Specific response to reviewer comments (including line numbers for the no-markup version)

Reviewer 1

It would be useful if the authors could develop or speculate on the wider implications of NO uptake for local and regional atmospheric chemistry, as I do not believe that our wider community has fully engaged with the notion of soils as NO sinks, given the past emphasis on soils as NO emission sources.

We agree that our observation of regular NO uptake by soils is worth exploring, given that until now the majority of studies have reported soils acting as net NO sources. However, we do not want to overemphasize this point, as our soils experienced unique ambient conditions (i.e. high atmospheric NO and O3) that may not occur in many other sites worldwide. However, in response to this comment, we have revised this paragraph in the discussion to emphasize the importance of these unusual results. The final sentence of Section 4.4 (Line 599-603) now reads: In summary, although the soils in our study sites can be a net source of NO, particularly during the dry season (Fig. 2d) and in sites where ambient air NO concentrations are low (Fig. 5), most of the time the soils acted as net sinks of NO, signifying the importance of soil and vegetation as NO sinks (Jacob and Bakwin, 1991; Sparks et al., 2001) in areas affected by anthropogenic NO sources.

First, it would be useful if the authors could make more use of multiple regression or the mixed effects models to determine the hierarchy (i.e. relative importance) of environmental drivers for different trace gases (i.e. which are the dominant and which are the lesser environmental controls?). While the authors have outlined the dominant role of soil moisture, it would be interesting to see a clearer description of the relative importance of the other drivers. Does the hierarchy of drivers vary among sites? Do the hierarchy of drivers vary among seasons?

In response to this comment and comments from the other reviewer (see below), we added Table S1, which shows the hierarchy of importance of the soil factors controlling soil GHG fluxes for each season (across sites) and within each site (across seasons).

Table S1 Ranking[a] of soil factors that control the soil-atmosphere trace gas exchange along orthogonal precipitation and fertility gradients in the Panama Canal watershed, central Panama (F- and P-value of the model ANOVA shown in brackets).

	CO_2	CH_4	N_2O	NO
Wet season (all sites)	1. NH_4^+ (F=24.5, P<0.01) 2. Temperature (F=9.4, P<0.01)	1. Moisture (F=59.1, P<0.01) 2. Temperature (F=10.0, P<0.01)	1. NO_3^- (F=6.1, P=0.01)	ns

		3. NO_3^- (F=5.6, P=0.02)		
Dry season (all sites)	1. Moisture (F=52.4, P<0.01) 2. Temperature (F=5.01, P=0.03)	1. Moisture (F=10.5, P<0.01) 2. NO_3^- (F=14.6, P<0.01) 3. NH_4^+ (F=7.8, P<0.01)	ns	ns
Met (wet/dry)	1. Moisture (F=38.0, P<0.01) 2. NH_4^+ (F=13.3, P<0.01)	ns	ns	ns
P27 (wet/dry)	1. Temperature (F=25.9, P<0.01) 2. Moisture (F=22.7, P<0.01)	1. Moisture (F=33.1, P<0.01) 2. Temperature (F=5.2, P=0.03)	ns	1. Temperature (F=10.1, P<0.01) 2. Moisture (F=7.4, P<0.01)
P08 (wet/dry)	1. Moisture (F=25.8, P<0.01) 2. Temperature (F=20.6, P<0.01)	1. Moisture (F=30.8, P<0.01)	1. Moisture (F=12.8, P<0.01)	1. Moisture (F=16.6, P<0.01)
P19 (wet/dry)	1. Moisture (F=44.2, P<0.01) 2. NH_4^+ (F=4.2, P=0.04)	1. Moisture (F=32.5, P<0.01)	1. Moisture (F=27.7, P<0.01) 2. NO_3^- (F=14.2, P<0.01)	ns
P32 (wet/dry)	1. Moisture (F=18.8, P<0.01) 2. Temperature (F=16.0, P<0.01) 3. NO_3^- (F=4.2, P=0.04)	1. Moisture (F=62.5, P<0.01) 2. NH_4^+ (F=7.8, P<0.01)	1. Moisture (F=7.2, P<0.01)	ns

[a] This ranking (denoted by numbers) signifies its hierarchy of importance based on the minimal adequate LME model, using a stepwise model simplification; ns – no soil factor showed significant relationship with the soil trace gas fluxes.

Second, in the section on soil CO_2 flux, I think it would be useful if the authors could revise the text to incorporate a slightly expanded discussion of how root respiration could be influencing variations in soil CO2 fluxes (see point 10 below). For example, could the differences in respiration between this study site and others be attributed to differences in belowground biomass or root/shoot allocation? Do data exist on belowground biomass in these sites? If so, do those data help explain patterns in soil respiration?

We do not know of any data existing on root biomass in any of our present sites. From our previous work and that of others, we know root respiration can contribute 30% - 35% of the soil CO_2 efflux (van Straaten et al. 2011, Silver et al. 2005). However, we do not have any root data to base any possible contribution of roots to the soil CO_2 fluxes at our present sites. Interestingly, regardless of the contribution of autotrophic respiration to the soil CO_2 fluxes, we did not detect any significant differences in soil CO_2 fluxes among sites, but only found that across our 5 sites the temporal pattern of soil CO_2 fluxes was strongly related to soil moisture contents (Fig. 3) [added at line 424-427]. The range of soil moisture contents in these 5 sites (Fig. 4a) also clearly showed that the low-rainfall sites varied from the lower end up to the mid-moisture range, the high-rainfall site varied from the mid to high-moisture ranges and there was a wide overlap among sites within the mid-moisture ranges (Fig. 4a). Thus, if both autotrophic and heterotrophic responded similarly to these ranges of soil moisture contents, then their relative contributions should be less important than their overall response, or the response of soil CO_2 fluxes as a whole, to soil moisture contents.

Thus, in order to avoid any unnecessary speculative discussion, we prefer to focus our discussion on the possible causes of the generally low soil CO_2 fluxes from our present sites as compared to the other lowland forests in Panama (lines 406-423) – possibly due to low root respiration as well as considerable variation in litterfall (as a substrate for heterotrophic respiration). Here, we speculate that autotrophic respiration could be low at two of our sites since they have lower tree densities (particularly at Met and P27; see 2.1) than the old growth, lowland forests on BCI and Gigante.

To summarize, we focused our discussion on the temporal pattern, which our data have clearly shown, as well as reporting on similarities and differences with other studies from CSA lowland forests.

Third, in section 4.2 of the Discussion, the authors have identified separate sets of controls on CH4 uptake that appear to be operating on different time scales; i.e., daily fluxes of CH4 appear to be more strongly linked to soil moisture, whereas soil fertility was a stronger constraint on annual CH4 fluxes. This is an important and interesting finding, as it highlights the scale-dependency of different environmental controls, and suggests that different environmental factors may be controlling different aspects/components of trace gas cycling; e.g. in the short-term, soil moisture may be regulating transport and supply of CH4 to methanotrophs (hence, regulating instantaneous fluxes), whereas in the long-term, site fertility may be influencing the

total amount of methanotrophic biomass or the overall methanotrophic potential of these soils. It would be useful if the authors could consider a way of revising the current text to better highlight this important finding, as it has wider implications for upscaling these results or incorporating these findings into process-based models.

We have made major revisions to Section 4.2 in order to highlight better the scale-dependency of different environmental drivers of soil CH_4 fluxes. See Lines 464-510.

Additional comments

1. Lines 158-165: It would be useful know the precision of the analysis; i.e. what was the coefficient of variation for the standards?
2. Lines 173-174: Ibid.

We added the detection limits of our instruments, which were calculated as 3 x standard error of the standard, which was used to check the instrument precision during the analysis. The average detection limit during the periods of our measurements was 50 ppm CO_2, 43 ppb N_2O, 45 ppb CH_4, and 0.04 ppb NO/mV (mV is the electrical signal from the produced chemiluminescence of the oxidized NO). (Lines 174-175, 194-195)

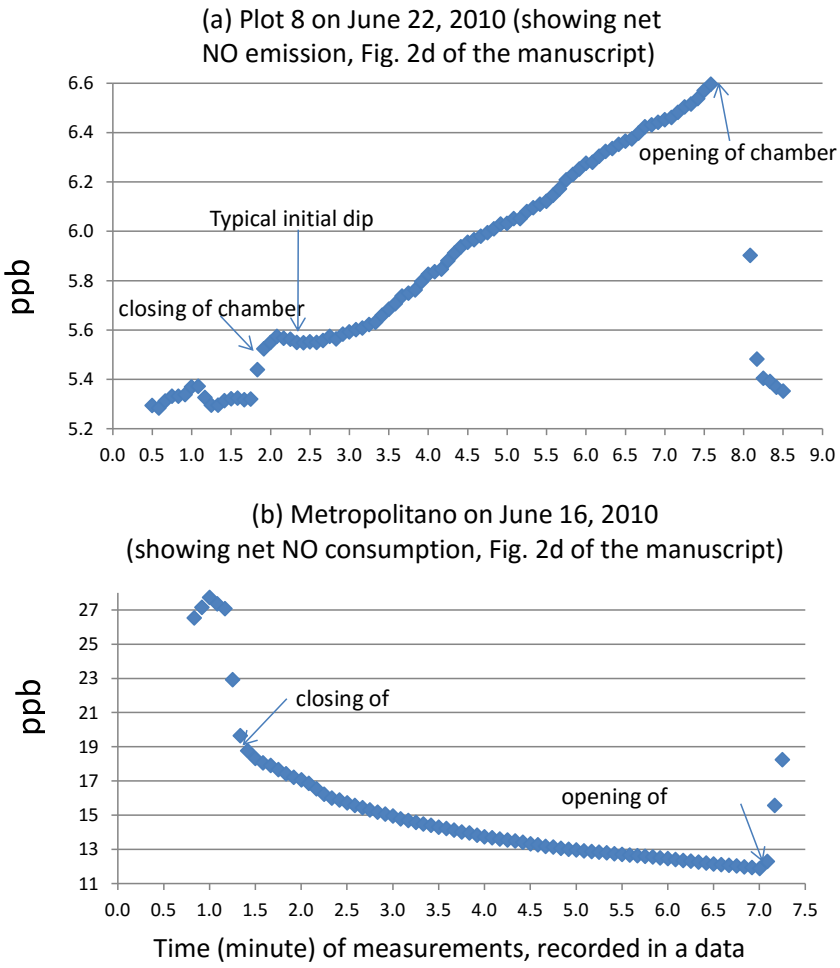
3. Lines 175-177: Were any fluxes non-linear? How were these data treated? Under more saturated soil moisture conditions, was there any evidence of ebullition? If so, how were these data treated?

Soil NO fluxes were always linear. We show below the typical soil NO fluxes where we observed net emission and net consumption. We considered the first 3-min. of linear change in NO concentrations with chamber closure time. (added at Lines 198-204)

For soil CO_2, N_2O and CH_4fluxes, all 3 gases were analyzed in our gas chromatograph sequentially from the same gas sample. Since these 3 gases come from the same sample, we based our best fit of gas concentration vs. time on the CO_2 concentration increase, as it is the gas with the highest concentration among these 3 gases. The CO_2 concentration always increased linearly with time of chamber closure. Hence, we used a linear fit for all the 3 gases, and zero fluxes and negative fluxes (i.e. for N_2O and CH_4) were all included in our data analysis. [added at Lines 198-204] This linear increase was not surprising, considering that the large volume of our chambers (11 L) decreases the likelihood of feedbacks on the diffusion gradient with increasing concentration; additionally, there was generally low soil CO_2 and N_2O fluxes at our sites (as we noted in the Discussion).

We also did not observe any evidence of ebullition (e.g. sudden increase of gas concentration during our 30-min chamber closure). (mentioned in Lines 198-204) Such a phenomenon is more likely under flooded conditions or in the transition periods to and from flooded conditions. We measured the volumetric moisture content continuously in our wettest site (plot 32) during the study period, using permanently installed water content probes (Campbell Scientific CS616, Logan, Utah), the same instrument we describe in our earlier studies in another lowland forest in Gigante, Panama (Koehler et al., 2010, Veldkamp et al. 2013, and Corre et al. 2014). The water-

filled pore space in the top 10 cm, recorded in the data logger every 4 hours, did not reach saturation at any time during our measurement period.



4. Lines 205-207: Are there any potential limitations associated with using this 15N natural abundance technique?

The potential limitations of using 15N natural abundance of the soil is its inherent high spatial variability brought about by 1) vegetation species differences, and 2) surface topography, which may drive differences in soil 15N natural abundance due to slope influences on water and solute distribution and ultimately on microbial N-cycling processes. These are the reasons why we used not only the 15N natural abundance of the surface depth but also of the 4 depth increments, and determined the overall 15N nat. abund. enrichment factor (ε), which considers the change in 15N natural abundance signature and total N concentration with depth in relation to the surface depth, as an integrative indicator of soil N availability (shown in our previous studies, e.g. Baldos et al. 2015). [summarized in Lines 233-236]

5. Lines 254-256: Have the authors considered using Box-Cox transformations to normalise the data? If successful, this would enable the authors to use parametric statistics (e.g. linear regression, multiple regression) rather than Spearman's Rank correlation. Moreover, even if the data do not fully meet the assumptions for parametric analyses, it may be useful/instructive to analyse the data using multiple regression techniques to evaluate the relative hierarchy of environmental drivers.

We have added an additional table (Table S1 above) to show the relative hierarchy of environmental drivers within sites (across seasons) and within seasons (across sites). Non-parametric statistics were only used to compare non-repeated measures with annual and seasonal averages.

6. Lines 271-286: It is worthwhile reporting the seasonal trends (or, lack of trends in NH4+) here as well. Does NH4+ show wet or dry season differences? I had assumed not given that this wasn't stated explicitly.

Lines 309-310 state that of the four repeated measures (temperature, moisture, extractable NO_3^- and extractable NH_4^+), only moisture and extractable NO_3^- exhibited strong seasonal differences. Additionally, we have added a statement (line 313-315) specifically clarifying that temperature and extractable NH_4^+ exhibited between-season differences at only one site each (temperature - P8, extractable NH_4^+ - P27).

7. Lines274-275: Do you have complementary measurements of net or gross N cycling processes to help interpret these field patterns? It's possible that the reduction in NO3 during the wet season may be linked to reduced nitrification (with a growth of anoxic microsites), or an increase in NO3- reduction (e.g. DNRA or denitrification).

These lines that the reviewer is referring to are presenting the total soil N, which is commonly 4 orders of magnitude (Table 2) higher than the mineral N (Table 3), the latter reflecting the actively cycling fraction of the total N. Thus, the rate of soil N cycling, being small compared to the total soil N, cannot make a big change to the amount of total N. Total soil N reflects the long-term accumulation of N in these sites.

We indeed have measured gross rates of soil-N cycling in the same sites and replicate plots in the wet season 2010 (Nov.) and the dry season 2011 (May). We do not report them here, as they are

included in a separate paper focusing on patterns of soil-N cycling and soil N availability along these orthogonal gradients of soil fertility and precipitation.

However, our interpretations in the present paper were considered in light of the rates of soil-N cycling that we measured. Across sites, gross N mineralization rates correlated with soil microbial biomass N, total soil N, 15N nat. abund. enrichment factor (ε), and 15N nat. abundance (Spearman rank correlation coefficients of 0.48-0.80, n=20, P<0.05). The patterns of microbial N and total N followed that of increasing annual precipitation, while 15N nat. abund. enrichment factor and 15N nat. abundance were low at the low- and high-rainfall sites and peaked at the mid-rainfall sites (Table 2). These patterns were opposite to those of soil pH, ECEC and exchangeable bases across sites (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 2). Thus, our interpretation of this pattern of total soil N with increasing precipitation was that the higher the total N (with increasing precip.), the higher the amount of microbial N and the higher the soil N availability, as indicated by the rate of actively cycling N (i.e. gross rates of N mineralization) and mineral N (i.e. soil NH4+ levels, Table 3).

Across sites and seasons, gross N mineralization was not correlated with gross nitrification but instead with NH4+ immobilization (suggesting that heterotrophic nitrification was possibly important rather than autotrophic nitrification). We cannot merely attribute the reduction of NO3- in the wet season to reduced nitrification because gross nitrification was only measured once in the wet and once in the dry season, and we did not see significant differences between wet and dry seasons across sites nor at each site. Additionally, gross nitrification was correlated with NO3- immobilization, but not with DNRA, suggesting that when there was high NO3- availability, this was preferably assimilated by the microbial biomass. On the other hand, the soil NO3- levels we show in Table 3 were measured repeatedly, parallel to soil trace gas flux measurement, over our 21-month study period (as opposed to the gross rate of soil-N cycling which, due to the intensive labor and cost required, was only measured twice). The soil NO3- levels (Table 3) reflected the concurrently occurring NO3- production and consumption processes, [included in Lines 534-543] and our discussion on the role of soil NO3- levels on the soil trace gas fluxes always considered the soil NO3- patterns between seasons, among sites, the inverse correlations of NO3- and soil moisture, and the correlations of NO3- with soil CO2, CH4, N2O and NO fluxes at a particular site.

8. Lines 293-297: Were these data from bivariate regressions or from a multiple regression model? If the second, it would be useful to indicate, based on the sum of squares, which variables accounted for a larger proportion of the variance and which variables accounted for less, in order to clearly establish the hierarchy of drivers.

As shown above, we have included a table (Table S1) showing the relative hierarchy of environmental drivers. As suggested by reviewer 2 above, we used the minimum adequate LME models in analyzing the hierarchy of drivers. This statistical analysis is also described in the revised manuscript (line 282-296).

9. Lines 317-319: Increased evidence for nutrient limitation of methanotrophy? What are the implications of this for process models (could be discussed in the Discussion)?

This question of the reviewer is related to the 3rd general comment above (please see our answer above as well). The sentences following these lines 317-319 presented the possible reasons (through correlations with controlling factors) for this pattern of differences among sites (see lines 318-331) and are discussed in lines 438-459 of the original manuscript.

The most important controlling factor on the long-term pattern of soil CH_4 fluxes across sites was soil fertility. Specifically, as shown by the strong inverse correlation between soil 15N natural abundance signatures and exchangeable cations (Table 5), the positive correlation between soil CH4 flux and fertility (Fig. 4b) likely reflected the long-term effects of soil development (Tables 1 and 2) - more CH4 uptake occurred in highly weathered soils with less rock-derived nutrients but high soil N availability (i.e. high 15N natural abundance signatures) (Tables 4 and 5). When separated by season, the correlation between average soil CH4 fluxes and soil 15N natural abundance was stronger in the dry season than the wet season (Table S2), supporting our claim that soil N availability enhanced CH4 uptake in soils when gas diffusion was favorable (dry season). (included in revised 4.2; See Lines 464-510)

10. Lines 339-341: Evidence for very active nitrifiers? Perhaps this could be explored further in the discussion.

This question is related to comment #7 above (please refer to our extended answer there). Our measured gross nitrification rates (measured once in the wet and once in the dry season at all sites) did not show significant differences among sites nor between seasons at each site. Thus, we cannot simply attribute the results presented in these lines (339-341) that the reviewer is asking (i.e. positive correlations between soil N2O emissions and moisture and negative correlations between soil N2O emissions and NO3- concentrations at the mid-rainfall sites (P8 andP19) to be due to active nitrifiers.

11. Lines 362-363: To what extent is inter-annual variability modified/affected by differences in belowground allocation and variations in root-rhizosphere respiration? Do data exist on the belowground biomass across your gradient or differences in root/shoot allocation? If so, this may help tease out the extent to which differences in total soil respiration are affected by differences in the fluxes from individual respiration components.

This question is related to the question about CO_2 above (please refer to our extended answer there). In brief, we do not know of any available datasets that could answer this question. However, we do think our results highlight another interesting facet of CO_2 emissions in these sites, namely, that despite the differences in soil factors between sites, we did not see differences in CO_2 fluxes. However, we did see strong temporal patterns, and therefore focused our discussion on short-term changes over time, as well as reporting on similarities and differences with other studies from CSA lowland forests.

Reviewer 2

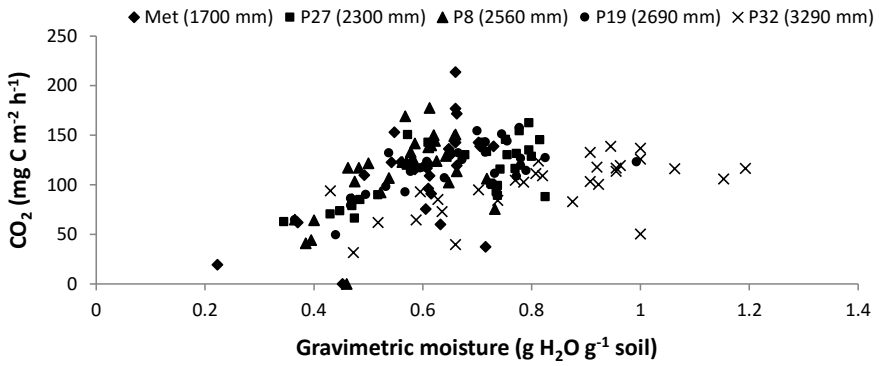
(1) Since in tropical ecosystems soil moisture is highly variable, while temperature is fairly constant (can be seen in your dataset: while gravimetric soil moisture changed from 1.2 to

0.4, soil temperature changed from 27 to 23°C. In other words 66% change of moisture, while temperature changed 15%.). Based on that it can be expected that changing soil moisture is the major driver of trace gas emissions. However, in your study a co-correlation of soil moisture and soil temperature is discussed. This is highly interesting, but not yet well presented. You should be able to demonstrate that air temperature at your sites was fairly constant, therefore the most of the change in soil temperature should be attributed to co-correlation to soil moisture changes. Based on theoretical considerations (e.g. Q10 value) you should be able to give an estimate about how much of the change in CO2, CH4, N2O emission could be caused by temperature only and by the combined soil moisture/temperature effect.

In response to this comment and the first comment of reviewer 2 (see above), we have used minimal adequate linear mixed effects models to identify a hierarchy of importance of the environmental drivers within and between sites/seasons, which addresses this concern by giving more details about the relative importance of moisture, temperature and extractable mineral N over our 21-month measurement period (Table S1).

(2) The general "parabolic relationship" of CO2 and soil moisture might be influenced by combining all data point from all sites. It seems actually that the emission follow more actual soil moisture than rainfall gradient. For a more comprehensive analysis, it might be helpful to include correlation coefficients for rainfall, soil moisture, soil temperature, NO3- and NH4+. Since in the whole paper all figures show data points with individual symbols for each site, it seems reasonable to use different symbols for each site (Fig3).

In response to this comment, we include below a revised version of Fig. 3 to show individual symbols for each site, which we also use to replace the previous version of Fig. 3 in the manuscript. As we discussed in lines 440-441, such parabolic relationships have also been observed by other studies in tropical forests of Costa Rica, Panama and Brazil. Indeed, we conducted correlation tests between annual soil CO2 emissions and annual rainfall but this was not statistically significant because their relationship was parabolic and not linearly correlated. For this parabolic relationship with annual rainfall, we decided it was better to present Fig. 3 as essentially the same pattern is depicted, but Figure 3 is better, as it depicts the actual measured daily values. All the other soil factors were tested for correlation with soil CO2 fluxes, and we have reported their relationships in lines 332-340. They are also summarized in Table S1 (see above).



Furthermore, is there a reason why N2O is not shown in relationship to soil moisture? It might be helpful for a more process based discussion and the role of aerobic CH4 oxidation coupled to denitrification in this soils? Predominantly the soils are a net-sink for CH4, and you measured N2O and NO3 but did not discuss the coupling of processes yet (see e.g. Zhu et al. 2016 aerobic methane oxidation coupled to denitrification).

As we mentioned in the text (lines 380-383), soil moisture was only strongly correlated with soil N_2O fluxes at two sites (P8 and P19), so including a figure showing the relationship with moisture across sites would not add anything to the results we were presenting. We have, indeed, analyzed our data to explore whether there was a link between soil N2O and CH4 fluxes – which would support what reviewer 1 is asking here. However, neither Table 5 nor Table S2 support such link (i.e. no significant correlation). Thus, we would have no basis to include this aspect in our discussion without being overly speculative. We do note, though, that the roles of NO3- on soil N2O fluxes as well as on CH4 uptake were discussed extensively (lines 482-492 and 530-538 of the manuscript).

It would be more appropriate to convert gravimetric soil moisture into either whc or WFPS to normalize somehow for the soils from different site.

We are unable to convert the gravimetric to WFPS mainly because the Metropolitan and P27 sites, whose parent materials are agglomerates, had fine stones making measurement of soil bulk density erroneous. We tried to do a more accurate estimate of soil bulk density but we were not confident that we were able to get out all of the gravel in these heavy clay soils (average soil texture within the top 50 cm was 60-62%) from the soil cores we used to measure soil bulk density. On the other hand, we made very careful measurements of gravimetric measure contents every time we took subsamples from the soils that were concurrently sampled during each soil gas flux measurements. Thus, our gravimetric moisture measurements were more reliable than converting to WFPS.

(3) If soil temperature, soil moisture, and soil properties would dominate the CO2, CH4, N2O, and NO fluxes, the data points (Fig.3) should result separate functions over time. The fact, that

they are overlaying each other suggests, that other parameters, which are not yet discussed might affect CO2, CH4, N2O, and NO fluxes. As such it should be discussed how abundance (and activity?) of functional microbial groups will change within the rainfall and fertility transect?

As mentioned above, we have now provided more information as to the relative hierarchy of the environmental drivers that we monitored. We agree that the abundance/activity of functional microbial groups would play a role and that such a dataset would definitely provide additional insight into trace gas fluxes along these gradients. However, as we did not take those measurements as part of this study, discussing how they may have affected our results would be purely speculative. We have added a sentence into the discussion to specifically mention that point (i.e. that in future studies, measurement of functional groups could add additional insight; Lines 611-612).

(4) Without any additional literature reference the transfer from Tamai et al., 2003 for methanotrophs to methanogens is hard to buy. In Tamai et al., 2003 a negative correlation between CH4 uptake rate and Al was found. Table 2 shows that your inhibition might be possible for P8, P19, P32, but not for the others. However, these 3 sites show actually the lowest CH4 fluxes in the rain season 2011 (Fig. 2). Shouldn't a correlation of net flux and Al result in a positive correlation if inhibition of methanotrophs based on Tamai et al., 2003 is assumed? If your assumption would be valid, how can you explain a simultaneous inhibition of methanotrophs which could cancel out your inhibition of methanogens? Since methanotrophs and methanogens are different functional groups of microbes, I think this is speculative.

We agree with this comment and this was removed in the revised version of section 4.2.

(5) For me it seems more plausible that a combination of pH, BS and ECEC which show strong correlations as well, might result a stronger impact for CH4 flux. And a correlation of 15N might point towards coupled methane oxidation and denitrification (e.g. Zhu et al., 2016)?

As mentioned above, we have substantially altered Section 4.2, which is the section of the discussion related to CH_4 fluxes. However, as we outlined in the comment above, our results do not show any correlation between CH_4 and N_2O fluxes, in the annual or seasonal averages, so we chose not to incorporate that into the discussion.

Based on the microbial processes it can be assumed that CH4 oxidation should contribute to CO2 formation. However, this is indicated by a correlation of only -0.24 (CH4 and CO2) in Table 5. Consequently, a potential coupling of aerobic methane oxidation and denitrification might result only -0.07 (CH4 and N2O) in table 5.

The correlation coefficients referred by reviewer 1 here are not statistically significant and therefore we chose not to incorporate them into the discussion. Additionally, even granting that this assumption of CH4 oxidation contributing to CO2 formation is valid, by looking at the magnitude of soil CO2 fluxes in comparison to soil CH4 uptake (Figs. 2a-b), such a contribution would be minute compared to the more conventional contributions of heterotrophic (oxidation of

organic C with O2) and autotrophic (plant roots) respiration. As to possible coupling of CH4 oxidation with denitrification, please see our answer to the same comment above.

Finally the introduction and discussion would highly benefit to be focused more on microbial processes.

We have changed the introduction in response to this comment. Although we still start with a general intro about trace gases from Central and South American forests, and possible temporal/spatial controlling factors, we then proceed to introduce each trace gas individually, before moving on to introduce the gradient study. See Lines 59-106.

Minor comments:
Introduction
It might be better for the reader to follow the different microbial processes which cause the production and consumption of each trace gas rather than jump from effects of temperature to moisture to soil properties on CO2, CH4, N2O and NO? Overall the introduction is missing a clear structure.

See comment above.

You are writing about methanotrophs and methanogens, but for the other trace gases you don't include any information about the processes and functional microbial groups.

In response to this and the other comments above, we now introduce each trace gas individually, briefly commenting on the processes of importance (i.e. autotrophic/heterotrophic respiration, methanotrophs/methanogens, nitrification/denitrification; See Lines 59-106).

Line 40: Studies (without references) either include references or refer to a comprehensive list in supplement.

This sentence has been revised so that the vague reference to "studies" is gone. (However, annual soil trace gas fluxes in Central and South American (CSA) tropical lowland forests can vary significantly; in one study…; Line 43)

Line 65/66: take care of terminology, maybe define once? Net CH4 flux consists of production (positive) and consumption (negative). Furthermore, it should be mentioned that production occurs even under negative net CH4 flux, but consumption is predominant.

This sentence has been revised as follows: Soil CH_4 fluxes (predominant flux indicated by positive values (net emissions) or negative values (net consumption)) in CSA tropical lowland forests… (Line 79)

Material and Methods
Line 149 "soil trace gas flux measurement": you can only measure mixing ratios. Fluxes are the result of a second order calculation.

Line 150 “fluxes were measured”?

We have changed the title of section 2.2 to “soil trace gas flux calculation” and altered the wording in that section to indicate that we determined fluxes rather than directly measuring them.

Line 168 Please specify what gas did you flow through the chambers? Ambient air, synthetic air?

Line 246 now specifies ambient air.

I recommend including the formulas to calculate CO2, CH4, N2O (static) and NO (dynamic), plus the trapezoid rule to calculate the annual fluxes that the reader does not have to look up several other papers to follow the calculations.

Fluxes were calculated using the linear change in concentration over time (now included at Lines 197 and 203). The trapezoid rule is an established method of filling in gaps between sample dates by assuming a linear relationship in gas fluxes between those two dates (Line 207-280). Neither of these calculations uses a specific formula.

Results
The results are majorly focusing on the descriptive correlations. Why the major results of CO2, CH4, N2O, NO fluxes is not presented here? For me these are the major results obtained from the field by hard work (Fig1 and Fig2).

The raw data can be made available for teams developing models and/or needing more specific information, but as the data was presented in Figure 1 and Figure 2, we chose to focus the results and discussions on patterns that we found in the data.

Line 291 Due to different soil properties for each site, it seems not very helpful to present Fig. 3 and talk about a “parabolic relationship”.

Please see our related comment above. As shown in the figure above, even once the different sites are identified with unique symbols, the data do not separate out, but instead, together, exhibit this parabolic relationship. It is also shown in Table S2 that moisture was a major controlling factor during the dry season and within each individual site.

Discussion
Statement about what might cause the NO3- differences? Wet deposition, if yes, are there values from literature?

We have measured the gross rates of soil-N cycling at these sites. The rates of gross N mineralization (2-5 mg N kg^{-1} d^{-1}, or about 68-170 mg N/m2/day in the top 5-cm depth, using our measured soil bulk density, averaged across sites, of 0.68 g/cm^3) and gross nitrification (1.2-2.4 mg N kg^{-1} d^{-1}, or about 41-82 mg N/m2/day in the top 5-cm depth) were much higher than our measured wet N deposition (9 kg N/ha/yr or only 2.4 mg N/m2/day) at the Gigante site (see map in Fig. S1; Gigante is across the Panama Canal from our present sites).

We would actually not assume that the mineral N in the soil is directly influenced by the external N input via wet N deposition. The soil N cycling rates are much larger than the wet deposition, based on our previous sites in Gigante (e.g. Corre et al. 2010, 2014), Ecuador (Baldos et al. 2015), and Indonesia (Allen et al. 2016).
We discussed the pattern of the soil NO3- levels among sites, or the mineral N pool for that matter, in perspective of the soil-N cycling, which influencse this mineral N levels, and ultimately reflected in our overall index of soil N availability status (low or high N availability), 15N natural abundance enrichment factor (which has been shown to correlate with soil N availability; see lines 228-237 of the manuscript).

Thus, we decided not to include in our discussion about wet deposition, which obviously will not directly influence the soil NO_3^- levels, but discussed the patterns of NO_3^- among sites with regards to soil N availability status of the sites.

The connection of the trace gas fluxes to microbial processes is missing. E.g. the correlation of CH4 fluxes (net uptake) is negatively correlated to 15N natural abundance. Does this point towards a CH4 production coupled to denitrification? And could this coupling be less relevant in the dry season versus the wet season and thereby result amplified correlations in the dry season?

The negative correlation of CH4 fluxes (net uptake) with 15N natural abundance was indeed discussed (lines 488-493). However, please refer to our explanation above as to why we don't think that this relationships points towards CH4 production being coupled to denitrification.

Figures:

Error bars are missing for Fig 3, 4, and 5
Fig. 4 a, b, c should include a 0 line for easier understanding. Fig. 4a might be better to bin data into moisture classes of 10%. Less data points will make the figure easier to understand and better show trends. Error bars can be included. Would it make more sense to average the single points and report error bars to highlight the grouping in different fertilizer regimes Fig 4b? That might be helpful for discussion?

We chose not to put error bars on the scatterplots, as their purpose was to highlight trends, which may have been masked by including so much additional information. However, in response to this comment, we have included a zero line for 4a (zero occurred at the top of b and c). We are reluctant to average the data, however, as the current figures allow readers to see the exact spread found within each site rather than simply the standard deviation shown on error bars.

Fig. 5: Where was the NO ambient mixing ratio measured? Close to the ground (chamber height) or 2m height? Are there references available for such high NO ambient mixing ratios and possible sources? Based on Remde et al (1989) it might be helpful to plot NO release rate versus ambient NO mixing ratio at same moisture and temperature for each site. Furthermore, only data points for a range of soil moisture and soil temperature should be selected.

The NO ambient mixing ratio was measured at a height of 2 m above the ground (prior to each chamber measurement) near to each of the 4 chamber locations at each of the 4 replicate plots per site on each sampling day. (added at Line 179-181)

As to the last comments (*to plot NO release rate versus ambient NO mixing ratio at same moisture and temperature for each site; only data points for a range of soil moisture and soil temperature should be selected)*, this would not be meaningful for our data sets, because such a way of analyzing data is driven by an inherent assumption that the ambient NO mixing ratio is influenced by biological processes in the soil. This is not the case at our study sites where anthropogenic ambient NO levels are prevalent, especially the site near to the Panama city and even the other sites along the Panamal canal, brought about by large shipping traffic. Such high NOx emission was also reported by Hietz et al. 2011.

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

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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

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). However, annual soil trace gas fluxes in Central and South American (CSA) tropical lowland forests can vary significantly; in one study~~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 moisture affects microbial activity both directly through water availability and indirectly through its influence on the soil oxygen status and gas diffusivity (Davidson and Schimel, 1995). Spatial variations in soil trace gas fluxes are largely controlled by

soil ~~physical and biochemical~~ characteristics. Soil texture, for example, 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 nutrient~~N~~ availability (Silver et al., 2000; Sotta et al., 2008; Allen et al., 2015).

~~Net s~~Soil CO_2 fluxes at the soil surface are the result of interacting belowground processes, including autotrophic (root) respiration ~~(from roots, rhizosphere and associated mycorrhiza)~~ and heterotrophic (microbes and soil fauna) ~~microbial~~ respiration (Raich and Schlesinger, 1992; Hanson et al., 2000). Although temporal and spatial drivers may be affecting these processes differently, the ~~overall~~net response of soil CO_2 fluxes shows some consistent trends. ~~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 CO_2 emissions from CSA tropical forest soils generally exhibit positive relationships with soil temperature (Chambers et al., 2004; Schwendenmann and Veldkamp, 2006; Sotta et al., 2006, Koehler et al., 2009a) and soil moisture (Davidson et al., 2000). ~~,~~ The relationship between CO_2 and moisture ~~which may be~~is often 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). Spatial differences in soil CO_2 emissions can be affected by soil characteristics. B~~In CSA tropical forests, b~~oth Silver et al. (2005) and Sotta et al. (2006) ~~observed~~noted a soil texture effect on net soil CO_2 emissions; higher ~~soil CO_2~~ emissions occurred in~~from~~ sandy ~~than~~as compared to clayey Ferralsol soils, which were attributed to

respiration from the higher fine root biomass in the sandy soils. Soil fertility can also affect net soil CO_2 emissions; ~~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). ~~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 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.~~

~~Net s~~Soil CH_4 fluxes reflect the combined activity of both methanotrophs (CH_4 consumers) and methanogens (CH_4 producers), the ratio of which can change in space and time. Since the activity of both functional groups 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 are more likely to 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 CH_4 fluxes (predominant flux indicated by positive values (net emissions) or negative values (net consumption)) ~~positive values for net~~

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~~emissions and negative values for net consumption)~~ in CSA tropical lowland forests ~~also~~ often~~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). Although they have less often been the focus of CH_4 studies, soil biochemical characteristics (i.e. soil fertility status) may also play an important role. 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. ~~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).~~

N-oxide gases (N_2O and NO) are produced and consumed through the microbial processes of nitrification and denitrification (Chapuis-Lardy et al., 2007). 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. Soil temperature can also be positively correlated with NO flux (Gut et al., 2002), and negatively correlated with soil N_2O emissions (Keller et al., 2005), though this

may be due to a co-correlation of soil temperature with soil moisture. 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). Finally, as an essential substrate for nitrification and denitrification, N availability in the soil is a primary controlling factor of soil N-oxide fluxes (Koehler et al., 2009b; Corre et al., 2014).

~~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 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 CH_4 fluxes (positive values for net emissions and negative values for net consumption) in GSA 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 GSA tropical forest studies (Keller and Reiners, 1994; Verchot et al., 1999; Davidson et al., 2004; Keller et al.,~~

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~~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.~~

~~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).~~

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712 Climate scenarios suggest that tropical regions may experience large changes in
713 precipitation regimes in the future, with moist tropical regions likely experiencing both higher
714 annual precipitation and more extreme precipitation events (Stocker et al., 2013). Such changes
715 could significantly alter current soil trace gas fluxes, since soil moisture – as described above –
716 plays an important role in both the temporal and spatial variability of soil trace gas fluxes. One
717 approach to studying how changes in precipitation may alter soil trace gas fluxes is to investigate
718 these fluxes along a natural gradient of climate (e.g. precipitation) in a localized region. This
719 approach was used by Holtgrieve et al. (2006) on the Kula volcanic series lava flow in Hawaii, to
720 show that soil N cycling and N-oxide fluxes were strongly affected by mean annual precipitation.
721 However, as suggested by Santiago et al. (2005), precipitation gradients in continental tropical
722 forests, where there are variations in species composition and soil parent material, may exhibit
723 different patterns than those from Hawaii. Additionally, precipitation (or climate) is itself a soil
724 forming factor (Jenny, 1945), and continental tropical lowland soils are considerably older than
725 the relatively young volcanic soils (i.e. Santiago et al., 2005). Therefore, soils of continental
726 precipitation gradients will reflect both the long-term effects of the precipitation regime (i.e. on
727 differences in soil physical and biochemical characteristics) in addition to short-term effects (i.e.
728 on soil moisture).
729 In this study, we quantified soil trace gas fluxes in tropical lowland forests of the Panama
730 Canal Watershed, spanning a precipitation gradient of 1700-3400 mm yr^{-1} (Figure S1). Soil
731 fertility (based on an aggregate index that included clay content, ^{15}N natural abundance, effective
732 cation exchange capacity (ECEC), organic C:N ratio, and exchangeable Al; see 2.4) varied
733 orthogonally with this precipitation gradient (Figure S2). The objectives of our study were to: (1)
734 determine how soil fluxes of CO_2, CH_4, N_2O and NO vary along orthogonal gradients of

735 precipitation and soil fertility, and (2) assess and compare the spatial and temporal controls of
736 soil trace gas fluxes in lowland tropical forests. By using orthogonal gradients of precipitation
737 and soil fertility, we were able to examine the relative importance of climatic factors vs. soil
738 biochemical characteristics for soil trace gas fluxes. We hypothesized that the temporal and
739 spatial patterns of soil trace gas fluxes across sites would follow the pattern of the most
740 important controlling soil factors: soil CO_2 fluxes would be parabolic in relation to increasing
741 soil moisture along the precipitation gradient; soil CH_4 fluxes would increase (or CH_4
742 consumption would decrease) with increasing soil moisture and decreasing soil fertility along the
743 precipitation gradient; and soil NO fluxes would decrease whereas soil N_2O fluxes would
744 increase with increasing soil moisture along the precipitation gradient.
745
746 **2 Methods**
747 **2.1 Study sites**
748 Soil trace gas fluxes were measured in five study sites of the Center for Tropical Forest Science
749 (CTFS) located in the Panama Canal Watershed, central Panama (Table 1; Figure S1). Mean
750 annual air temperature is 27 °C (Windsor, 1990); the soil temperature across all sites fluctuated
751 between 22.5 and 27.5 °C during our study years (Fig. 1a). The five sites span a gradient of
752 annual precipitation from 1700 mm yr^{-1} in Metropolitan National Park (Met) on the Pacific side
753 to 3400 mm yr^{-1} in P32 on the Atlantic side; the dry season generally lasts from January through
754 April (Corre et al., 2014). The sites were located in either old growth (P8 and P32) or mature
755 secondary (Met, P27, and P19) lowland forests, with tree densities (≥10 cm diameter at breast
756 height, DBH) of: 322 stems ha^{-1} in Met, 395 stems ha^{-1} in P27, 560 stems ha^{-1} in P8, 520 stems
757 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 attributes (Pyke et al., 2001). The amounts and forms of soil organic P are strongly controlled by soil properties whereas the proportion of soil organic P to total P is insensitive to the variation in rainfall and soil properties (Turner and Engelbrecht, 2011).

2.2 Soil trace gas flux ~~measurement~~calculation

Soil CO_2, CH_4 and N_2O fluxes were ~~measured~~ determined every 2-4 weeks from June 2010 through February 2012 (28-31 sampling dates) using static vented chambers. Within each of the five sites, a 20 m grid was placed over a 1 ha area and we randomly chose four 20 m x 20 m replicate plots with a minimum distance of 20 m between plots. In each replicate plot, four permanent chamber bases were installed (0.04 m^2 area and 0.25 m height after inserting 2 cm into the soil) at the ends of two perpendicular 20 m transects that crossed in the plot's center. The total volume of the chamber (with cover) was 11 L. To ~~measure~~ determine soil trace gas fluxes, chamber covers were placed on the bases and gas samples (100 mL) were taken 2, 12, 22 and 32 min later. Samples were stored in pre-evacuated glass containers with Teflon-coated stopcocks. At the Gamboa field laboratory, gas samples were then analyzed for CO_2, CH_4 and N_2O concentrations using a gas chromatograph (Shimadzu GC-14B, Columbia, MD, USA) equipped with a flame ionization detector (FID), an electron capture detector (ECD) and an autosampler, the same instrument that was used in our earlier studies (Koehler et al. 2009a, 2009b, 2010, 2012; Veldkamp et al., 2013; Corre et al. 2014). The instrument's detection limits were 50 ppm CO_2, 43 ppb N_2O and 45 ppb CH_4. Gas concentrations were ~~determined~~ measured by comparing

integration peaks with those of three or four standard gases containing increasing concentrations of CO_2, CH_4 and N_2O (Deuste Steininger GmbH, Mühlhausen, Germany).

Soil NO fluxes were ~~measured~~ determined every 2-4 weeks from June 2010 through June 2011 (18-21 sampling dates) using open dynamic chambers (11 L volume) placed for 5-7 minutes on the same permanent bases described above. The NO ambient mixing ratio was measured at a height of 2 m above the ground (prior to each chamber measurement) near to each of the 4 chamber locations at each of the 4 replicate plots per site on each sampling day. To measure NO, ~~T~~the air from the chamber (ambient air) 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). The instrument's detection limit was 0.04 ppb NO/mV; mV is the electrical signal from the produced chemiluminescence.

-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. To calculate soil NO fluxes, we considered the first 3 minutes of linear change in NO

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concentrations with chamber closure time. For CO_2, N_2O and CH_4 fluxes, all 3 gases were analyzed in our gas chromatograph sequentially from the same gas sample. Thus, we based our best fit of gas concentration vs. time on the CO_2 concentration increase, as it is the gas with the highest concentration among these 3 gases. We did not observe any evidence of ebullition (e.g. sudden increase of gas concentration during our 30-min chamber closure), and the CO_2 concentration always increased linearly with time of chamber closure, so a linear fit was used for all 3 gases. Zero fluxes and negative fluxes (i.e. for N_2O and CH_4) were all included in our data analysis.

~~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, assuming a linear relationship in fluxes between sampling ~~d~~days ~~with measured fluxes~~ (Koehler et al. 2009a, 2009b, 2010; Veldkamp et al., 2013; Corre et al. 2014).

2.3 Soil biochemical characteristics

In each replicate plot after each soil trace gas flux measurement, samples of the top 5 cm of soil were taken about 1 m from each of the 4 chamber bases, pooled and mixed thoroughly in the field to measure soil extractable NH_4^+ and NO_3^- concentrations and gravimetric water content. In the field, soil samples were placed into prepared extraction bottles containing 150 mL of 0.5M K_2SO_4 and shaken thoroughly. Back at the field station ($\leq$ 6 h after samples were taken), the extraction bottles were again shaken (~ 1 h) and then the extracts were filtered and frozen immediately. The remaining soil was oven-dried at 105 °C for 1 day in order to ascertain

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828 gravimetric water content; this was then used to calculate the dry mass of the soil that had been
829 extracted for mineral N. The frozen extracts were sent by air to the University of Göttingen,
830 Germany for analysis by continuous flow injection colorimetry (Cenco/Skalar Instruments,
831 Breda, Netherlands). The Berthelot reaction method was used to determine NH_4^+ (Skalar Method
832 155-000) and the copper-cadmium reduction method was used to determine NO_3^- (NH_4Cl buffer
833 without ethylenediaminetetraacetic acid; Skalar Method 461-000).
834 Soil pits were dug in the center of each of the four replicate plots per site and soil samples
835 were taken for the depth intervals of 0-5, 5-10, 10-25 and 25-50 cm. Soil samples were air-dried
836 and sieved through a 2-mm sieve. Natural abundance ^{15}N signatures were determined from the
837 ground soil samples using isotope ratio mass spectrometry (IRMS; Delta Plus, Finnigan MAT,
838 Bremen, Germany). We calculated the $\delta^{15}N$enrichment factor (ε) using the Rayleigh equation
839 (Mariotti et al., 1981): $\varepsilon = d_s - d_{so} / \ln f$, where d_s is the $\delta^{15}N$ natural abundance at different depths
840 in the soil profile, d_{so} is the $\delta^{15}N$ natural abundance of the reference depth (top 5 cm), and f is the
841 fraction of total N remaining (i.e. the total N concentration at a given depth divided by the total
842 N concentration in the top 5 cm). The use of only surface $\delta^{15}N$ natural abundance values can be
843 limited, given its inherently high spatial variability (i.e. due to vegetation species differences and
844 surface topography). Therefore, we used not only the surface depth but also 4 depth increments
845 to determine the overall natural abundance enrichment factor (ε). The ε value was used as an
846 integrative indicator of soil N availability, as this correlates with internal soil-N cycling rates
847 (Sotta et al., 2008; Baldos et al., 2015). Total organic C and N were measured from the ground
848 soil samples by dry combustion using a CN analyzer (ElementarVario EL; Elementar Analysis
849 Systems GmbH, Hanau, Germany). ECEC was determined from the sieved soil samples by
850 percolating with unbuffered 1M NH_4Cl and measuring the exchangeable element concentrations

(Ca, Mg, K, Mn, Na, Fe and Al) in the percolates using an inductively coupled plasma-atomic emission spectrometer (ICP-AES; Spectroflame, Spectro Analytical Instruments, Kleve, Germany). Base saturation was calculated as the ratio of exchangeable base cations to the ECEC. Soil pH (H_2O) was analyzed from a 1:4 soil-to-water ratio. Particle size distribution of the mineral soil was determined using the pipette method with pyrophosphate as a dispersing agent (König and Fortmann, 1996).

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2.4. Soil fertility index

The variation in soil types along our rainfall gradient (Table 1) was paralleled with variations in soil biochemical characteristics (Table 2; see 3.1). Thus, we developed a soil fertility index using principal component analysis (PCA), similar to the approach employed by Swaine (1996); for each site, the index was based on five soil physical and biochemical properties: 1) clay content, which reflects water- and nutrient-holding capacity, 2) ε that signifies long-term soil N status, 3) ECEC and soil C:N ratio, which indicate bioavailability of rock-derived nutrients and soil organic matter, and 4) exchangeable Al, which implies soil chemical suitability. We used the depth-weighted average of these soil parameters (Table 2), measured at various depth intervals in the top 50 cm depth (except for ε that is calculated for the whole depth; see above). The first component factor of this PCA analysis explained 42 % of the variation in these soil characteristics among sites (Figure S2) and the factor scores were used as the quantitative index 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).

873 **2.4 Statistical analyses**

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

878 Soil trace gas fluxes (based on the average of the four chambers per replicate plot on each
879 sampling day) and the accompanying soil explanatory variables (soil temperature, gravimetric
880 moisture, NH_4^+ concentration and NO_3^- concentration) were tested for normality using Shapiro-
881 Wilk's test; variables with non-normal distributions were square root or log transformed. We
882 then used linear mixed effects models (LMEs) to assess the differences in these repeatedly-
883 measured variables along the orthogonal precipitation and soil fertility gradients, with site and/or
884 season as the fixed effect(s) and sampling days and replicate plots as random effects. If the
885 Akaike information criterion (AIC) showed an improvement in the LME models, we included a
886 first-order temporal autoregressive function to account for the decreasing correlation of
887 measurements with increasing time (Zuur et al., 2009) and/or a variance function (varIdent) to
888 account for heteroscedasticity of fixed-factor variances (Crawley, 2012). To assess the
889 relationships between soil trace gas fluxes and soil explanatory variables, we used the mean
890 values of the four replicate plots on each sampling date, and conducted Pearson correlation tests
891 over the entire sampling period across the five sites and for each site. Lastly, we analyzed the
892 hierarchy of importance of the soil controlling factors of soil trace gas fluxes by selecting the
893 minimal adequate LME model. For this, we used a stepwise model simplification in which each
894 controlling factor was tested against a null model and the soil factor that showed the lowest AIC
895 value was ranked as the most important; the soil factors with the next lowest AIC values were

added step-wise into the model if this significantly improve the model fit. This analysis was conducted on the mean values of the four replicate plots on each sampling date over the sampling period across the five sites and for each site.

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, correlation coefficients and minimal adequate LME models were considered significant at $P \leq 0.05$. ~~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).

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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 in the wet season that the dry season at all sites but P19. Temperature and extractable NH_4^+ exhibited between-season differences at only one site each (temperature - P8, extractable NH_4^+ - P27; Table 3). Within each season, all four soil controlling factors differed along the precipitation gradient (all $P < 0.01$ except $P = 0.04$ for extractable NH_4^+ in the wet season; Table 3). Soil temperatures in both seasons were lower at P32 (3400 mm) than at all other sites (not significant at P27 in the dry season), and also lower at P27 (2030 mm) than Met (1700 mm). Soil moisture contents, in contrast, were higher in both seasons at P32 than at the other four sites. Extractable soil NO_3^- concentrations in both seasons were higher at Met and P8 (2360 mm) than at P27, P19 (2690 mm) and P32, and in the wet season, also higher at Met than P8. Extractable soil NH_4^+ concentrations were higher at P32 than Met in both seasons. Across sites, over the 21-month measurement period, soil moisture was inversely correlated with temperature ($r = -0.28$, $P < 0.01$, $n = 145$) and extractable soil NO_3^- ($r = -0.51$, $P < 0.01$, $n = 145$) and directly correlated with extractable soil NH_4^+ ($r = 0.46$, $P < 0.01$, $n = 145$).

3.2 CO_2 fluxes

Although soil CO_2 emissions did not differ among the five sites over the 21-month measurement period ($P = 0.40$; Fig. 2a; Table 3), emissions exhibited a parabolic relationship with soil

moisture across sites (Fig. 3) and were higher in the wet season than the dry season at each site ($P \leq 0.05$; Table 3). Over the 21-month sampling period, average daily soil CO_2 emissions from the five sites were correlated with soil moisture (r = 0.35, $P < 0.01$, n = 145; Fig. 3), soil temperature (r = 0.46, $P < 0.01$, n = 145), ~~soil moisture (r = 0.35, $P < 0.01$, n = 145; Fig. 3),~~ extractable soil NH_4^+ (r = 0.32, $P < 0.01$, n = 145) and extractable soil NO_3^- (r = -0.21, $P = 0.01$, n = 145~~).~~); the dominant drivers in the wet season were extractable NH_4^+ followed by temperature, while the dominant drivers in the dry season were moisture, followed by temperature (Table S~~2~~1). Within individual sites, daily soil CO_2 emissions exhibited negative correlations with extractable soil NO_3^- at Met (r = -0.48, $P = 0.01$, n = 27), P8 (r = -0.39, $P =$ 0.03, n = 30), and P32 (r = -0.54, $P < 0.01$, n = 30). Moisture was a dominant driver of CO_2 emissions from soils at all sites, with temperature (P27, P8 and P32) and mineral N (Met, P19 and P32) both playing important roles as well (Table S1).

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 S~~1~~2).

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). Moisture was a dominant

driver of CH_4 flux in both seasons, but was stronger in the wet season (Table S1). ~~.~~ ~~-~~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); moisture was also the dominant within-site driving factor at all sites except Met (Table S1). ~~.~~ Across sites, mineral N was a significant explanatory factor in both seasons; within sites, this was only reflected in the model at P32 (Table S1) but ~~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 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 S2~~1~~); 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

($P < 0.01$). Notably, the model fit also indicated no significant soil factors for the dry season, but did identify NO_3^- as a driving factor across sites in the wet season (Table S1). Within individual sites, moisture was a controlling factor of N_2O emissions at P8, P19 and P32, with NO_3^- availability also important at P19 (Table S1). Comparing between 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 S2~~1~~).

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) ($P < 0.01$; Table 3). Over the 13-month measurement period, there were no driving factors significant across sites in the model fit (Table S1) but 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 sites, ~~only~~ dominant drivers (Table S1) were moisture (P27 and P8) and temperature

(P27), with soil NO fluxes at P8 ~~showed~~ also exhibiting 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 S2~~4~~).

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 with ~~that~~those of a mature secondary forest (P15 site, 7-18 Mg C ha^{-1} yr^{-1} in 2007/2008; Notthingham et al., 2010) close to our P8 and P19 sites (Figure S1). Finally, three of our sites

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(Met, P27 and P19) were mature secondary forests, with tree densities (particularly at Met and P27; see 2.1) lower than the old growth forests on BCI (Pyke et al., 2001) and Gigante (Koehler et al., 2009a). This may have additionally influenced soil CO_2 fluxes since up to 35 % of CO_2 emissions can be contributed by root respiration (Silver et al., 2005). Interestingly, regardless of the contribution of autotrophic respiration to soil CO_2 fluxes, we did not detect any significant differences in soil CO_2 fluxes among sites, but only found that across our 5 sites the temporal pattern of soil CO_2 fluxes was strongly related to soil moisture.

Net ~~S~~soil CO_2 emissions responded to changes in climatic factors on a seasonal scale (i.e. higher soil CO_2 fluxes in the wet than dry season at all sites; Table 3) and to daily fluctuations in soil temperature and moisture across the five sites (see 3.2). The hierarchy of importance of the soil factors are ~~also~~ shown in Table S1: at each site (except P27) and during the dry season across sites, soil moisture was the most important ~~factor~~ driving factor, ~~the~~ followed by soil temperature, NH_4^+ or NO_3^-, while during the wet season, when soil moisture was sufficient, the most important soil factors ~~was~~were NH_4^+ and soil temperature (Table S1). The higher CO_2 emissions in the wet season were likely due to the alleviation of water competition between decomposers and vegetation; in seasonal tropical forests, litter tends to fall in the dry season, but low soil moisture limits decomposition until the start of the wet season (Yavitt et al., 2004). Other studies from CSA lowland forests have also reported a positive relationship between soil CO_2 emissions and soil temperature (Chambers et al., 2004; Schwendenmann and Veldkamp, 2006; Sotta et al., 2006, Koehler et al., 2009a), and parabolic relationships (Fig. 3) between soil CO_2 emissions and soil moisture (Schwendenmann et al., 2003; Sotta et al., 2006; Kohler et al., 2009). Additionally, soil CO_2 emissions responded to changes in soil mineral N both on the plot level and across sites (see 3.2). Relationships between soil CO_2 emissions and soil mineral N concentrations have not been reported in other studies, although Schwendenmann et al. (2003)

observed that spatial differences in soil total N were positively correlated with soil CO_2 fluxes, and Koehler et al. (2009a) found that chronic N addition decreased soil CO_2 fluxes in a montane tropical forest (although not in a lowland forest). However, the correlations between CO_2 emissions and both NH_4^+ (positive correlation) and NO_3^- (negative correlation) may also simply be reflecting a co-correlation between extractable mineral N and soil moisture (see 3.2).

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

4.2 CH_4 fluxes

Our findings show~~ed~~ the scale-dependency of environmental controls ~~of~~on soil CH_4 fluxes – the short-term (seasonal) pattern within and across sites were dominantly controlled by soil

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moisture, temperature and mineral N (Table S1~~ the above table~~) whereas the long-term pattern based on annual fluxes across sites was largely controlled by soil fertility (Fig. 4b).

The control of soil moisture on soil CH_4 fluxes has been shown in several CSA tropical forest studies (Keller and Reiners, 1994; Verchot et al., 2000; Davidson et al., 2004; Veldkamp et al., 2013). This was also observed at our sites, with less CH_4 uptake during periods of high water content (i.e. wet vs. dry season; Table 3), soil moisture being the dominant controlling factor at each site (except Met) and across sites during each season (Table S1), as well as a positive correlation of soil CH_4 fluxes with water content (Fig. 4a). We attribute the dominant role of soil moisture to controlling gas diffusivity from the atmosphere into the soil and/or methanogenic activity during periods of high moisture. Our annual soil CH_4 uptake (Table 4) was within the range of other reported values from Brazil and Panama (Verchot et al., 2000; Davidson et al., 2004; Keller et al., 2005; Silver et al., 2005; Veldkamp et al., 2013). ~~although studies have also~~Studies that have measured stronger uptake in CSA lowland forests (up to 4.90 kg C ha^{-1} yr^{-1}; Keller and Reiners, 1994; Steudler et al., 1996; Keller et al., 2005; Sousa Neto et al., 2011)~~. Studies that measured higher uptake~~ may have had soils with higher gas diffusivity due to lower soil water content and/or lower clay content (see Veldkamp et al., 2013); in our five sites, the two sites with the highest sand content (P8 and P19; Table 1) exhibited the highest soil CH_4 uptake (Tables 3 and 4). In addition to moisture,

~~Another soil factor controlling the~~ soil NO_3^- may also have been an important driver of temporal soil CH_4 uptake in our sites; ~~may have been soil NO_3^-, as~~ we observed increased CH_4 uptake as NO_3^- concentrations increased in P8, P19 and P32 (see 3.3) and it was a dominant controlling factor across sites in both seasons (Table S1). Although this may have reflected a co-correlation between soil NO_3^- concentration and soil moisture (see 3.1), increasing CH_4 uptake in

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the soil with increasing mineral N has been observed in tropical forest soils of Australia (Kiese et al., 2003), Panama (Veldkamp et al., 2013) and Indonesia (Hassler et al., 2013). Additionally, our soils exhibited a correlation between annual soil CH_4 fluxes and soil ^{15}N natural abundance signatures (Table 5), the latter being an indicator of soil N availability (Sotta et al. 2008; Arnold et al. 2009; Baldos et al. 2015). When separated by season, the correlation between soil CH_4 fluxes and soil ^{15}N natural abundance was stronger in the dry season than the wet season (Table S2), supporting our claim that soil N availability enhanced CH_4 uptake in soils when gas diffusion was favorable (dry season).

~~Our annual soil CH_4 uptake (Table 4) was within the range of other reported values from Brazil and Panama (Verchot et al., 2000; Davidson et al., 2004; Keller et al., 2005; Silver et al., 2005; Veldkamp et al., 2013) although studies have also measured stronger uptake in CSA lowland forests (up to 4.90 kg C ha^{-1} yr^{-1}; Keller and Reiners, 1994; Steudler et al., 1996; Keller et al., 2005; Sousa Neto et al., 2011). Studies that measured higher uptake may have had soils with higher gas diffusivity due to lower soil water content and/or lower clay content (see Veldkamp et al., 2013); in our five sites, the two sites with the highest sand content (P8 and P19; Table 1) exhibited the highest soil CH_4 uptake (Tables 3 and 4).~~

~~As shown in several CSA tropical forest studies (Keller and Reiners, 1994; Verchot et al., 2000; Davidson et al., 2004; Veldkamp et al., 2013), soil CH_4 fluxes are strongly regulated by soil moisture content. Soil CH_4 fluxes from our sites exhibited this expected pattern, with regards to less uptake during periods of high water content (i.e. wet vs. dry season; Table 3), soil moisture being the dominant controlling factor at each site and across sites during each season (Table S1), as well as a positive correlation of soil CH_4 fluxes with water content (Fig. 4a). This~~ The dominant role of soil moisture can we attributed to limited gas diffusivity

~~from the atmosphere into the soil as well as~~and/or ~~methanogenic activity during periods of high moisture. Another soil factor controlling the temporal soil CH_4 uptake in our sites may have been soil NO_3^-, as we observed increased CH_4 uptake as NO_3^- concentrations increased in P8, P19 and P32 (see 3.3) and it was a dominant controlling factor across sites in both seasons (Table S1). Although this could be~~may have reflected a co-correlation between soil NO_3^- concentration and soil moisture (see 3.1), increasing CH_4 uptake in the soil with increasing mineral N has been observed in tropical forest soils of Australia (Kiese et al., 2003), Panama (Veldkamp et al., 2013) and Indonesia (Hassler et al., 2013). Additionally, our soils exhibited a correlation between annual soil CH_4 fluxes and soil ^{15}N natural abundance signatures (Table 5), the latter being an indicator of soil N availability (Sotta et al. 2008; Arnold et al. 2009; Baldos et al. 2015). When separated by season, the correlation between soil CH_4 fluxes and soil ^{15}N natural abundance was stronger in the dry season than the wet season (Table S21), supporting our claim that soil N availability enhanced CH_4 uptake in soils when gas diffusion was favorable (dry season).

The control of soil fertility on the long-term pattern of soil CH_4 fluxes across sites was depicted by a correlation between annual soil CH_4 fluxes and oure calculated soil fertility index (Fig. 4b), which exhibited an opposite pattern to that of annual precipitation (Figure S2). This soil fertility control was supported by the strong correlations of both annual (Table 5) and seasonal (Table S2) soil CH_4 fluxes with ECEC and exchangeable Al, both included in the soil fertility index (Figure S2; see 2.4). The correlations between soil CH_4 fluxes and fertility indicators reflected the site differences in soil biochemical characteristics (Table 2). Specifically, as shown by the strong inverse correlation between soil $\delta^{15}N$ natural abundance signatures and exchangeable cations (Table 5), the positive correlation between soil CH_4 flux and fertility (Fig. 4b) likely reflected the long-term effects of soil development (Tables 1 and 2) - more CH_4 uptake

occurred in highly weathered soils with less rock-derived nutrients but high soil N availability (i.e. high $\delta^{15}N$ natural abundance signatures) (Tables 4 and 5). This supports our hypothesis that soil CH_4 uptake reflected the control of soil moisture and N availability across sites along this precipitation gradient. Our results also highlight the importance of considering soil properties - in particular the degree of soil development - rather than simply climatic factors, when predicting/modeling soil CH_4 fluxes on a large scale.

~~The negative correlation between annual soil CH_4 uptake and annual precipitation (Fig. 4c; see 3.3) seemed at first to conflict with the mechanism we explained above for the positive correlation with soil moisture content (Fig. 4a). However, we attribute this to the fact that annual precipitation was not the underlying factor controlling the annual soil CH_4 fluxes across these sites. Instead, the best indicator for annual soil CH_4 flux across the five sites was soil fertility (Fig. 4b), which showed an opposite pattern to that of annual precipitation (Figure S2). This soil fertility control was supported by the strong correlations of both annual (Table 5) and seasonal (Table S21) soil CH_4 fluxes with ECEC and exchangeable Al, both included in the soil fertility index (Figure S2; see 2.4). The negative correlation of soil CH_4 fluxes with exchangeable Al, which was clearly observed in the wet season (Table S21), could suggest an inhibition of methanogens by water-soluble Al (as opposed to inhibiting methanotrophs, as seen by Tamai et al., 2003). The correlations between soil CH_4 fluxes and fertility indicators reflected the site differences in soil biochemical characteristics (Table 2). Specifically, as shown by the strong inverse correlation between soil $\delta^{15}N$ natural abundance signatures and exchangeable cations (Table 5), the positive correlation between soil CH_4 flux and fertility (Fig. 4b) likely reflected the long-term effects of soil development (Tables 1 and 2) - more CH_4 uptake occurred in highly weathered soils with less rock-derived nutrients but high soil N availability (i.e. high $\delta^{15}N$~~

~~natural abundance signatures) (Tables 4 and 5). This supports our hypothesis that soil CH_4 uptake reflected the control of soil moisture and N availability across sites along this precipitation gradient. Our results also highlight the importance of considering soil properties – in particular the degree of soil development – rather than simply climatic factors, when predicting/modeling soil CH_4 fluxes on a large scale.~~

4.3 N_2O fluxes

Our annual soil N_2O fluxes (Table 4) were within the lower end of the range (1.23 - 11.4 kg N ha^{-1} yr^{-1}) reported from other CSA forest studies (Keller and Reiners 1994, Verchot et al., 1999, Keller et al., 2005, Silver et al., 2005). In comparison with other studies from Panama, our N_2O fluxes were similar to those measured from Gigante during dry years (0.5 ± 0.2 kg N ha^{-1} yr^{-1} in 2008–2009 with annual precipitation 5–26 % lower than the 12-year average; Corre et al. 2014) but slightly lower than those measured from the same site during wet years (1.0 - 1.4 kg N ha^{-1} yr^{-1} in 2006–2007 with annual precipitation 5–17 % higher than the 12-year average; Koehler et al., 2009b). The low soil N_2O fluxes at our sites were likely caused by the generally lower soil N availability compared to the Gigante site; the five sites in our present study had an average gross N mineralization rate of 4 ± 1 mg N kg^{-1} d^{-1} in the 2010 wet season (Corre et al. unpublished data), which was significantly lower than those from Gigante (29 ± 6 mg N kg^{-1} d^{-1} in the 2006 wet season; Corre et al. 2010).

~~In addition, i~~Inter-annual variation in rainfall and hence soil moisture can also strongly affect soil N_2O emissions (Corre et al., 2014). Our measured soil N_2O emissions exhibited a tendency to be higher in the wet season than the dry season (P8 and P19; Table 3), highest at the mid-rainfall site of P8 (which could mean that at the high-rainfall sites N_2O could have been

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1194 further denitrified to N_2), and were only correlated with the soil ^{15}N natural abundance signatures
1195 (as an indicator of soil N availability) in the wet season (Table S2~~1~~). At the sites (P8 and P19),
1196 where N_2O emissions were higher in the wet than dry season and soil NO_3^- levels were lower in
1197 the wet than dry season (Table 3), the inverse correlation between daily soil N_2O emissions with
1198 NO_3^- concentrations over the 21-month measurement period suggests that during the wet season
1199 N_2O production could have been high but might have been further denitrified to N_2, and hence
1200 resulted in low soil NO_3^- concentrations. ~~This argument is supported by our earlier study in~~
1201 ~~Gigante, where nitrification and denitrification contributed equally to soil N_2O emissions during~~
1202 ~~the dry season but denitrification was the main process contributing to soil N_2O emission in the~~
1203 ~~wet season (Koehler et al., 2012; Corre et al. 2014).~~ Although the reduction of NO_3^- in the wet
1204 season could also be caused by reduced nitrification, measurements in our study area (once in the
1205 wet and once in the dry season) showed no significant differences between wet and dry seasons
1206 across sites nor at each site (Corre et al. unpublished data). Additionally, gross nitrification was
1207 correlated with NO_3^- immobilization, but not with DNRA, suggesting that when there was high
1208 NO_3^- availability, this was preferably assimilated by the microbial biomass (Corre et al.
1209 unpublished data). On the other hand, the soil NO_3^- levels we show in Table 3 were measured
1210 repeatedly, parallel to soil trace gas flux measurement, over our 21-month study period. The soil
1211 NO_3^- levels (Table 3) therefore reflected the concurrently occurring NO_3^- production and
1212 consumption processes. The argument that these reflect further denitrification to N_2 ~~This~~
1213 ~~argument~~ is supported by our earlier study in Gigante, where nitrification and denitrification
1214 contributed equally to soil N_2O emissions during the dry season but denitrification was the main
1215 process contributing to soil N_2O emission in the wet season (Koehler et al., 2012; Corre et al.
1216 2014). Our results partly supported our initial hypothesis, in that soil N_2O emissions were highest

at the mid-precipitation site (with the highest soil N availability as indicated by ^{15}N natural abundance; Table 2) due to possible reduction of N_2O to N_2 at the high precipitation site.

4.4 NO fluxes

Our annual soil NO uptake (Table 4) was considerably lower than other reported NO fluxes, which are usually small net emissions rather than net uptake. Soil NO emissions from Panama, Costa Rica and Brazil range from 0.26 to 7.88 kg N $ha^{-1}yr^{-1}$ (Keller and Reiners 1994, Verchot et al., 1999, Gut et al., 2002, Keller et al., 2005, Silver et al., 2005, Koehler et al., 2009b; Corre et al. 2014). However, the net uptake that we measured may be reflecting unusually high ambient air NO concentrations in our forest sites as compared to forests from other studies. Although all of our sites were located in mature-secondary or old-growth forests, the forests were located within the Panama Canal watershed, where there is heavy, year-round marine traffic (~13,000 cargo ships in 2011; Hricko, 2012). Furthermore, the highest levels of soil NO uptake that we measured were in the Met site (Table 4); in addition to being in the vicinity of the Panama Canal, the park is located within the city limits of Panama City, which has a population of approximately 1.6 million people (The World Factbook, 2015). Therefore, elevated ambient air NO concentrations from anthropogenic emissions may be driving the NO uptake that we measured. Our instrument cannot measure O_3 concentration, which could be high in these sites influenced by anthropogenic emissions. Thus, the NO uptake that we saw may have been driven by both chemical (Pape et al. 2009) and microbiological reactions (as NO is an intermediate product of nitrification and denitrification; Davidson et al. 2000). The dominance of a chemical reaction of NO uptake at our sites was supported by the fact that we observed a negative 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 between dry-season soil NO fluxes and clay contents of the sites (Table S2~~1~~), suggesting that soil

NO fluxes were responding to conditions favourable for NO production. Favourable soil conditions were most visible at P8, which had the highest soil NO emissions (with low ambient air NO concentrations) in the dry season (Table 3; Fig. 2d); soil NO fluxes at this site increased when aerobic soil conditions prevailed (i.e. negative correlation with soil moisture; see 3.5) and increased with substrate availability (i.e. positive correlation with soil NO_3^-; see 3.5).

In summary, although the soils in our study sites can be a net source of NO, particularly during the dry season (Fig. 2d) and in sites where ambient air NO concentrations were low (Fig. 5), most of the time the soils acted as net sink of NO, signifying the importance of soil and vegetation as NO sinks (Jacob and Bakwin, 1991; Sparks et al., 2001) in areas affected by anthropogenic NO sources.

4.5 Implications for climate change

It is notable that, although all four trace gases were strongly correlated with the temporal variation in soil moisture and had clear differences between seasons (Table 3), there were no correlations between the soil trace gases when looking at the annual fluxes (Table 5) or seasonal averages (Table S2~~4~~). This lack of correlation is presumably rooted in the interaction of other soil and/or climatic factors with known drivers of soil trace gas production and consumption; one future direction could be to do an in-depth analysis of the abundance/activity of functional microbial groups along these gradients of precipitation and fertility~~.~~

We have shown that in the short term, soil trace gas fluxes were largely controlled by soil moisture, with the additional influences of soil temperature and mineral N concentration. However, in the long term and/or over large spatial scales, the degree of soil development and related soil fertility had a strong influence. Additionally, we have shown that even in presently

undisturbed forests, gas fluxes can be affected by 'upstream' anthropogenic activities. Therefore, in order to understand and be able to predict soil trace gas fluxes under future climate scenarios, research needs to focus on identifying and predicting interacting effects of soil and site, as well as climatic characteristics, on soil-atmosphere trace gas exchange.

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References

Allen, K., Corre, M. D., Tjoa, A. and Veldkamp, E.: Soil nitrogen-cycling responses to conversion of lowland forests to oil palm and rubber plantations in Sumatra, Indonesia, PLoS ONE, 10(7), e0133325, doi:10.1371/journal.pone.0133325, 2015.

Bouwman, A. F., Fung, I., Matthews, E., and John, J.: Global analysis of the potential for N2O production in natural soils. Global Biogeochem. Cy., 7, 557–597, 1993.

Butterbach-Bahl, K., Baggs, E. M., Dannenmann, M., Kiese, R., and Zechmeister-Boltenstern, S.: Nitrous oxide emissions from soils: how well do we understand the processes and their controls? Phil. Trans. R. Soc., 368, 20130122, 2013.

Chambers, J. Q., Tibuzy, E. S., Toledo, L. C., Crispim, B. F., Iguchi, N., dos Santos, J., Araujo, A. C., Kruijt, B., Nobre, A. D., and Trumbore, S. E.: Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. Ecol. Appl., 14, S72–S88, 2004.

Chameides, W. L., Fehsenfeld, F., and Rodgers, M. O.: Ozone precursor relationships in the ambient atmosphere. J. Geophys. Res., 97, 6037–6055, 1992.

Chin, K. J., Lukow, T., and Conrad, R.: Effect of temperature on structure and function of the methanogenic archaeal community in an anoxic rice field soil. Appl. Environ. Microbiol., 65, 2341–2349, 1999.

Conrad, R.: Soil microorganisms as controllers of atmospheric trace gases (H2, CO, CH4, OCS, N2O, and NO). Microbiol. Rev., 60, 609–640, 1996.

Conrad, R.: Microbiological and biochemical background of production and consumption of NO and N_2O in soil. In: Trace Gas Exchange in Forest Ecosystems, (eds Gasche R, Papen H, Rennenberg H), Dordrecht, Kluwer Academic Publishers, pp 3–33, 2002.

Corre, M. D., Veldkamp, E., Arnold, J., and Wright, S. J.: Impact of elevated N input on soil N cycling and losses in old-growth lowland and montane forests in Panama. Ecology, 91, 1715–1729, 2010.

Corre, M. D., Sueta, J. P., and Veldkamp, E.: Nitrogen-oxide emissions from tropical forest soils exposed to elevated nitrogen input strongly interact with rainfall quantity and seasonality. Biogeochemistry, 118, 103-120, 2014.

Crawley, M. J.: The R book, Chichester: John Wiley, 2012.

Davidson, E. A., and Schimel, J. P.: Microbial processes of production and consumption of nitric oxide, nitrous oxide and methane. In: Biogenic trace gases: measuring emissions from

soil and water (eds Matson PA, Harriss RC), Blackwell Science, Oxford, pp 327–357, 1995.

Davidson, E. A., Verchot, L. V., Cattânio, J. H., Ackerman, I. L. and Carvalho, J. E. M.: Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. Biogeochemistry, 48, 53–69, 2000.

Davidson, E. A., Yoko Ishida, F., and Nepstad, D. C.: Effects of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. Glob. Change Biol., 10, 718–730, doi: 10.1111/j.1529-8817.2003.00762.x, 2004.

Gut, A., S. M. van Dijk, M. Scheibe, U. Rummel, M. Welling, C. Ammann, F. X. Meixner, G. A. Kirkman, M. O. Andreae, and B. E. Lehmann, NO emission from an Amazonian rain forest soil: Continuous measurements of NO flux and soil concentration, J. Geophys. Res., 107(D20), 8057, doi:10.1029/2001JD000521, 2002.

Hanson, P. J., N. T. Edwards, C. T. Garten, and J. A. Andrews, Separating root and soil microbial contributions to soil respiration: a review of methods and observations, Biogeochemistry, 48(1), 115-146. 2000.

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

Holtgrieve, G. W., Jewett, P. K. and Matson, P. A.: Variations in soil N cycling and trace gas emissions in wet tropical forests. Oecologia, 146, 584–594, 2006.

Hricko, A.: Progress and pollution: port cities prepare for the Panama Canal expansion. Environ. Health Persp., 120, A470–32012, 2012.

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Jacob, D. and Bakwin, P.: Cycling of NOx in tropical forest canopies, in: Microbial production and consumption of greenhouse gases: methane, nitrogen oxides and halomethanes, edited by: Rogers, J. E. and Whitman, W. B., American Society for Microbiology, Washington, DC, USA, 237–253, 1991.

Jenny, H.: Arrangement of soil series and types according to functions of soil-forming factors. Soil Sci., 61, 375–392, 1946.

Keller, M., and Reiners, W. A.: Soil-atmosphere exchange of nitrous oxide, nitric oxide, and methane under secondary succession of pasture to forest in the Atlantic lowlands of Costa Rica. Global Biogeochem. Cy., 8, 399–409, 1994.

Keller, M., Jacob, D. J., Wofsy S. C., and Harriss, R. C.: Effects of tropical deforestation on global and regional atmospheric chemistry. Climatic Change, 19, 139–158, 1991.

Keller, M., Varner, R., Dias, J. D., Silva, H., Crill, P., de Oliveira, R. C., and Asner, G. P.: Soil–atmosphere exchange of nitrous oxide, nitric oxide, methane, and carbon dioxide in logged and undisturbed forest in the Tapajos national forest. Brazil, Earth Interact., 9, 1–28, 2005.

Kiese, R., Hewett, B., Graham, A., and Butterbach-Bahl, K.: Seasonal variability of N_2O and CH_4 uptake by tropical rainforest soils of Queensland, Australia. Global Biogeochem. Cy.,25 17, 1043, doi:10.1029/2002GB002014, 2003.

Koehler, B., Corre, M. D., Veldkamp, E., and Sueta, J. P.: Chronic nitrogen addition causes a reduction in soil carbon dioxide efflux during the high stem-growth period in a tropical montane forest but no response from a tropical lowland forest on a decadal time scale. Biogeosciences, 6, 2973–2983, 2009a.

Koehler, B., Corre, M. D., Veldkamp, E., Wullaert. H., and Wright, S. J.: Immediate and long-term nitrogen oxide emissions from tropical forest soils exposed to elevated nitrogen input. Glob. Change Biol., 15, 2049–2066, 2009b.

Koehler, B., Zehe, E., Corre, M. D., and Veldkamp, E. An inverse analysis reveals limitations of the soil- CO_2 profile method to calculate CO_2 production for well-structured soils. Biogeosciences, 7: 2311–2325, 2010.

Koehler, B., Corre, M. D., Steger, K., Well, R., Zehe, E., Sueta, J. P. and Veldkamp, E. An in-depth look into a tropical lowland forest soil: how 9-11 years experimental nitrogen addition affected the contents of N_2O, CO_2 and CH_4 down to 2-m depth. Biogeochemistry 111: 695-713. Erratum in 111: 715-717, 2012.

Kursar, T. A.: Evaluation of soil respiration and soil CO_2 concentration in a lowland moist forest in Panama. Plant Soil, 113, 21–29, 1989.

Le Mer, J., and Roger, P.: Production, oxidation, emission and consumption of methane by soils: a review. Eur. J. Soil Biol., 37, 25–50, 2001.

Mariotti, A., Germon, J. C., Hubert, P., Kaiser, P., Letolle, R., Tardieux, A., and Tardieux, P.: Experimental determination of nitrogen kinetic isotope fractionation: some principles; illustration for the denitrification and nitrification processes. Plant Soil, 62, 413–430, 1981.

Mohanty, S. R., Bodelier, P. L. E., and Conrad, R.: Effect of temperature on composition of the methanotrophic community in rice field and forest soil. FEMS Microbiol. Ecol., 62, 24–31, 2007.

1398 Nottingham, A. T., Turner, B. L., Winter, K., van der Heijden, M. G., and Tanner, E. V.:
1399 Arbuscular mycorrhizal mycelial respiration in a moist tropical forest. New Phytol., 186,
1400 957-967, 2010.
1401 Pape, L., Ammann, C., Nyfeler-Brunner, A., Spirig, C., Hens, K., and Meixner, F. X.: An
1402 automated dynamic chamber system for surface exchange measurement of non-reactive
1403 and reactive trace gases of grasslandecosystems. Biogeosciences, 6, 405-429, 2009.
1404 Prather, M., Derwent, R., Ehhalt, D., Fraser, P., Sanhueza, E., and Zhou, X.: Other trace gases
1405 and atmospheric chemistry. In: Climate Change 1994 (eds Houghton JT, Meira Filho LG,
1406 Bruce J, Lee H, Callander BA, Haites E, Harris N, Maskell K), Cambridge University
1407 Press, Cambridge, UK, 73–126, 1995.
1408 Pyke, C. R., Condit, R., Aguilar, S., and Lao, S.: Floristic composition across a climatic gradient
1409 in a neotropical lowland forest. J. Veg. Sci., 12, 553–566, 2001.
1410 R Core Team. R: A language and environment for statistical computing. R Foundation for
1411 Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, URL: http://www.R-
1412 project.org/, 2013.
1413 Raich, J. W., and Schlesinger, W. H.: The global carbon dioxide flux in soil respiration and
1414 relationship to vegetation and climate. Tellus, 44B, 81–99, 1992.
1415 Rummel, U., C. Ammann, A. Gut, F. X. Meixner, and M. O. Andreae, Eddy covariance
1416 measurements of nitric oxide flux within an Amazonian rain forest, J. Geophys. Res.,
1417 107(D20), 8050, doi:10.1029/2001JD000520, 2002
1418 Saikawa, E., Schlosser, C. A., and Prinn, R. G.: Global modeling of soil nitrous oxide emissions
1419 from natural processes. Global Biogeochem. Cy., 27, doi:10.1002/gbc.20087, 2013.

Santiago, L.S., Schuur, E.A. and Silvera, K.: Nutrient cycling and plant–soil feedbacks along a precipitation gradient in lowland Panama. J. Trop. Ecol., 21, 461–470, 2005.

Schwendenmann, L., and Veldkamp, E.: Long-term CO2 production from deeply weathered soils of a tropical rain forest: Evidence for a potential positive feedback to climate warming. Glob. Change Biol., 12, 1878–1893, 2006.

Schwendenmann, L., Veldkamp, E., Brenes, T., O'Brien J. J., and Mackensen, J.: Spatial and temporal variation in soil CO2 efflux in an old-growth neotropical rain forest, La Selva, Costa Rica. Biogeochemistry, 64, 111–128, 2003.

Silver, W.L., Neff, J., McGroddy, M., Veldkamp, E., Keller, M., and Cosme, R., Effects of Soil Texture on Belowground Carbon and Nutrient Storage in a Lowland Amazonian Forest Ecosystem. Ecosystems, 3, 193–209. doi:10.1007/s100210000019, 2000.

Silver, W. L., Thompson, A. W., McGroddy, M. E., Varner, R. K., Dias, J. D., Silva, H., Crill, P. M., and Keller, M.: Fine root dynamics and trace gas fluxes in two lowland tropical forest soils. Glob. Change Biol., 11, 290–306, doi: 10.1111/j.1365-2486.2005.00903.x, 2005.

Sotta, E. D., Veldkamp, E., Guimaraes, B. R., Paixao, R. K., Ruivo, M. L. P., and Almeida, S. S.: Landscape and climatic controls on spatial and temporal variation in soil CO2 efflux in an Eastern Amazonian Rainforest, Caxiuana, Brazil. Forest Ecol. Manag., 237, 57–64, 2006.

Sotta, E. D., Corre, M. D., and Veldkamp, E.: Differing N status and N retention processes of soils under old-growth lowland forest in Eastern Amazonia, Caxiuanã, Brazil. Soil Biol. Biochem., 40, 740–750, 2008.

Sousa Neto, E., Carmo, J. B., Keller, M., Martins, S. C., Alves, L. F., Vieira, S. A., Piccolo, M. C., Camargo, P., Couto, H. T. Z., Joly, C. A., and Martinelli, L. A.: Soil-atmosphere exchange of nitrous oxide, methane and carbon dioxide in a gradient of elevation in the

coastal Brazilian Atlantic forest. Biogeosciences, 8, 733–742, doi:10.5194/bg-8-733-2011, 2011.

Sparks, J. P., Monson, R. K., Sparks, K. L., and Lerdau, M.: Leaf uptake of nitrogen dioxide (NO2) in a tropical wet forest: Implications for tropospheric chemistry, Oecologia, 127(2), 214–221, doi:10.1007/s004420000594, 2001.

Steudler, P. A., Melillo, J. M., Feigl, B. J., Neill, C., Piccolo, M. C., and Cerri., C. C.: Consequences of forest-to-pasture conversion on CH4 fluxes in the Brazilian Amazon Basin. J. Geophys. Res.-Atmos., 101, 18547–18554, doi:10.1029/96JD01551, 1996.

Stocker, T. F., Qin, D., Plattner, G. K., Tignor, M., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, B., and Midgley, B. M.: IPCC, 2013: climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. 2013.

Swaine MD. Rainfall and soil fertility as factors limiting forest species distributions in Ghana. J. Ecol., 84, 419-428, 1996.

Tamai, N., Takenaka, C., Ishizuka, S., and Tezuka, T.: Methane flux and regulatory variables in soils of three equal-aged Japanese cypress (Chamaecyparis obtusa) forests in central Japan. Soil Biol. Biochem., 35, 633–641, 2003.

The World Factbook. https://www.cia.gov/library/publications/the-world-factbook/geos/pm.html [Accessed: March, 2015]

Townsend, A. R., Asner, G. P., and Cleveland, C. C.: The biogeochemical heterogeneity of tropical forests. Trends Ecol. Evol., 23, 424–431, 2008.

Turner, B. L., and Engelbrecht, B. M. J.: Soil organic phosphorus in lowland tropical rain forests. Biogeochemistry, 103, 295–315, 2011.

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

Verchot, L. V., Davidson, E. A., Cattânio, H., Ackerman, I. L., Erickson, H. E., and Keller, M.: Land use change and biogeochemical controls of nitrogen oxide emissions from soils in eastern Amazonia. Global Biogeochem. Cy., 13(1), 31–46, 1999.

Verchot, L. V., Davidson, E. A., Cattanio, J. H., and Ackerman, I. L.: Land-use change and biogeochemical controls of methane fluxes in soils of eastern Amazonia. Ecosystems, 3, 41–56, doi:10.1007/s100210000009, 2000.

Windsor, D. M.: Climate and moisture availability in a tropical forest, long term record for Barro Colorado Island, Panama. Smithson. Contrib. Earth Sci., 29, 1–145, 1990.

Wright, S. J., Yavitt, J. B., Wurzburger, N., Turner, B. L., Tanner, E. V., Sayer, E. J., Santiago, L. S., Kaspari, M., Hedin, L. O., Harms, K. E., Garcia, M. N., and Corre, M. D. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology, 92, 1616–1625, 2011.

Yavitt, J. B., Wright, S. J., and Kelman Wieder, R.: Seasonal drought and dry-season irrigation influence leaf-litter nutrients and soil enzymes in a moist, lowland forest in Panama. Austral Ecol., 29, 177–188, 2004.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M.: Mixed effects models and extensions in ecology with R. Springer, New York., 2009.

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

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

[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.

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

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}

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 $P \leq 0.05$).

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.

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).

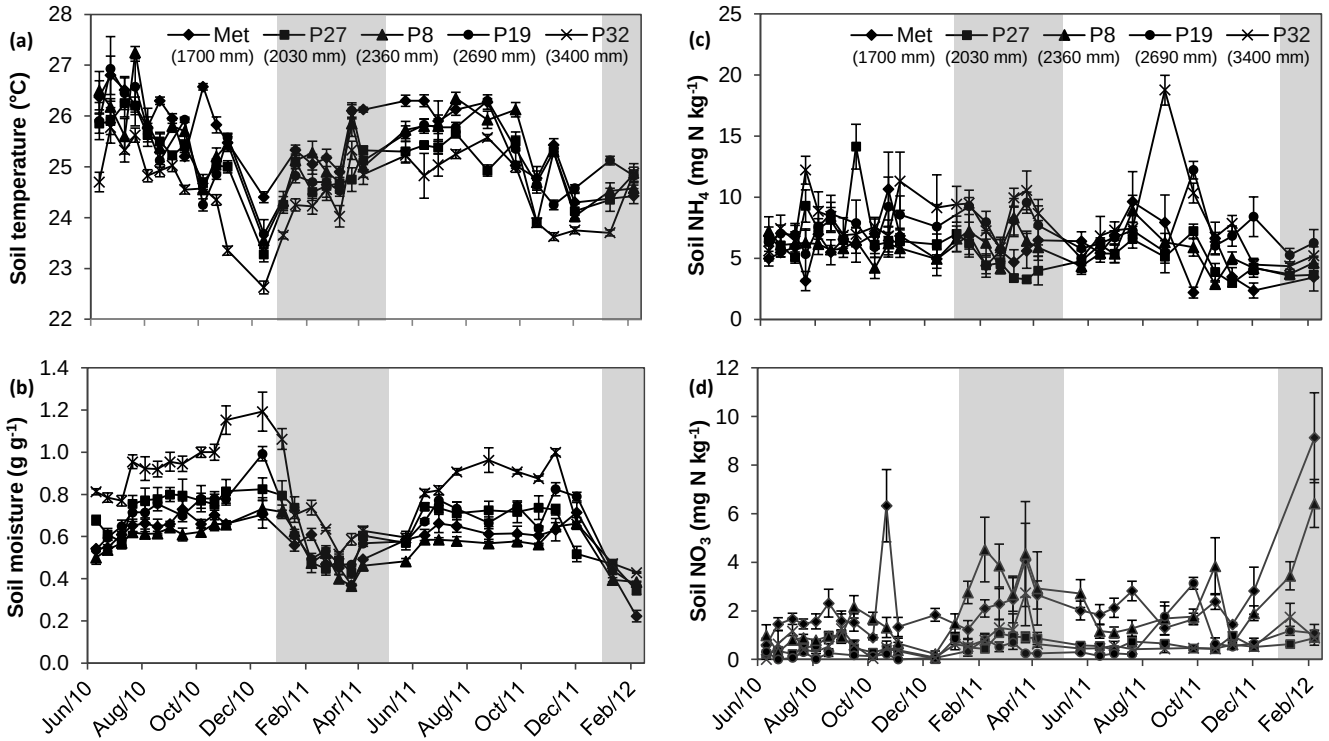

Fig. 1 Mean (±SE, n = 4) soil **(a)** temperature, **(b)** moisture, **(c)** NH_4^+ and **(d)** NO_3^- concentrations measured in the top 5 cm of soil in lowland forests along orthogonal gradients of annual precipitation and soil fertility in the Panama Canal watershed, central Panama. Gray shading indicates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

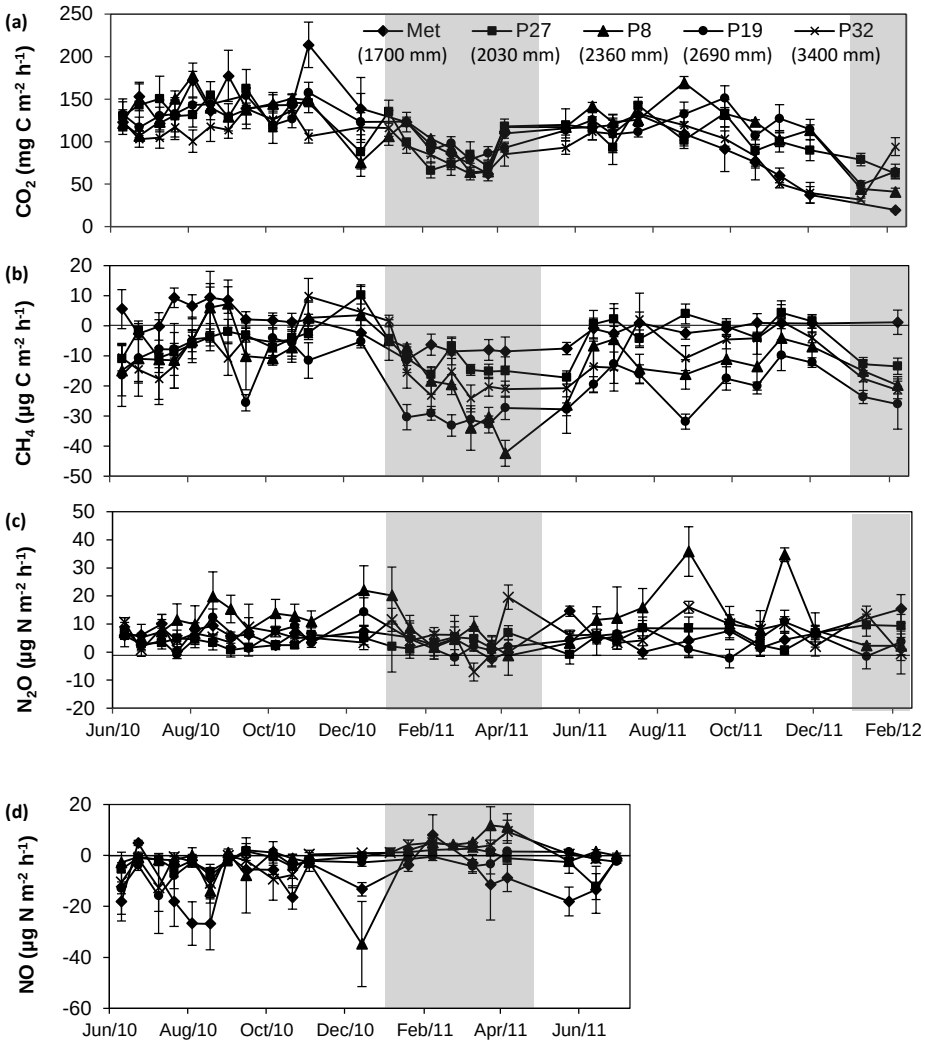

Fig. 2 Mean (±SE, n = 4) soil **(a)** CO_2, **(b)** CH_4, **(c)** N_2O and **(d)** NO fluxes from lowland forests along orthogonal gradients of annual precipitation and soil fertility in the Panama Canal watershed, central Panama. Gray shading indicates the dry season (January through April).

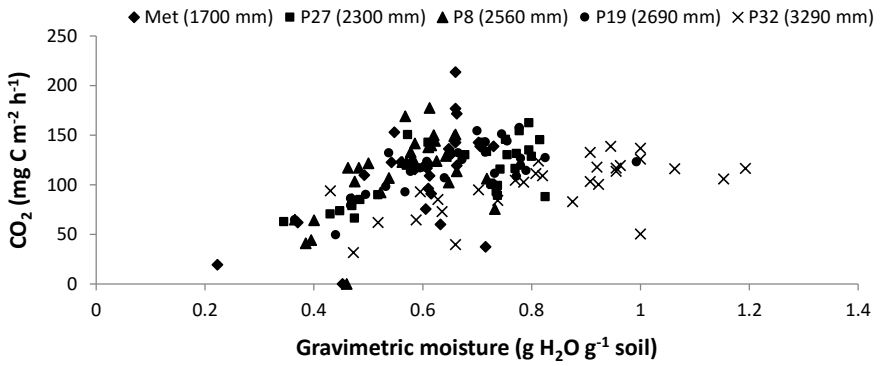

Fig. 3 Soil CO_2 fluxes and moisture contents (top 5 cm) in five lowland forests along orthogonal gradients of annual precipitation (shown in brackets) and soil fertility in the Panama Canal watershed, central Panama. Each data point is the average of four replicate plots on one sampling day from one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

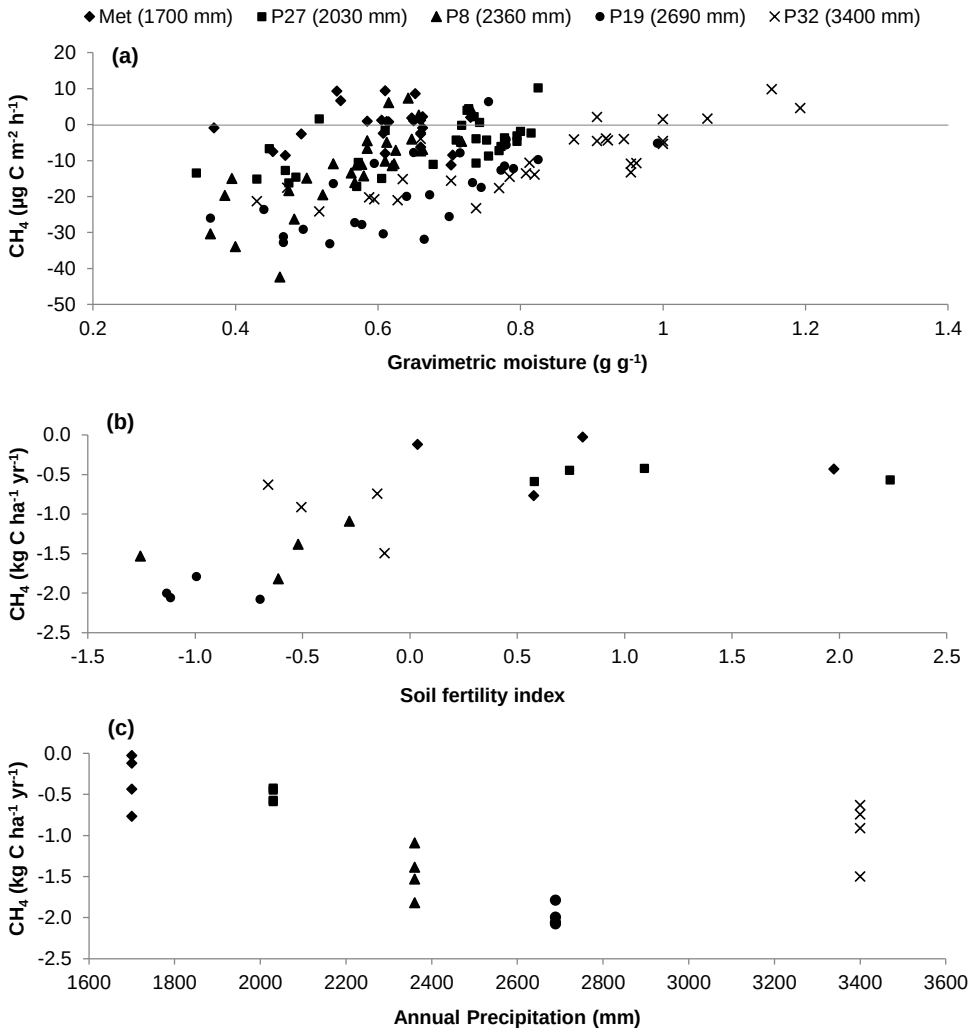

Fig. 4 Average daily soil CH_4 fluxes plotted against (a) soil moisture (top 5 cm), and annual soil CH_4 fluxes plotted against (b) soil fertility index and (c) annual precipitation. For (a), each data point is the average of four replicate plots on each sampling day of each of the five sites, measured 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.

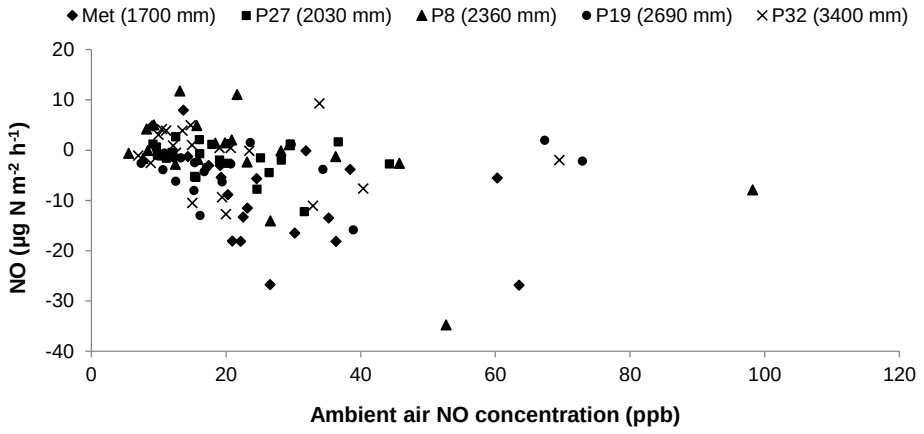

Fig. 5 Soil NO fluxes plotted against ambient air NO concentrations; each data point is the average of four replicate plots on each sampling day in each of the five sites, measured from June 2010 to June 2011. The five lowland forests are located along orthogonal gradients of annual precipitation and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