



ENSO-Influenced Drought Drives Methane Flux Dynamics in a Tropical Wet Forest Soil

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Key Points:

- We measured methane flux in a Costa Rican lowland tropical wet forest through a severe drought during the end of the 2015–2016 El Niño
- Soil moisture varied across the El Niño and into the following La Niña and significantly impacted methane flux
- Predicted drying of the tropics may lead to negative climate feedbacks, which could increase soil methane consumption

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Abstract Global atmospheric methane growth rates have wildly fluctuated over the past three decades, which may be driven by the proportion of tropical land surface saturated by water. The El Niño/Southern Oscillation Event (ENSO) cycle drives large-scale climatic trends globally, with El Niño events typically bringing drier weather than La Niña. In a lowland tropical wet forest in Costa Rica, we measured methane flux bimonthly from March 2016 to June 2017 and using an automated chamber system. We observed a strong drying trend for several weeks during the El Niño in 2016, reducing soil moisture below normal levels. In contrast, soil conditions had high water content prior to the drought and during the moderate La Niña that followed. Soil moisture varied across the period studied and significantly impacted methane flux. Methane consumption was greater during the driest part of the El Niño period, while during La Niña and other time periods, soils had lower methane consumption. The mean methane flux observed was $-0.022 \text{ mg CH}_4\text{-C m}^{-2} \text{ hr}^{-1}$, and methane was consumed at all timepoints, with lower consumption in saturated soils. Our data show that month studied, and the correlation between soil type and month significantly drove methane flux trends. Our data indicate that ENSO cycles may impact biogenic methane fluxes, mediated by soil moisture conditions. Climate projections for Central America show dryer conditions and increased El Niño frequency, further exacerbating predicted drought. These trends may lead to negative climate feedbacks, with drier conditions increasing soil methane consumption from the atmosphere.

1. Introduction

Methane (CH_4) is an important anthropogenic greenhouse gas, responsible for 20%–30% of total greenhouse gas radiative forcing (Intergovernmental Panel on Climate Change, 2013). While CH_4 is more than 100 times less concentrated in the atmosphere than carbon dioxide, each CH_4 molecule holds 25 times more heat (Lelieveld et al., 1998). With anthropogenic influences on the composition of atmospheric greenhouse gases, atmospheric CH_4 concentrations have increased ~150% from a preindustrial mixing ratio of about 0.7 ppm (Etheridge et al., 1998) to approximately 1.84 ppm today (Nisbet et al., 2016). Further, as carbon dioxide levels and global temperatures increase, so do CH_4 emissions from natural and anthropogenic wetland soils (Zhang et al., 2017).

Soil CH_4 fluxes are regulated by a phylogenetically constrained and well characterized group of soil microorganisms, making this flux system ideal for analyses of the connection between soil community structure and functioning. Most field and modeling studies of the carbon cycle focus solely on CO_2 fluxes, despite the importance of CH_4 as a greenhouse gas. Globally, CH_4 emissions from anthropogenic and biogenic sources are on the rise, although total CH_4 sinks are uncertain (Aronson, Allison, et al., 2013). Total CH_4 emissions have been recently calculated to be between 553 and 756 Tg $\text{CH}_4 \text{ year}^{-1}$ (Saunio et al., 2016). The largest natural CH_4 sources are wetlands, which contribute around 33% of annual natural and anthropogenic CH_4 emissions (Zhang et al., 2017). Most of the CH_4 produced annually is removed from the atmosphere within the same year as it is produced. The largest CH_4 sink is chemical loss due to oxidation in the atmosphere (approximately 85%–95% annually; Kirschke et al., 2013; Lelieveld et al., 1998). There are wide

discrepancies in the estimates of gross oxidation by soil microorganisms in terrestrial environments (Aronson, Allison, et al., 2013). The most widely used sink strength estimate is $\sim 30 \pm 15$ Tg/CH₄ (Intergovernmental Panel on Climate Change, 2013), which corresponds to $\sim 5\%$ of the CH₄ produced each year (Kirschke et al., 2013).

Atmospheric CH₄ concentrations had risen steadily since the industrial revolution and then became erratic and did not increase overall from 2000 to 2006. They began increasing again in 2007 (Rigby et al., 2008) and continue to increase rapidly today (Nisbet et al., 2016; Schwietzke et al., 2016). One proposed explanation for the variability is that in the late 1990s and early 2000s, wetland sources emitted less CH₄ (Bousquet et al., 2006), including reduced emissions from tropical wetlands in particular (Nisbet et al., 2016). Isotopic measurements and models confirmed these sources (Kai et al., 2011), which could also indicate increased soil microbial consumption. This reveals that the interplay between terrestrial sinks and sources from year to year could drive global trends in CH₄ atmospheric concentrations, and the tropics may be the most variable in terms of biogenic fluxes. Understanding which mechanisms drive fluctuations in atmospheric CH₄ concentrations at multiple scales helps improve our ability to budget this important greenhouse gas.

The soil microorganisms responsible for CH₄ production and consumption are methanogens and methanotrophs, respectively. These groups have disparate environmental niches, particularly with regards to soil oxygen concentration and water content (Aronson, Allison, et al., 2013). Methane consumption dominates in high oxygen, low moisture soil conditions, and production dominates in low oxygen, saturated soil moisture conditions. Microbial oxidation of CH₄ by methanotrophs yields CO₂ as a byproduct (Hanson & Hanson, 1996), while several groups of methanogens can generate CH₄ from the carbon in CO₂. However, acetate from the partial breakdown of organic matter is a more common substrate for CH₄ production. Soil temperature and nutrient status, particularly nitrogen content and species, are considered secondary in driving CH₄ fluxes (Bodelier, 2011). When soils are saturated, either in a wetland or in a nonwetland soil that is inundated with rain, the diffusion of gases between the soil and the atmosphere is limited. This is particularly true of soils with a high clay content, where some precursors for both CH₄ production (CO₂) and oxidation (CH₄ and O₂) in the soil become more plentiful (Fernandez-Bou et al., 2019).

Tropical forest ecosystems cover 17% of Earth's land area and store approximately 40% of all terrestrial carbon (e.g., Clark et al., 2003; Vargas et al., 2008). However, environmental change, from land use changes to shifts in tropical storm patterns to climate change, may have major repercussions in tropical ecosystem carbon storage and allocation (Clark et al., 2013) with a largely unquantified impact on soil carbon storage (Vargas et al., 2009; Vargas & Allen, 2008). The tropical biome can be both a large producer and consumer of CH₄, and broadleaf evergreen-covered, nonwetland soils are possibly the greatest consumers of methane of all vegetation types (Aronson, Allison, et al., 2013).

The El Niño/Southern Oscillation Event (ENSO) cycle is a characteristic set of climatic events, which includes drought in tropical forest areas in Central America, the Amazon Basin, Southern Africa, India, and Indonesia under El Niño conditions. Pandey et al. (2017) recently showed, using satellite observations, that La Niña conditions increase atmospheric CH₄ concentrations globally, due to wetter conditions in the tropics. Zhang et al. (2018) further demonstrate that the shrinking of the tropical wetland areal extent during El Niño events causes an initial decrease in emissions rates and a later increase in emissions rates from a smaller wetland surface area. As tropical wetlands shrink due to El Niño, unsaturated zones become larger and may become dryer, leading to greater CH₄ consumption by these soils. Higher temperatures in the tropics, as compared to ecosystems of higher latitudes, correlate with higher rates in microbial reactions, including those that cycle methane (Hanson & Hanson, 1996).

In this study, we investigated the influence of the ENSO cycle on soil moisture and related impacts of soil moisture on CH₄ fluxes in a tropical wet forest. We measured in situ rainfall, soil moisture, soil oxygen and carbon dioxide concentrations, and CH₄ fluxes at the La Selva Biological Station, Costa Rica. We hypothesized that extreme drought in this wet forest soil would correlate with greater CH₄ consumption, as well as lower CO₂ concentrations in the soil, due to rapid diffusion of gases between soils and the atmosphere. We further hypothesized that soil moisture would be low, with period(s) of extreme drought, during El Niño conditions and high during La Niña conditions.

2. Materials and Methods

2.1. Study Site

This study was conducted in an old growth tropical wet forest at the La Selva Biological Station (Figure 1) on the Caribbean slope of the Cordillera Central, Atlantic lowlands of Costa Rica (10°25′51″N, 84°00′59″W). La Selva is a 1,500-ha reserve of premontane wet forest, with an elevation range from 80 to 150 m.a.s.l. and soils that have been classified as oxisols (Kleber et al., 2007). Lower elevation soils are characterized by “alluvial” or colluvial deposits whereas weathered “residual” soils of volcanic origin are found at higher elevations (Kleber et al., 2007). The station has a mean annual rainfall of 4,354 mm from 1963 to 2016, with mean monthly rainfall above 300 mm from May to December (<https://archive.tropicalstudies.org>). Generally, there are peaks of precipitation above 400 mm/month in June–August and November–December and a drier period from January to April. Even in the driest period of February and March, however, rainfall averages above 150 mm each month. Mean monthly maximum and minimum temperatures show very little seasonal change, with mean highs of 30–31 °C each month and mean monthly lows ranging only from 20 to 22 °C. The average annual temperature at the study site is 26.0 °C (Sanford et al., 1994), with little change in recent years, and an average annual temperature of 25.07 °C from 1992 to 2017 (<https://archive.tropicalstudies.org>). The soil characteristics of the top 1 m include bulk density of 0.81 and 0.79, with total C content of 2.02 and 2.80, total N of 0.19 and 0.24, total P of 0.96 and 0.62, and pH of 3.97 and 4.11, for alluvial and residual soils, respectively (Schwendenmann et al., 2003).

2.2. Field Sampling Design

Duplicate plots were established in each soil type, residual and alluvial, where four 20-cm diameter PVC collars were permanently installed near the corners of each plot to measure soil gas fluxes. Plots were all in similar topographic positions with minimal slope. Between March 2016 and June 2017, measurement campaigns were conducted at 2-month intervals to characterize soil gas fluxes, soil gas concentrations and soil abiotic factors. The El Niño event of 2015–2016 began as a weak event in summer 2015 and waned in June 2016, and our study started observing CH₄ flux in March 2016 due to logistical constraints. We had anticipated a lag between the onset of the El Niño event and observed tropical drought event(s).

Soil fluxes of CH₄ (f_{CH_4} , mg CH₄-C m⁻² hr⁻¹) were measured using a closed chamber system. A fitting PVC cap with silicone rubber gasket was placed on the collars to create a closed chamber and left to incubate for 40 min. Chamber air was sampled through a port with septa at minutes 0, 20, and 40 into the incubation and 20-ml samples were stored in exetainers. Samples were analyzed for CH₄ on a gas chromatograph (7890B, Agilent Technologies, Santa Clara, California, USA) equipped with FID and a HP-PLOT/Q column within 48 hr of collecting (Aronson et al., 2012).

Adjacent to each measurement collar, volumetric water content (VWC, %) and soil temperature (T_{soil} , °C) were measured in the 5-cm top soil using a ProCheck handheld datalogger with GS3 sensor (Decagon Devices, Pullman, WA, USA), installed vertically into the soil surface to integrate the top 5 cm. Air temperature (T_{air} , °C) was recorded at the start of measurements at each plot using the same device.

In addition to bimonthly sampling for 16 months, we deployed an auto-chamber system built around a Li8100 CO₂ analyzer and Li8150 multiplexer (LICOR, Nebraska, US) with a Greenhouse Gas Analyzer (Los Gatos Research, San Jose, California, USA) for measuring CH₄. In addition, soil moisture and temperature were measured continuously during flux measurements. Methane fluxes were measured continuously for one month, due to logistical constraints, from 26 March 2016 to 26 April 2016, with most dates falling between the first and second repeated sampling events. The automated chamber system was located 1.5 km away from the other plots, in residual soil. We used four 20-cm diameter collars; each fitted with automated chambers. The measuring interval was 30 min with a measurement duration of 5 min. Soil moisture was collected with three CS615 soil moisture sensors (Campbell Scientific, Logan, Utah, USA) installed vertically between 0- and 30-cm depth, and soil temperature was measured with two T-type thermocouples at 5-cm depth. Moisture and temperature data were logged on a CR10X at 30-min intervals.

In February 2015, two Soil Ecosystem Observatory (SEO) systems were installed to continuously monitor soil gas concentrations and moisture, while two more were added in February 2016. Our focus here makes use of the SEO data from one of the first SEOs on alluvial soil, where four additional flux collars were installed. Methane flux from these additional collars were measured at the same sampling periods as the

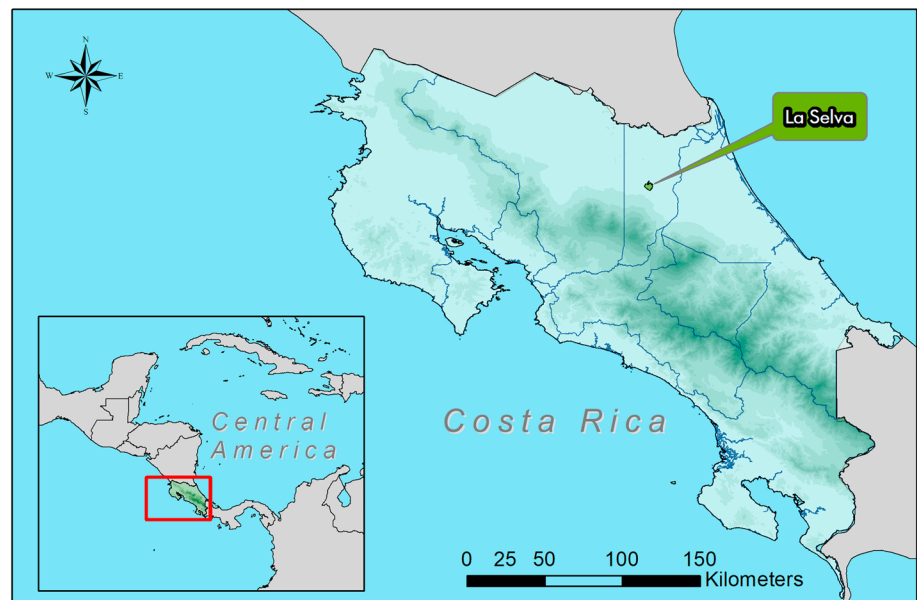


Figure 1. Map of Costa Rica with location of La Selva Biological Station and inlay of position within Central America. Green shading indicates elevation; blue lines depicts the border of each province or administrative division of the country.

plots. Other SEOs, which were located further from the study plots here described, showed similar temporal patterns from gas, temperature and moisture sensors. Each SEO consisted of an array of sensors installed at 2-, 8-, 16-, and 50-cm depths to measure soil water content and temperature (Campbell Scientific CS650), CO₂ (Vaisala GMT221; Allen & Kitajima, 2013; Vargas & Allen, 2008), and O₂ (Apogee O₂ sensors; Hall et al., 2013). Sensors were calibrated prior to installation using standard methods described in the manuals for each sensor.

2.3. Data Analysis

Soil fluxes were calculated based on a linear fit to the change in gas concentration over time, accounting for total chamber volume, soil area and air temperature, and assuming standard atmospheric pressure. All data was analyzed using a mixed model repeated measure analysis of variance (ANOVA) in JMP Pro 12 software. Data that does not pass Mauchly's test for sphericity in variance (chi-square $p < 0.05$) may distort variance calculations resulting in an F ratio that would be inflated, indicating that the variances of the differences between all possible pairs of within-subject conditions are not equal. When this occurred, we used the Greenhouse-Geisser Epsilon to adjust the degrees of freedom, and the F ratio to test for significance in variables and interactions. We used a stepwise multiple regression to evaluate the impact of continuous variables on the total variance in CH₄ flux data.

3. Results

Soils were moist to the point of saturation in March, with an average of 52.4% VWC, according to discrete measurements taken at the top 5 cm at each sampling date and location. Between March and early May 2016, as the El Niño progressed, soil moisture dramatically declined to an average of 38.6% VWC (−0.5 MPa), with the lowest observed moisture according to the SEO sensors at 27%. Rainfall in April was significantly lower in 2016 than the 60-year average (Figure 2). The SEO showed a decrease in soil moisture and CO₂ concentrations, extending into early May 2016, when we performed our bimonthly sampling of CH₄ fluxes. Soil moisture began to stabilize at a saturated level again around July 2016. Soil CO₂ concentrations increased significantly, corresponding with a slight increase in soil moisture, in November 2016 (Figure 3) correlated with the start of La Niña. May is typically part of the “rainy” season in this location within Costa Rica, so the observed drought may indicate a strong El Niño. By the time the

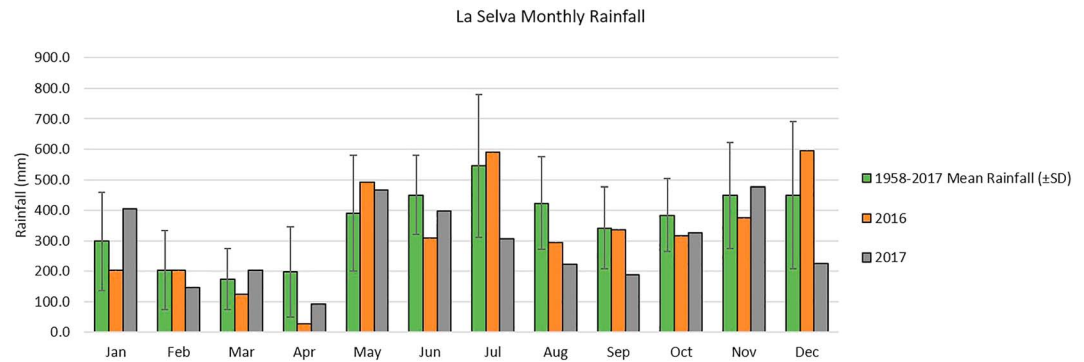


Figure 2. Monthly rainfall at La Selva Biological Station, Costa Rica. Green bars show average rainfall in the 60 years up to and including those of the study period, while orange bars indicate 2016 and grey bars indicate 2017 monthly data.

La Niña of 2016 began in November at the end of the rainy season, the VWC was again up to saturation, 51.4%.

On average, we found CH₄ was consumed by soils at all time points (Figure 4), even when soils were found to be at or close to moisture saturation. The average CH₄ consumption rate (mean ± standard error) was $-0.022 \text{ mg CH}_4\text{-C m}^{-2} \text{ hr}^{-1} \pm 1.28 \times 10^{-3}$ (negative numbers indicating consumption). The CH₄ consumption was greatest in May 2016, at $-0.041 \text{ mg CH}_4\text{-C m}^{-2} \text{ hr}^{-1}$ and lowest in March 2016, at -0.011 and November 2016, at $-0.012 \text{ mg CH}_4\text{-C m}^{-2} \text{ hr}^{-1}$. We found that CH₄ fluxes did not significantly differ between alluvial and residual soils but fluxes varied significantly by month sampled ($p < 0.001$), and there was a significant interaction between month sampled and soil type ($p < 0.009$; Figure 4), using the Greenhouse-Geisser Epsilon. Soil VWC and temperature significantly differed across time ($p < 0.003$ and $p < 0.001$), with the Greenhouse-Geisser Epsilon correction; the interaction of time and soil type was also a significant source of variation (0.0003). In a stepwise multiple regression, only VWC was found to significantly correlate with CH₄ flux ($r^2 = 0.256$, $p < 0.0001$) but not temperature ($p < 0.091$). In a single regression between soil VWC and CH₄ flux, we found even closer agreement ($r^2 = 0.362$; Figure 5b).

We also investigated the correlation between soil parameters measured by the SEO at various depths (2, 8, 16, or 50 cm) and CH₄ flux from the collars located in the same plots as the SEOs, by a stepwise multiple regression. While the temperature in the air, at 2 and 50 cm, CO₂ at 2 and 8 cm and VWC at 8 cm entered the regression, only CO₂ at 2 cm and temperature at 2 cm were significant ($p < 0.0124$ and $p < 0.0093$, respectively). Also, CO₂ and VWC at 8 cm and temperature at 50 cm were marginally significant ($p < 0.0800$, $p < 0.0803$, and $p < 0.0747$, respectively). In the stepwise regression, soil O₂ did not enter the

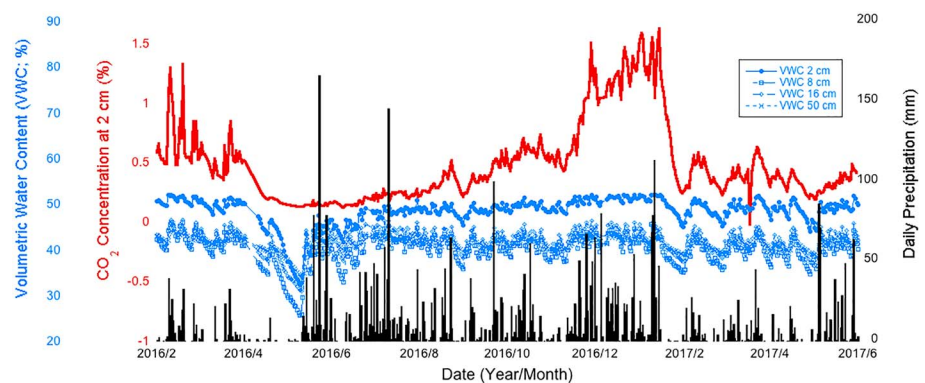


Figure 3. Daily average of soil moisture (blue lines) at depths of 2 (circles), 8 (squares), 16 (diamonds), and 50 cm (X marks), as well as CO₂ concentrations (red line) at 2-cm depth and daily precipitation (black bars), from 1 February 2016 to 1 June 2017, at the control SEO location. VWC = volumetric water content.

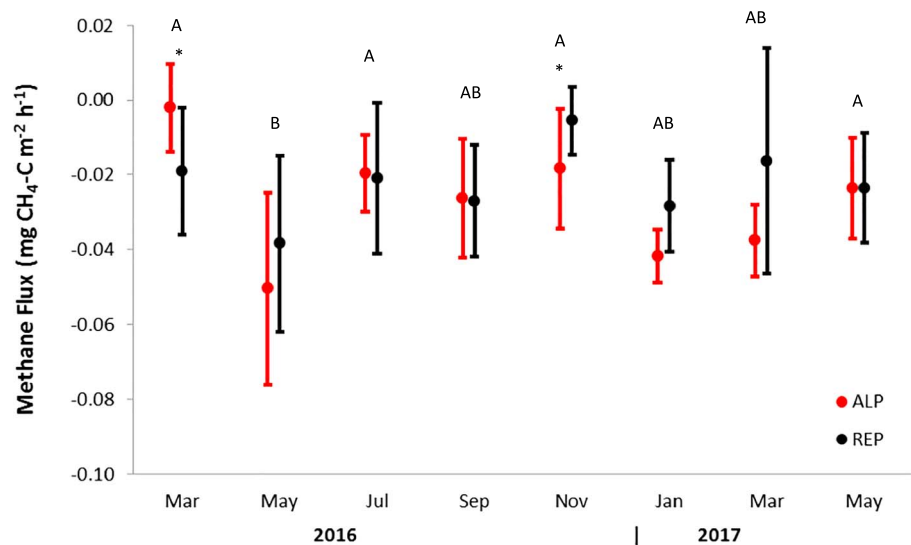


Figure 4. Methane flux by month during the study period in residual (black) and alluvial (red) soils. Asterisks indicate significant differences between soil types for the date noted from one-way ANOVA, while letters represent significant differences between dates from a one-way ANOVA using Tukey's HSD. Note that methane fluxes that are negative represent consumption by the soil.

model nor did CH_4 flux significantly correlate with O_2 observed at any depth; when compared to methane flux in a single regression, soil O_2 was also not found to significantly correlate with methane flux at any depth ($p < 0.190$ at 8 cm; $p < 0.073$ at 16 cm; $p < 0.308$ at 50 cm). Soil O_2 was erratic during the study period and did not closely follow the trends of the other gases.

During the 30 days that the automated chamber system was deployed (mid-March to mid-April), rainfall was 40.6 mm (Organization of Tropical Studies (OTS) meteorological data, www.ots.ac.cr/meteoro/default.php?pestacion=2), far lower than average for this station. The average volumetric soil moisture was $36.6\% \pm 5.59$ (mean \pm standard error) but declined across the study period (Figure 6); the soil moisture in mid-March was 44.1%, while it was 29.1% in mid-April. The average soil temperature was 24.2 ± 0.28 , which did not vary greatly. The average CH_4 flux was $-0.083 \text{ mg CH}_4\text{-C m}^{-2} \text{ hr}^{-1} \pm 0.018$, which doubled during the study period, starting at $-0.058 \text{ mg CH}_4\text{-C m}^{-2} \text{ hr}^{-1}$ in mid-March, and ending at $-0.108 \text{ mg CH}_4\text{-C m}^{-2} \text{ hr}^{-1}$ in mid-April. The single regression of VWC by CH_4 flux showed a tight correlation ($r^2 = 0.972$; Figure 5a).

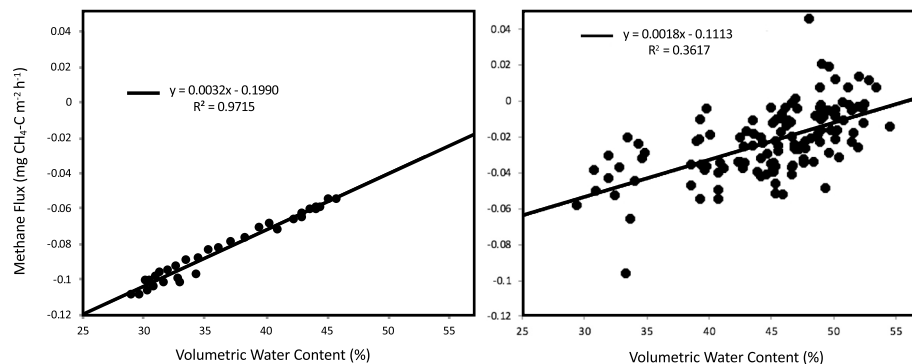


Figure 5. Regression of methane flux by volumetric water content for the automated chamber system (left) and manual sampling (right). The data presented for the automated system (left) are the daily means for four automated chambers (methane flux), each measured every half hour, and two soil VWC sensors. The data presented for the manual sampling are bimonthly measurements from individual chamber bases, from four bases per plot in four separate plots, including both soil types. Note that methane fluxes that are negative represent consumption by the soil.

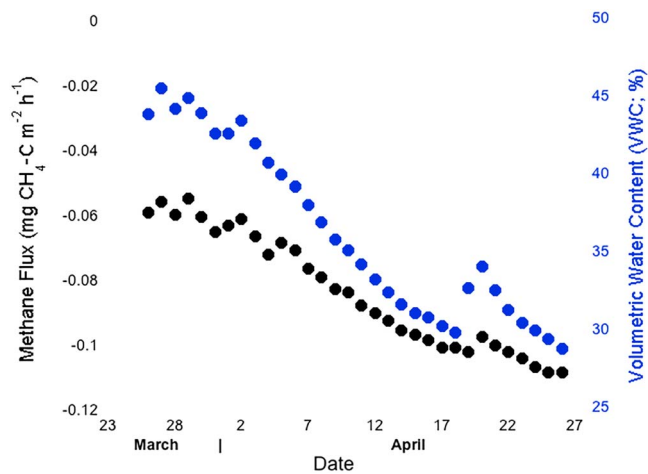


Figure 6. Regression of methane flux and volumetric water content by date for the automated chamber system. The data presented are the daily means for four automated chambers (methane flux), each measured every half hour, and two soil VWC sensors. Note that methane fluxes that are negative represent consumption by the soil. VWC = volumetric water content.

4. Discussion and Conclusions

Climate predictions suggest that Costa Rica, and much of Central America, will be drier in coming decades (Castillo et al., 2018). Further, El Niño drives negative precipitation anomalies along the Pacific slope of Central America in the “Dry Corridor” (Cid-Serrano et al., 2015). La Selva Biological Station, located in a tropical wet forest, where this research was performed, is within a moderate (wetter) zone of this Dry Corridor, which experiences lower monthly rainfall levels for up to four months of the year. During El Niño, the precipitation in this region and the rest of the Dry Corridor is reduced (Sanchez-Murillo et al., 2016), with opposite conditions during La Niña. This indicates a lower CH_4 sink strength in nonwetland tropical forest soils during the La Niña than the El Niño, confirming recent hypotheses for the 2011 La Niña event in the tropics (Pandey et al., 2017). While this study represents a relatively low rate of sampling, with one date every ~8 weeks and 1 month of auto-chamber data, it is structured to capture landscape variability in this important tropical ecosystem.

The ENSO cycle is expected to shift under global climate change scenarios. El Niño conditions are predicted to become more frequent due in general to a warming global climate (Timmermann et al.,

1999). In addition, warm temperature anomalies in the tropical Pacific Ocean in particular are likely to increase ENSO frequencies (Collins et al., 2010). Indeed, El Niño has generally shifted from the Eastern Pacific to the Central Pacific, with unknown consequences for land surface weather patterns (Yeh et al., 2009). Carbon flux changes in response to these climate shifts have the potential to feedback to climate change.

During the El Niño of 2015–2016, one of the three strongest such events on record (Sanchez-Murillo et al., 2016), we observed very low rainfall, associated with drought soil conditions at La Selva in April and May. That month is typically the beginning of the rainy season. Dry soils in May were associated with high rates of consumption of CH_4 . Further, wet soil conditions prevailed in rainy season months during October–November of the moderate La Niña of 2016–2017 and were associated with less soil methane consumption, at rates more similar to what we observed at times not influenced by an ENSO phase. While restricted to one study area, our results support other studies that show the ENSO cycle driving tropical soil moisture conditions (Poveda et al., 2001). We also showed that drought conditions increase CH_4 consumption by these tropical wet forest soils, which are otherwise quite consistent in background levels of CH_4 consumption. Our findings do not support nor contradict reports that tropical responses to the 2011 La Niña event led to significant increases in global atmospheric CH_4 growth rates (Pandey et al., 2017), as saturated soils did not respond to increases in rainfall with different CH_4 fluxes in our study. Overall, this is evidence that ENSO-related conditions in the tropics can drive important shifts in tropical wet forest exchange of atmospheric CH_4 .

When rainfall increases in tropical zones, it induces higher soil moisture across the entire area, which promotes the generation of CH_4 from wetlands and reduces the total consumption of dry soils, such as those reported here. However, these impacts on nonwetland soils have only recently been incorporated into global budgets and models (Curry, 2007; Murguía-Flores et al., 2018). While we had hypothesized that drought conditions would drive higher CH_4 consumption by the soil and that hypothesis was confirmed by this study, we had not anticipated that even at the highest VWC levels observed we would also observe consumption (Figure 5). This observation in a tropical wet forest is startling and calls into question assumptions made about the relationship between water content and CH_4 production and consumption rates included in global models (Aronson, Allison, et al., 2013). Most data on the environmental regulation of CH_4 fluxes comes from temperate biomes (Aronson, Allison, et al., 2013). It may be that these standard assumptions are generated from, and more relevant to, other ecosystems, such as in temperate rather than tropical zones or even tropical seasonal forests which have been shown to contrast with these observations (O’Connell et al., 2018).

Redox variability in seasonal tropical (Singh et al., 1997) and even subtropical wet forest soils (Silver et al., 1999; O'Connell et al., 2018) can be dramatic, leading to large fluxes in CH₄. In the subtropical wet forest at Luquillo, oxygen concentration is the main factor determining CH₄ oxidation rates, with both topographical position and rainfall determining soil oxygen content (Teh et al., 2005). Many tropical studies have shown a negative correlation between seasonal precipitation and net CH₄ uptake, which is due to the increased activity of methanogens (CH₄ producers) relative to methanotrophs (CH₄ consumers) in waterlogged, anoxic soil conditions (Aronson, Dubinsky, et al., 2013). In forests within the tropical biome, these impacts can be extreme: rain throughfall exclusion in the Amazon basin caused CH₄ consumption to more than quadruple compared to plots receiving natural precipitation levels (Davidson et al., 2004). A seasonal tropical forest in Peru showed significantly greater methane uptake in the dry than the wet season across forest types (Teh et al., 2014). Similarly, a dry tropical forest study showed that in the rainy season, CH₄ consumption was inversely related to water content and precipitation (Singh et al., 1997), which is similar to trends we present here. In the dry season, the trend observed by Singh et al. (1997) was reversed, with CH₄ consumption stimulated by additional moisture. The study described here was performed in a tropical wet forest more similar to a subtropical wet forest (O'Connell et al., 2018), than a dry tropical forest (Singh et al., 1997); however, in this site the drought experienced during the El Niño of 2015–2016 was an extreme negative precipitation anomaly, and the observed increase in methane consumption was dramatically different from all other dates studied.

Both of the soil types studied had high clay content, a common trait in tropical forests, which when saturated leads to poor diffusion (Fernandez-Bou et al., 2019). We observed low VWC and low soil CO₂ concentrations in the soil during the drought period, as we had hypothesized, likely due to more rapid gas diffusion with less water filled pore space in the soil (Vargas & Allen, 2008). In our limited automated chamber measurements, which included one site and only 1 month as the drought was increasing, VWC explained almost all of the methane flux variability. Our expanded static chamber measurements across several plots and a longer time-frame added in landscape-scale, temporal, and soil type variability. In these measurements, we found other factors were also important, such as date, soil temperature, soil CO₂ concentration, and date by soil type. Across these plots, soil VWC was still an important factor but was mediated by other variables. Further, we found that the soil O₂ concentration was highly variable and did not explain the CH₄ variability in this study. This is unexpected and deserves further study.

The tropics, because of high moisture and temperatures, have extremely high rates of microbial production, turnover, and activity. As the climate warms, this may drive greater consumption of methane by nonwetland soils, as shown from our SEO data, but also greater emissions from wetlands. Predicted drying and warming trends with climate change and El Niño will likely dramatically shift the rates of CH₄ production and consumption in tropical regions and therefore globally (Kai et al., 2011; Nisbet et al., 2016). Our data show that it is possible for predicted tropical drying and warming to have a negative feedback effect on climate in tropical wet forests, with upland soil CH₄ consumption possibly being stimulated (leading to landscape or regional dampening of CH₄ release) with more frequent El Niño cycles. Further, the impacts of increased or changing El Niño patterns may be amplified under a changing climate. In particular, as the Intertropical Convergence Zone is already expanding, both southward and northward (Allen et al., 2012), leading to more land surface area that could be covered by tropical wet forest, where El Niño events can decrease the release of CH₄, possibly increasing the negative feedback to climate change.

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