.01 (4.20)^{Aa}	4.15 (2.56)^{b}	-3.24 (2.68)^{Ba}
P8 (2360)	25.6 (0.4)^{Aab}	0.60 (0.03)^{Ac}	5.68 (0.94)^{ab}	1.32 (0.54)^{Bb}	131 (19)^{A}	-7.87 (6.95)^{Abc}	13.5 (7.0)^{Aa}	-3.95 (6.60)^{Ba}
P19 (2690)	25.5 (0.5)^{ab}	0.72 (0.06)^{Ab}	7.29 (1.39)^{ab}	0.46 (0.39)^{c}	129 (15)^{A}	-13.0 (6.92)^{Ac}	5.58 (3.13)^{Ab}	-3.98 (4.95)^{a}
P32 (3400)	24.6 (0.4)^{c}	0.90 (0.08)^{Aa}	8.21 (1.87)^{Aa}	0.49 (0.27)^{Bc}	107 (17)^{A}	-6.79 (6.09)^{Aab}	6.41 (3.09)^{b}	-4.01 (4.34)^{Ba}
Dry season								
Metropolitan (1700)	25.3 (0.3)^{a}	0.45 (0.06)^{Bb}	5.32 (1.26)^{bc}	3.42 (1.55)^{Aa}	82.7 (19)^{B}	-6.88 (4.14)^{Ba}	4.18 (4.62)	-4.05 (7.21)^{Aab}

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P27 (2030)	24.7 (0.2)^{bc}	0.53 (0.08)^{Bab}	4.46 (0.89)^{Bc}	0.79 (0.18)^{Ab}	87.7 (14)^{B}	-12.1 (3.1)^{Bab}	4.87 (4.70)	1.09 (1.23)^{Aab}
P8 (2360)	24.9 (0.3)^{Bab}	0.48 (0.06)^{Bb}	6.04 (1.15)^{abc}	3.68 (1.16)^{Aa}	85.7 (17)^{B}	-21.3 (8.37)^{Bbc}	5.64 (5.75)^{B}	6.50 (3.76)^{Aa}
P19 (2690)	25.0 (0.3)^{ab}	0.49 (0.04)^{Bb}	7.47 (1.22)^{ab}	0.64 (0.26)^{b}	85.5 (12)^{B}	-29.2 (4.08)^{Bc}	1.30 (3.09)^{B}	-2.41 (2.35)^{b}
P32 (3400)	24.4 (0.3)^{c}	0.64 (0.09)^{Ba}	7.86 (1.37)^{a}	1.17 (0.61)^{Ab}	78.5 (15)^{B}	-17.4 (5.09)^{Bab}	5.89 (5.51)	4.34 (2.23)^{Aa}

[a] Means ((±SE, n = 4) followed by different lowercase letters indicate significant differences among sites within each season and different uppercase letters indicate significant differences between seasons within each site (linear mixed effects model with Tukey HSD test at $P \leq 0.05$).

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Table 4 Annual[a] trace gas fluxes (mean (SE), n = 4) from lowland tropical forest soils along orthogonal gradients of annual precipitation and soil fertility in the Panama Canal watershed, central Panama.

Site (annual precipitation)	CO_2 (Mg C ha^{-1} yr^{-1})	CH_4 (kg C ha^{-1} yr^{-1})	N_2O (kg N ha^{-1} yr^{-1})	NO (kg N ha^{-1} yr^{-1})
Met (1700 mm)	8.48 (0.70)	-0.34 (0.17)	0.41 (0.06)	-0.82 (0.16)
P27 (2030 mm)	9.16 (0.62)	-0.51 (0.04)	0.43 (0.06)	-0.12 (0.04)
P8 (2360 mm)	10.14 (0.76)	-1.45 (0.15)	1.07 (0.15)	-0.17 (0.17)
P19 (2690 mm)	9.89 (0.49)	-1.98 (0.07)	0.35 (0.05)	-0.21 (0.10)
P32 (3400 mm)	7.89 (0.84)	-0.94 (0.19)	0.66 (0.18)	-0.03 (0.09)

[a] Calculated using the trapezoidal rule between fluxes and time interval, covering the measurement periods of January - December 2011 for CO_2 , CH_4 and N_2O, and June 2010 - May 2011 for NO. Annual fluxes were not tested statically for differences among sites since these are trapezoidal extrapolations.

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Table 5 Spearman correlations of soil biochemical characteristics[a] and annual (measured in 2011) soil trace gas fluxes from five lowland tropical forests along orthogonal precipitation and fertility gradients in the Panama Canal watershed, central Panama.

	ECEC	BS	Na	Al	pH	Clay	CO_2	CH_4	N_2O	NO
^{15}N sig.	-0.87**	-0.67**	-0.30	0.42	-0.61**	-0.15	0.41	-0.70**	0.30	0.16
ECEC		0.80**	0.34	-0.50	0.76**	-0.12	-0.33	0.77**	-0.09	-0.17
BS			-0.13	-0.87**	0.96**	-0.12	-0.40	0.78**	-0.12	-0.54
Na				0.45	-0.18	-0.15	0.04	0.01	-0.01	0.60**
Al					-0.87**	0.04	0.24	-0.71**	0.17	0.58**
pH						-0.04	-0.34	0.76**	-0.12	-0.54
Clay							-0.13	-0.17	-0.67**	-0.34
CO_2								-0.24	0.26	0.10
CH_4									-0.07	-0.31
N_2O										0.19

** $P < 0.01$, $n = 20$ (4 replicate plots in each of the 5 forest sites)

[a] Soil parameter abbreviations: ^{15}N natural abundance signature (^{15}N sig.), effective cation exchange capacity (ECEC) and base saturation (BS).

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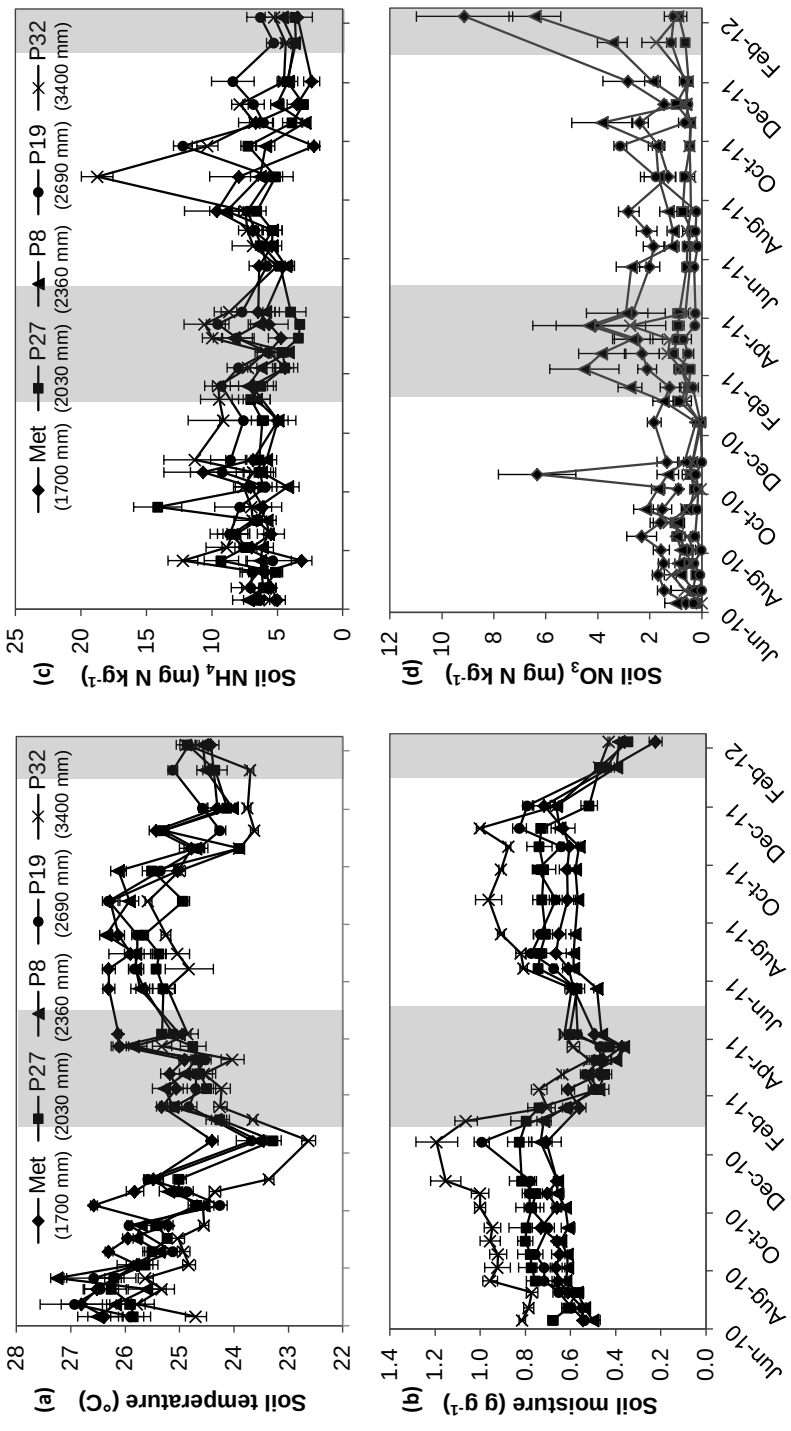

Fig. 1 Mean (±SE, n = 4) soil **(a)** temperature, **(b)** moisture, **(c)** NH_4^+ and **(d)** NO_3^- concentrations measured in the top 5 cm of soil in lowland forests along orthogonal gradients of annual precipitation and soil fertility in the Panama Canal watershed, central Panama. Gray shading indicates the dry season (January through April).

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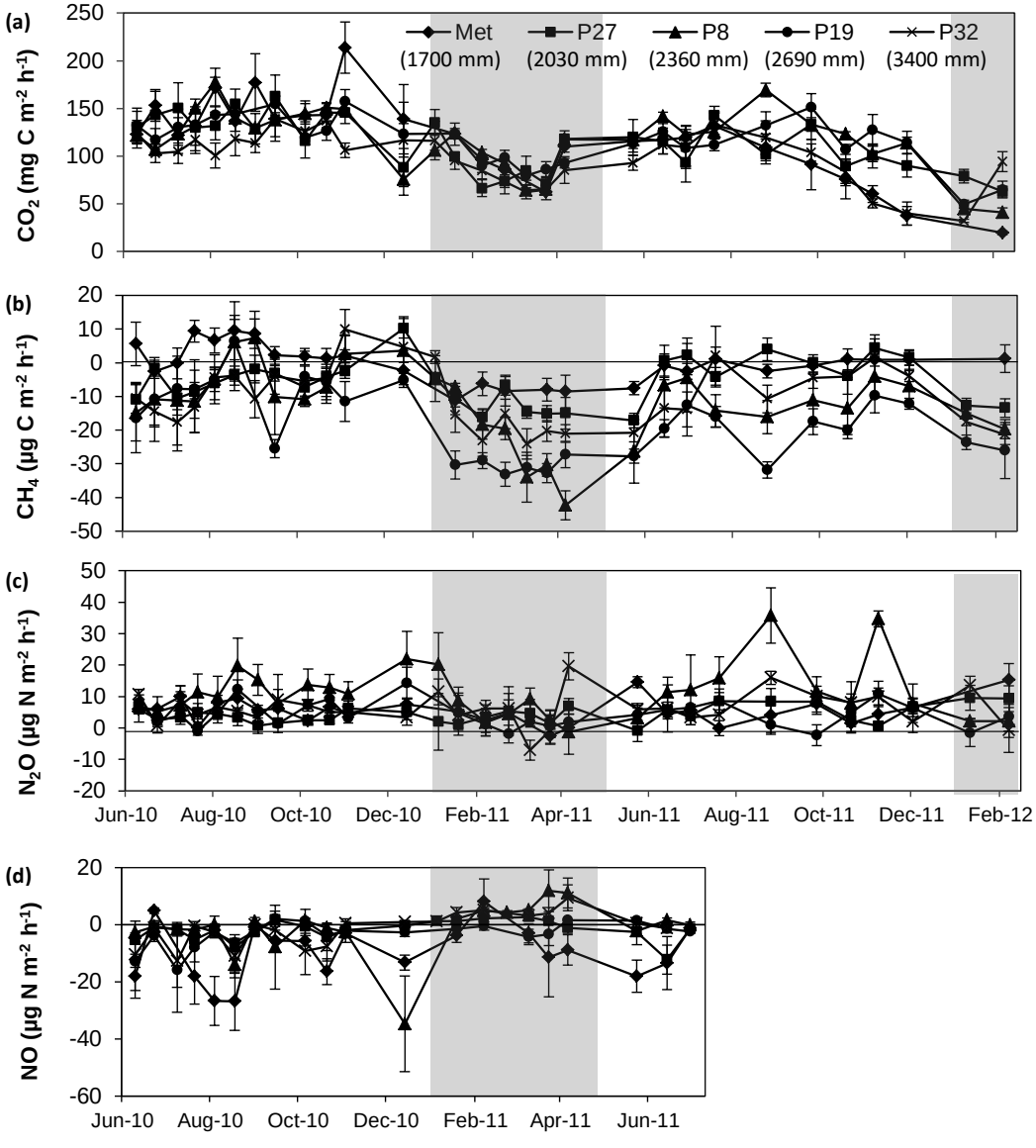

Fig. 2 Mean (±SE, n = 4) soil **(a)** CO_2, **(b)** CH_4, **(c)** N_2O and **(d)** NO fluxes from lowland forests along orthogonal gradients of annual precipitation and soil fertility in the Panama Canal watershed, central Panama. Gray shading indicates the dry season (January through April).

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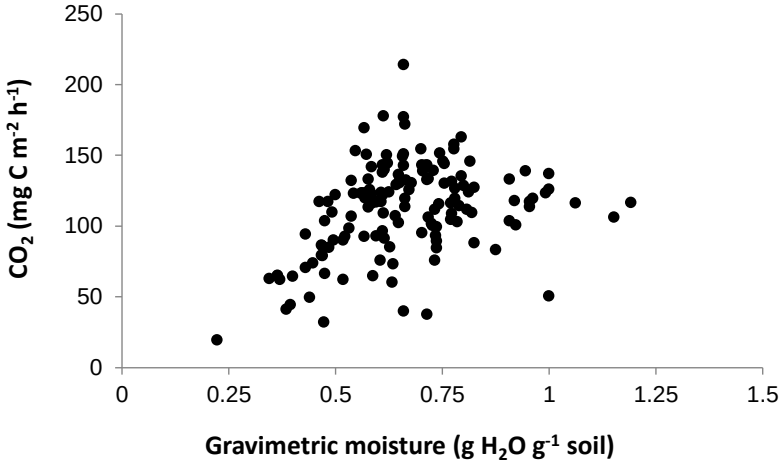

Fig. 3 Soil CO_2 fluxes and moisture contents (top 5 cm) in five lowland forests along orthogonal gradients of annual precipitation and soil fertility in the Panama Canal watershed, central Panama. Each data point is the average of four replicate plots on one sampling day from one of the five sites, measured from June 2010 to February 2012 (n = 145).

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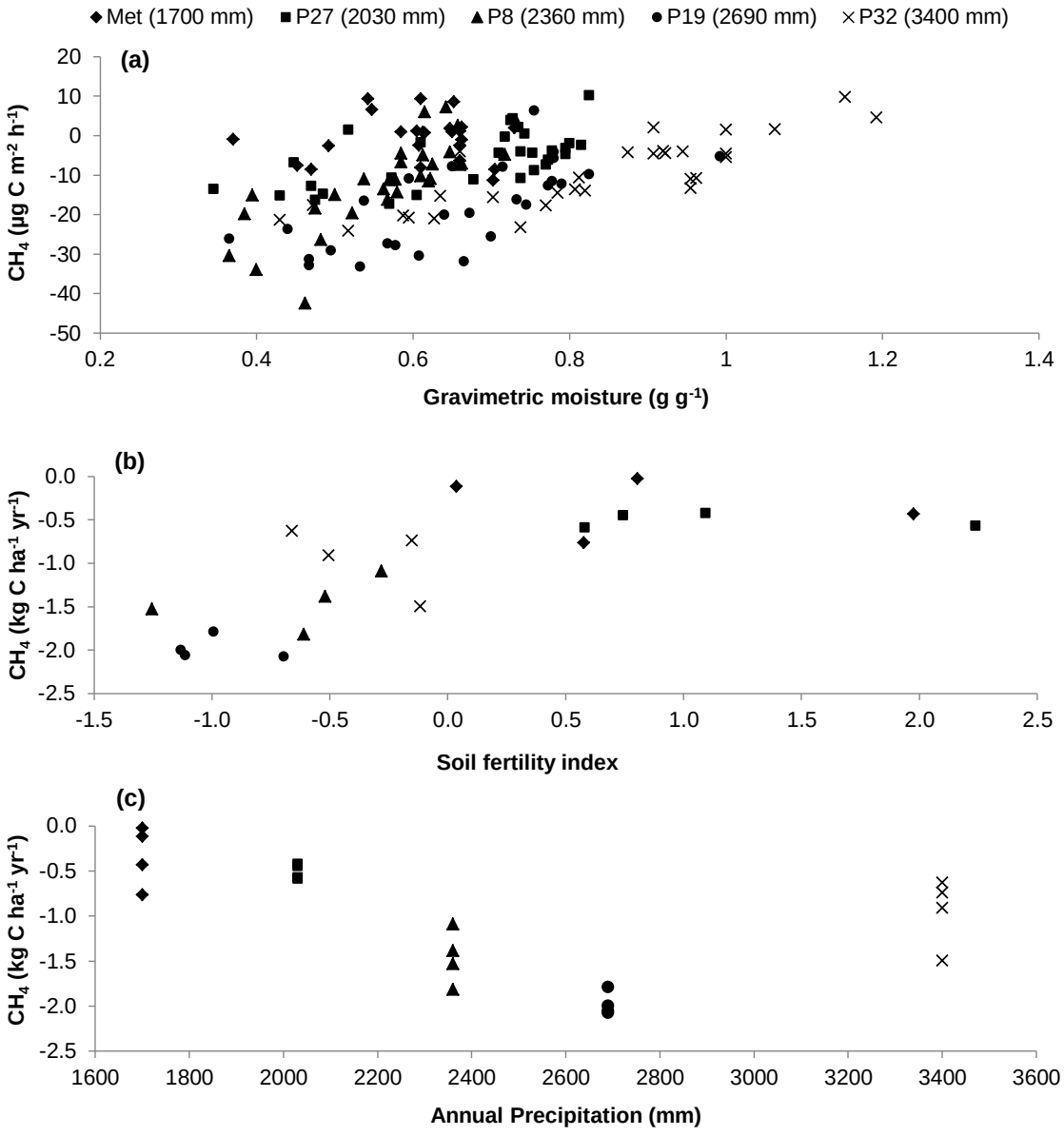

Fig. 4 Average daily soil CH_4 fluxes plotted against (a) soil moisture (top 5 cm), and annual soil CH_4 fluxes plotted against (b) soil fertility index and (c) annual precipitation. For (a), each data point is the average of four replicate plots on each sampling day of each of the five sites, measured from June 2010 to February 2012. The five lowland forests are located along orthogonal gradients of annual precipitation and soil fertility in the Panama Canal watershed, central Panama.

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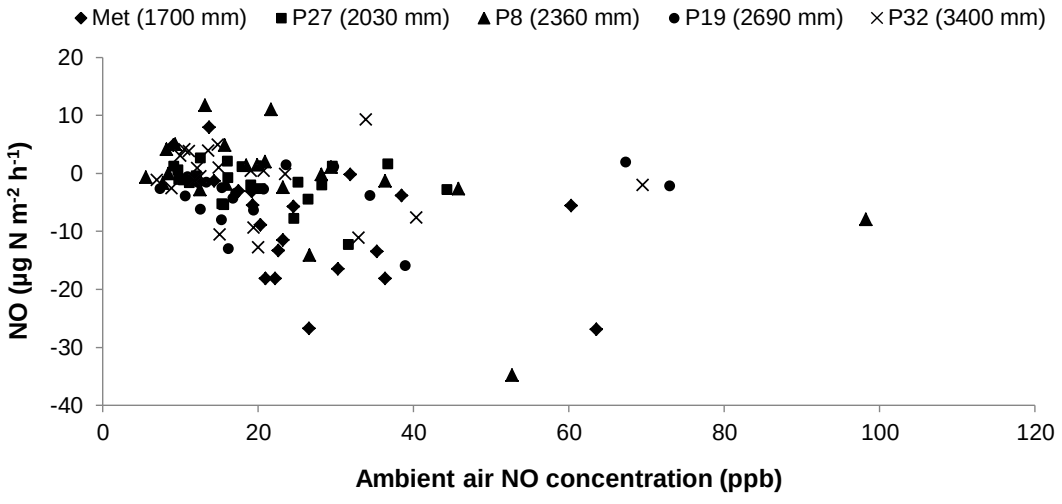

Fig. 5 Soil NO fluxes plotted against ambient air NO concentrations; each data point is the average of four replicate plots on each sampling day in each of the five sites, measured from June 2010 to June 2011. The five lowland forests are located along orthogonal gradients of annual precipitation and soil fertility in the Panama Canal watershed, central Panama.