The effects of topography on leaf litter decomposition in a humid tropical forest ecosystem

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ABSTRACT

Tropical forests are a major natural source of greenhouse gases affecting the global climate, including carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). Greenhouse gas emissions can vary along a small spatial range due to spatial heterogeneity in tropical forests created by factors like topography. Leaf litter decomposition is likely to provide important substrates for greenhouse gas emissions. To explore this, I conducted a 7-month litterbag decomposition experiment along a topographic gradient in the Luquillo Experimental Forest in Puerto Rico and compared results with high frequency soil moisture, soil oxygen, and greenhouse gas measurements. Litterbags were placed at four topographic locations (ridge, upper slope, lower slope, and valley) and collected and analyzed for mass remaining, C content, and N content over time. Decomposition rates were lower in the valleys, which matched the anaerobic conditions characterized by low soil oxygen and high soil moisture. The decay rates for other topographic locations did not differ significantly from one another, suggesting a threshold effect on decomposition. The valley also had the highest emission of CH_4, a by-product of anaerobic decomposition, but overall C emissions were dominated by the production of CO_2 on the ridge. Decomposition rates and C gas fluxes had a strong correlation, mostly indicating a turnover from aerobic to anaerobic decomposition. A link between N_2O and CO_2 emissions is evident as well, connecting faster decomposition rates to higher N-gas emissions. These results indicate significant variation in microbial activity linked to greenhouse gas emissions within a small, spatial range.

KEYWORDS

microbial decomposition, spatial heterogeneity, carbon dioxide, methane, nitrous oxide

INTRODUCTION

Increasing concentrations of greenhouse gases in the Earth's atmosphere is causing global climate change. Warmer temperatures and shifting precipitation regimes produced by anthropogenic climate change have an added positive feedback on greenhouse gases emitted by natural ecosystems (Bonan 2008). Forest ecosystems play a major role in the global carbon (C) cycle as they sequester C through photosynthesis and emit C through soil respiration (Raich and Schlesinger 1992). Forests store roughly 45% of terrestrial C (Bonan 2008) with the majority stored in the soils (Dixon et al. 1994). As global warming progresses, the C stored in forest soils is at increased risk of emissions as carbon dioxide (CO_2) and methane (CH_4), two of the main greenhouse gases causing climate change (Raich and Schlesinger 1992). Tropical forests are an especially significant natural source of C (Raich and Schlesinger 1992); tropical forests alone store about 20% of the world's terrestrial C, but they have a rapid turnover rate which means that their C reservoir is very sensitive to any changes in the environment (Brown and Lugo 1982). Tropical forests are also the largest natural source of nitrous oxide (N_2O), a more potent greenhouse gas than CO_2 or CH_4 (Matson and Vitousek 1990). Less is known about how these greenhouse gas emissions vary across the landscape, or the drivers of this variability (McGroddy and Silver 2000, Wood and Silver 2012).

Greenhouse gas emissions in tropical forests can vary significantly along multiple scales due to natural environmental gradients in biota and abiotic conditions (Silver et al. 1999, McGroddy and Silver 2000, Epron et al. 2006, Kosugi et al. 2007, Wood and Silver 2012). Ecosystem scale (approximately 10^3 m) studies observed significant differences in CO_2 fluxes, largely due to high differences in temperature, soil moisture, and soil type (McGroddy and Silver 2000, Kosugi et al. 2007). Colder, wetter sites tended to have lower C emissions, which may have been caused by lower levels of heterotrophic respiration (McGroddy and Silver 2000). Additionally, tropical soil gas emissions varied with subtle changes in soil conditions along small-scale, topographic gradients (approximately 10 m) (Epron et al. 2006, Wood and Silver 2012). CO_2 and N_2O emissions were linked to microclimate conditions created by the topography (ridge, slope, valley); differences in conditions such as soil nutrients and soil moisture correlated with emissions (Epron et al. 2006, Wood and Silver 2012). Small-scale variations in greenhouse gas emissions, and associated drivers, is thus important in understanding ecosystem-scale fluxes.

Furthermore, higher temperatures, prolonged droughts, and concentrated rainfall events associated with climate change in tropical forests (Malhi et al. 2009) are likely to differentially impact biogeochemical cycling in these different topographic zones (Heartsill-Scalley et al. 2007). Understanding how differences in environmental conditions within ecosystems affect greenhouse gas fluxes can help create better models that predict the trajectory of our climate. This is critical to ensure better decision making and policy to reduce the effects of climate change.

One of the major biological mechanisms that may impact soil greenhouse gas fluxes is microbial decomposition, a process strongly influenced by environmental variables that are also related to variations in fluxes. Decomposition is the process by which heterotrophic organisms break down dead organic matter in order to recycle essential nutrients that are consumed by plants and microbes (Chapin et al. 2002). CO_2 and CH_4 are both direct byproducts of decomposition, but some microbes also consume CH_4 as an energy source and hence act as a CH_4 sink (Le Mer and Roger 2001, Chapin et al. 2002). Decomposition is also related to N_2O emissions because C and nitrogen (N) cycles are closely linked (McGill et al. 1975, Firestone et al. 1980). N_2O is emitted during nitrification and denitrification, which are microbial processes that recycle N into forms usable by plants and microbes, and such processes tend to occur more rapidly with faster decomposition (Matson and Vitousek 1990). Higher N_2O emissions is also associated with higher concentrations of available inorganic N in the soil (Matson and Vitousek 1987, Venterea et al. 2012), and tropical forest soils tend to have a high abundance of inorganic N resulting in lower soil carbon-to-nitrogen (C:N) ratios (Vitousek and Sanford 1986, Chapin et al. 2002). This has implications for both decomposition and N mineralization (Chapin et al. 2002). Higher temperatures promote microbial activity and increased rates of chemical reactions, resulting in a higher decomposition rate (Meentemeyer 1978). Soil water availability increases decomposition rate by creating favorable moisture conditions for microbial decomposers and through leaching, which dissolves minerals and organic compounds in water and increases material transport (Chapin et al. 2002). However, as soils become saturated with water, it creates low oxygen environments (Cornejo et al. 1994, Silver et al. 1999). This anoxic environment leads to anaerobic decomposition, which is slower than aerobic decomposition and produces CH_4 (Kristensen et al. 1995, Chapin et al. 2002). While information exists about the general relationships between decomposition and greenhouse gases, and between decomposition and environmental conditions,

few studies have directly compared rates of decomposition and greenhouse gas emissions along small-scale gradients.

A study in the tropical forest of Puerto Rico monitoring greenhouse gas emissions along a topographic gradient aims to address this knowledge gap. At the Luquillo Experimental Forest, there is an ongoing project measuring CO_2, CH_4, and N_2O fluxes along a topographic gradient with a 5-meter elevation change. Soil moisture and oxygen content vary along this gradient of ridge, slope, and valley. Ridge soils have higher relative porosity due, at least partially, to the rooting patterns on tree species that favor ridge tops (Álvarez Ruiz and Lugo 2012), which increases aeration (Silver et al. 1999). In contrast, water accumulates in the valleys, which have lower porosity (Wood and Silver 2012). Therefore, soil oxygen tends to decrease from ridges to slopes to valleys as soil moisture increases (Silver et al. 1999). Although there is still limited data on N_2O emissions, the data gathered in this study thus far show that CH_4 production is highest in the valleys while CO_2 production is highest along the slopes. There is clear evidence for microclimate variations in tropical forests resulting in dramatic differences in greenhouse gas emissions, but it is still unknown how decomposition differs along this topographic gradient.

My research examines how decomposition rates differ along a topographic gradient and how these relate to the variations in measured greenhouse gas fluxes. Specifically, I addressed the following questions: (1) How do decomposition rates of leaf litter differ along ridge, slope, and valley? (2) How does the change in C:N ratios in the leaf litter differ at each topographic location as the leaves decompose? and (3) Is there a correlation between decomposition rates and emission rates of CO_2, CH_4, and N_2O? I hypothesized that (1) decomposition rates will differ along the topographic gradient, largely related to the variations in soil moisture causing a shift from rapid aerobic decomposition to slower anaerobic decomposition; (2) topographic locations will likely experience differences in the change of C:N ratios as anaerobic decomposition slows the recycling of C relative to N; (3) there will be positive correlations between decomposition rates and emissions of CO_2 and CH_4 due to the gases being a direct byproduct of decomposition. However, a relationship between decomposition rates and N_2O emissions may be much harder to distinguish; the change in C:N ratios may be a better indicator of N_2O emissions than the overall decomposition rates. For my research, I measured the mass loss of leaf litter over seven months to determine decomposition rates, and I analyzed C and N content in the leaf litter to obtain changes in C:N ratio.

METHODS

Study Site

The study was conducted in the Luquillo Experimental Forest in El Yunque National Forest in Puerto Rico. It is a subtropical forest dominated by tabonuco trees (*Dacryodes excelsa*) at 350 meters above sea level (Brown et al. 1983). Mean annual rainfall is approximately 3500 mm with drier periods occurring between January and April (Harris et al. 2012). Mean monthly air temperatures are relatively constant year around, staying between 21 and 25 °C (Harris et al. 2012). The field site (N 18.32112, W 65.81750) is approximately 15 x 15 m along a hillslope with a 5-m elevation difference between the valley and the ridge and an average incline of 25 degrees. The incline is steeper at the upper half of the slope than at the lower slope. This field site was simultaneously being used to monitor greenhouse gas flux rates and soil conditions along topographic gradients by the Silver Lab at the University of California, Berkeley.

Experimental Design

Leaf litter collection and litterbag preparation

In June 2016, I collected freshly fallen leaves of mixed tree species by laying out three tarps at the forest floor within 5 m of the field site. I gathered the leaves that had fallen onto the tarp every three days to assure that the leaves were fresh. I oven-dried the leaves at 50 °C for 72 hours and using a digital scale, weighed out approximately 5 g (± 1.0 g) of dried leaves into each litterbag, being careful not the crush or break the leaves. The litterbags were made of window screening (1 mm mesh) sewn together on two sides by polyester core thread and closed with Monel staples to an inner dimension of 15 x 15 cm. The mesh size was assumed to be small enough to limit the physical loss of leaf litter as it decomposed and to keep invertebrates out of the bags to limit decomposition to only microbial activities.

Litterbag decomposition experiment

I conducted the litterbag field experiment from July 2016 to February 2017. I deployed the bags along a topographic gradient of ridge, upper slope, lower slope, and valley with six litterbags per time point in each topographic location (Fig 1). I chose the topographic locations based on clearly visible characteristics: the ridge was located at the top of the hillslope where the land leveled out, the upper slope was located just below the ridge line where the slope was steep, the lower slope was located above the valley where the slope was gradual, and the valley was located at the bottom of the hillslope where the land became concave. I placed the litterbags in a line with six groups in such a way that at each collection time, one litterbag would be taken from each group to account for any spatial variations within each topographic location. At each time point, I collected a total of 24 litterbags across all topographic locations (six litterbags per location). The time points were broken down to months 1, 3, 5, and 7 with an initial measurement at month 0. This equals 120 litterbags (4 topographic locations x 6 replicates x 5 time points). Before weighing the litterbags, I cleaned the bags of any extra plant parts or soil and oven-dried them at 50 °C for 72 hours to obtain the dry weights of the mass remaining. For litterbags with a substantial amount of soil contamination, I removed the leaves from the litterbag and sorted out large clumps of soil before obtaining the dry weight (methods adapted from Bloomfield et al. 1993).

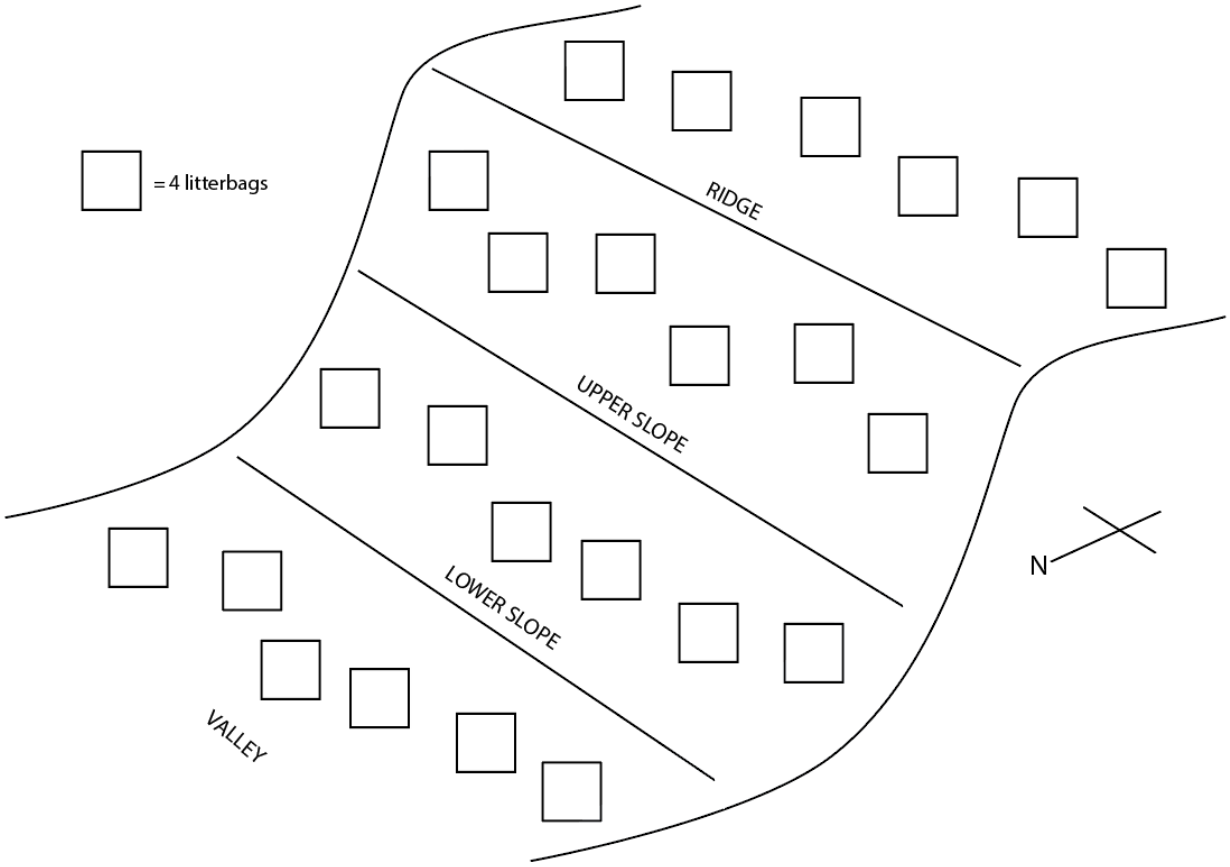

Figure 1. 96 litterbags were deployed along a topographic gradient of ridge, upper slope, lower slope, and valley (Month 0 was not deployed into the field). Each box represents 4 litterbags. This figure is not drawn to scale.

Greenhouse gas fluxes and environmental gradient

The field data on gas fluxes and abiotic factors were provided by the Silver Lab to help compare the decomposition rates. Automatic gas chambers placed along the same topographic gradient as the litterbags at the same study site continuously measured the fluxes of CO_2, CH_4, and N_2O from the soil. Each gas chamber measures gas fluxes from a 6-inch diameter patch of soil. There were 21 chambers in the field; the ridge, upper slope and lower slope have five chambers each and the valley has six chambers. Field sensors were also placed along the topographic gradient to monitor soil moisture, soil oxygen, and soil temperature.

Lab Analysis

Ashing

After measuring the dry weights, I used a mill to grind the leaves in each litterbag until they were homogenized. Approximately 1 g (± 0.1 g) of each sample was placed in a ceramic crucible and burned in a muffle furnace at 500 °C over night to determine the proportion of minerals (% weight) in the sample. This ashing process corrects the dry weight of the harvested leaves for any added soils that may have penetrated the litterbags while they were out in the field by comparing the mineral content of the intial litter to the litter from later time points.

C and N contents

I prepared aluminum capsules containing 10 – 15 mg of the ground litter samples with 2 replicates for each litterbag. I ran the capsules through an elemental analyzer to obtain the C and N concentrations (% weight) for each litter sample. The C and N concentration results were averaged for each litter sample for the final data analysis.

Data Analysis

Decomposition rate

I corrected the measured mass remaining using the proportion of mineral to organic matter obtained after ashing the samples and converted the mass to percent dry mass remaining at each time point. Then I fit the decomposition data into an exponential decay model to determine the decay rate, k, using the equation:

$$\ln(M_t/M_0) = -kt$$

where M_t/M_0 = the ratio of leaf litter mass remaining at time t, k = the decay rate in $year^{-1}$ (k-values), and t = the time it was out in the field in years. Because this study was less than a year long, I calculated t as a proportion of a year by dividing the number of days the litter was out in

the field by 365 days. I compared the k-values using one-way ANOVA and Tukey test on a statistical software, R (analysis adapted from Ostertag et al. 2003).

Change in C:N ratio

I calculated the C:N ratio by dividing the average C and N concentrations at each time point for each topographic location. I fit the change in C:N ratio into a linear model to obtain the slope to determine the rate of change of C:N. I also ran a one-way ANOVA and a Tukey test for the C:N ratio for Month 7. All statistical analyses were performed using R.

Comparing greenhouse gas flux to decomposition

Unfortunately, the real-time greenhouse gas data were not available when the decomposition study took place. Instead, I calculated monthly average fluxes of CO_2, CH_4, and N_2O over the three months prior to the start of my field experiment for each topographic location and compared them using one-way ANOVA and Tukey test. Then I ran three separate linear regression analyses comparing the k-values and the average flux rates of CO_2, CH_4, and N_2O to obtain R^2 values. As this is a relatively aseasonal environment, these greenhouse gas data provide a reasonable estimate of fluxes in these topographic zones.

RESULTS

Environmental characteristics along topographic gradient

The four topographic regions varied in soil moisture content ($P < 0.001$) and soil oxygen content ($P < 0.001$) but not in soil temperature ($P = 0.55$; Fig 2). Water content was highest in the valleys, and there was a gradual decrease in water content along the slopes and to the ridges (mean ± SD: valley = 51.0 ± 1.2%, lower = 45.8 ± 5.7%, upper = 44.9 ± 5.0%, ridge = 41.5 ± 6.5%; Fig 2a). In contrast, the oxygen content was lowest in the valleys and gradually increased along the slopes and to the ridge (mean ± SD: valley = 1.0 ± 4.2%, lower = 13.5 ± 3.0%, upper = 16.2 ± 2.1%, ridge = 16.3 ± 1.8%; Fig 2b). The temperature along the topography stayed relatively

constant (overall mean = 21.6 °C, overall SE = 0.02 °C) with monthly mean temperature ranging from 19.8 °C in January to 24.6 °C in August (Fig 2c).

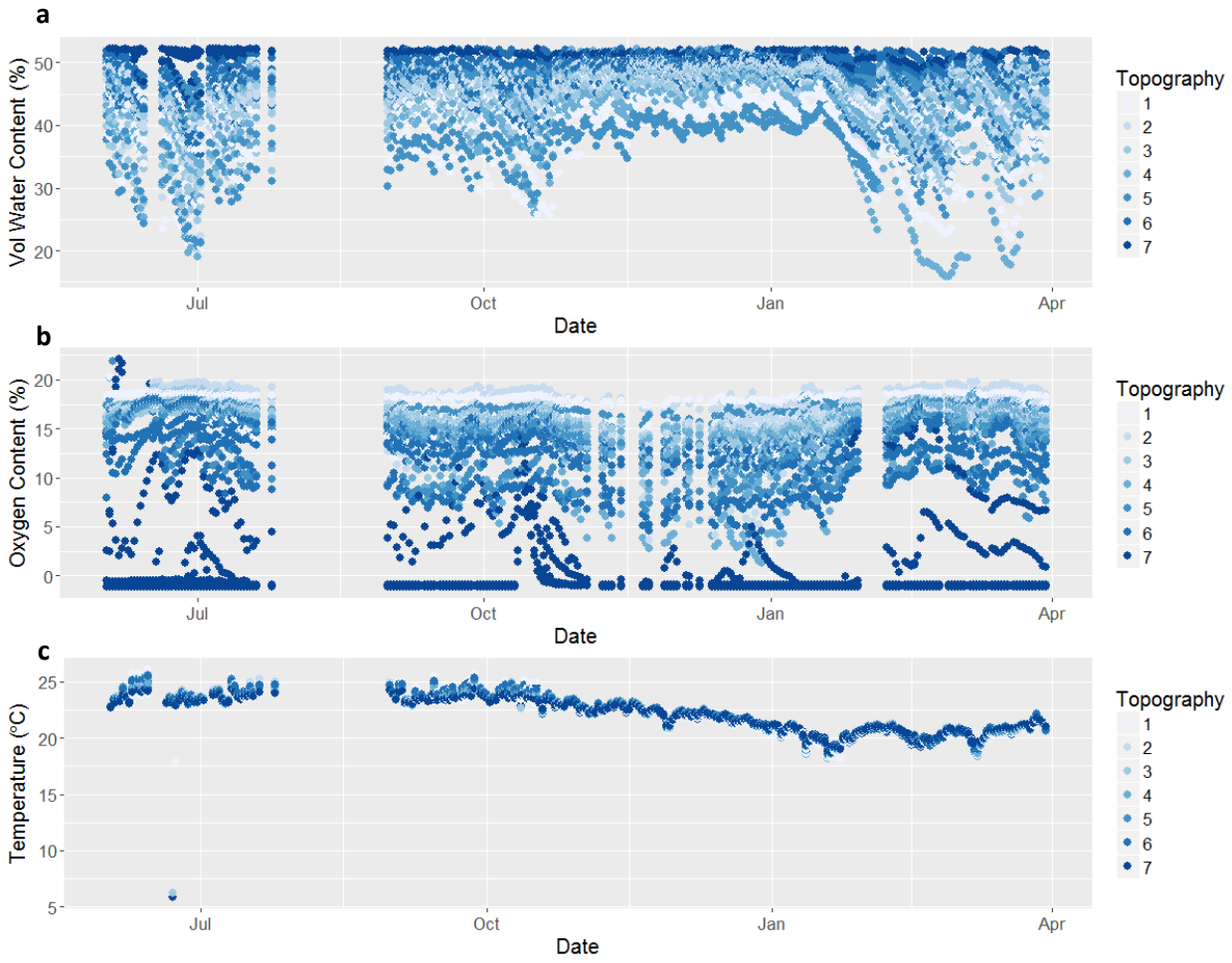

Figure 2. The effects of topography on environmental variables. Topography 1 is the ridge and the number increases as we go down the topography, ending at 7 on the valley. (a) Volumetric water content decreases as the topography changes from the valley to the ridge. (b) Oxygen content follows the inverse of the water content and increases as the topography changes from the valley to the ridge. (c) Soil temperature stays relatively constant along the topographic gradient, but experiences minimal seasonal fluctuations.

Decomposition rates

Percent mass remaining decreased from Month 0 to Month 5, but increased from Month 5 to Month 7 for most of the locations (Fig 3) due to soil contamination of the litterbags. Therefore, I calculated decomposition rates using data up to Month 5. Decomposition rates were higher at

upper topographic locations than the valley (Fig 4). The rates were fastest for lower slope and ridge (mean k ± SD: lower = 1.49 ± 0.17; ridge = 1.46 ± 0.12) with no significant difference between the two; rates were slowest for valley (valley = 1.17 ± 0.23). The rates for upper slope were in between (upper = 1.32 ± 0.25). The only significant difference of k-values was for lower slope and valley (P = 0.045).

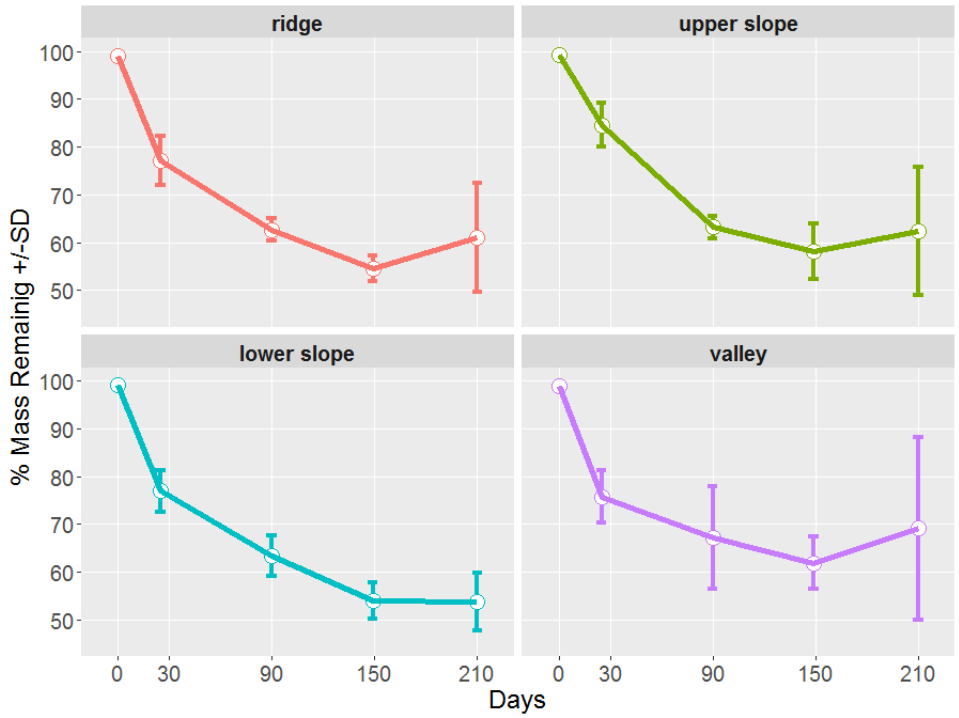

Figure 3. Mean mass loss by percentage with standard deviation over time for each topographic location. Mass decreased up through Month 5, but there was an increase in mass for most of the locations in Month 7, likely due to soil contamination.

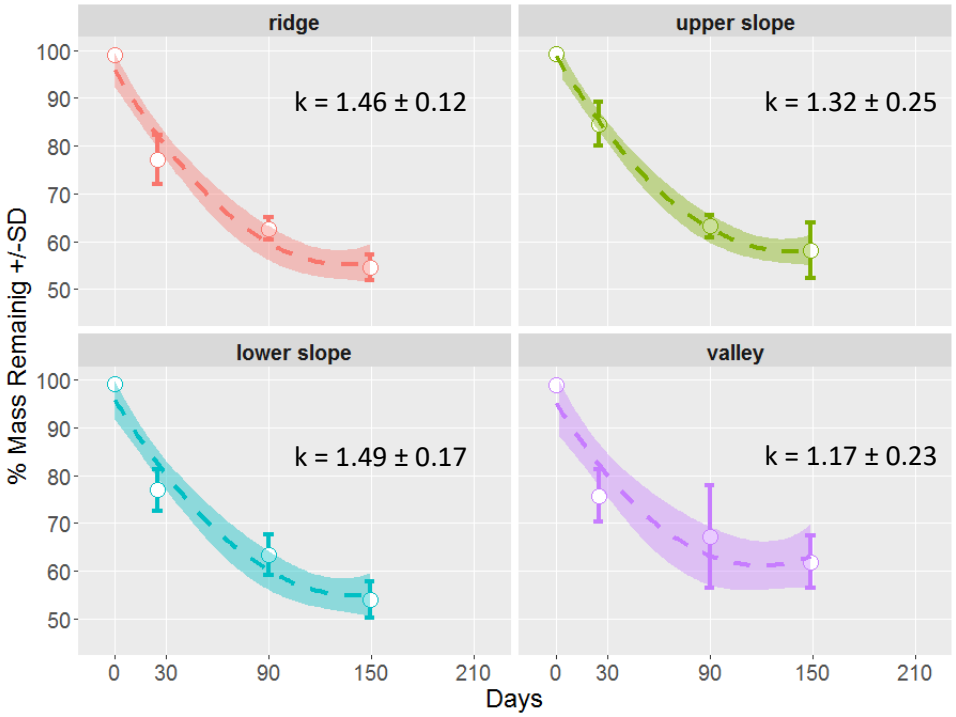

Figure 4. Exponential decay models with k-values for data up through Month 5 for each topographic location. Upper topographic locations had faster decomposition rates and there was a dramatic decrease in decomposition rate at the valley. Only the k-values for lower slope and valley were significantly different (P = 0.045).

Change in C:N

For all topographic locations, change in C:N over 7 months were negative (Fig 5), meaning loss of C was much faster than loss of N. The rate of change in C:N is reported by the slope (m) of the linear model in units of C:N/day. For ridge, m = -0.170 (R^2 = 0.890); for upper slope, m = -0.175 (R^2 = 0.828); for lower slope, m = -0.143 (R^2 = 0.819); and for valley, m = -0.171 (R^2 = 0.848). One-way ANOVA comparing C:N for Month 7 showed that there was no significant difference among the topographic locations (P = 0.381; Fig 6).

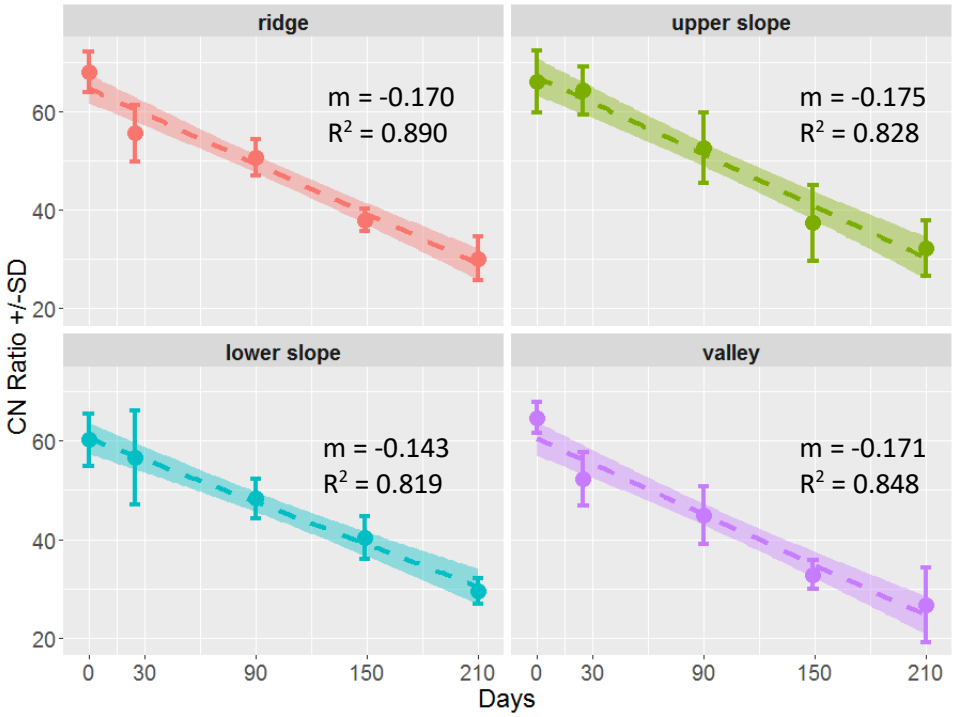

Figure 5. Linear model of C:N over time for each topographic location with mean C:N ratio and standard deviation. All four sites had a negative change in C:N ratio over the 7-month period.

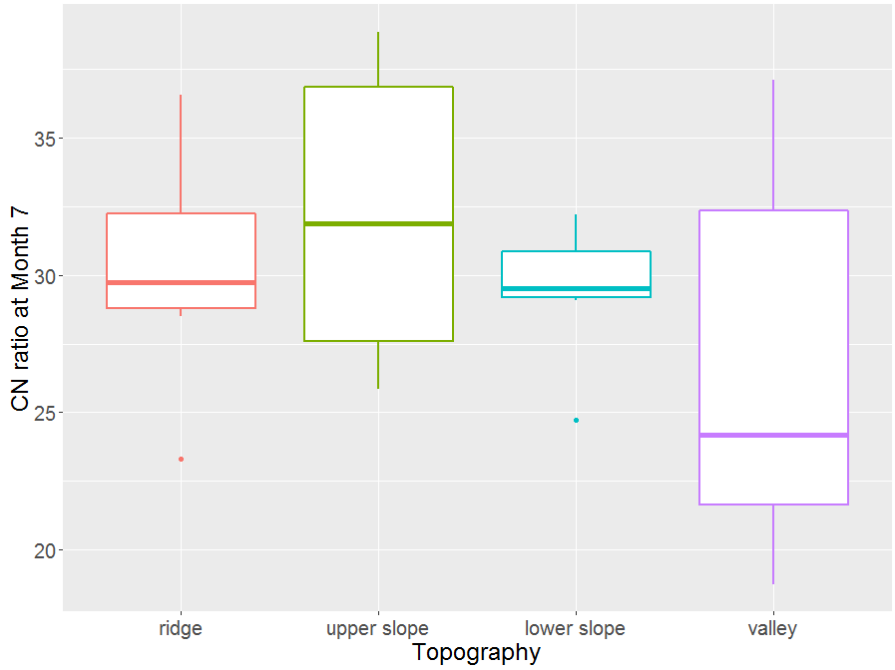

Figure 6. Distribution of C:N ratio at Month 7 for each topographic location. There were no significant differences among sites (P = 0.381).

Decomposition and greenhouse gases

I found a strong, positive linear correlation between decomposition rates and CO_2 fluxes ($m = 7.390$, $R^2 = 0.637$) and a strong, negative linear correlation between decomposition rates and CH_4 fluxes ($m = -27.92$, $R^2 = 0.704$). However, the positive correlation between decomposition rates and N_2O fluxes were weak ($m = 0.167$, $R^2 = 0.263$; Fig 7). CO_2 fluxes were highest along the ridge and decreased down to the valley (mean flux ± SE, units of umol m^{-2} s^{-1}: ridge = 4.03 ± 0.07, lower = 2.48 ± 0.04, valley = 0.98 ± 0.02) with significant differences among ridge, lower slope, and valley (all $P < 0.001$); but the upper slope had similar emissions as the valley (upper = 1.22 ± 0.03, $P = 0.104$; Fig 8a). CH_4 emissions were high in the valley (mean flux ± SE, units of nmol m^{-2} s^{-1}: valley = 9.40 ± 0.71), while ridge, upper slope, and lower slope consumed CH_4 (ridge = -0.35 ± 0.04, upper = -0.96 ± 0.29, lower = -0.62 ± 0.18; Fig 8b). CH_4 flux from the valley was significantly different from all other locations (all $P < 0.001$), but there was no significant difference of flux among ridge, upper slope, and lower slope (all $P > 0.9$). N_2O emissions were highest along the ridge and decreased from ridge to lower slope to valley (mean flux ± SE, units of nmol m^{-2} s^{-1}: ridge = 0.172 ± 0.014, lower = 0.139 ± 0.005, valley = 0.116 ± 0.004), but the upper slope had the lowest emissions (upper = 0.055 ± 0.003; Fig 8c); emissions from all locations were significantly different ($P < 0.01$).

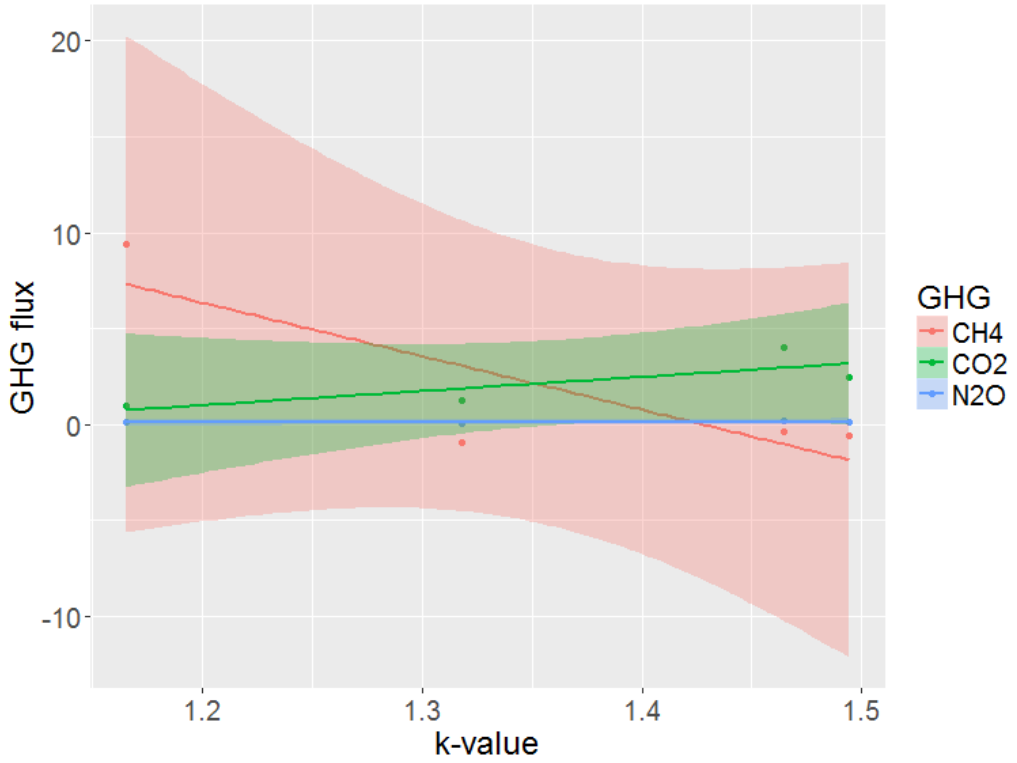

Figure 7. Linear regression of k-values as a predicting variable for fluxes for each greenhouse gas. The k-values had strong positive correlations with both CO_2 ($R^2 = 0.637$) and CH_4 fluxes ($R^2 = 0.704$), but the correlation with N_2O flux was weak ($R^2 = 0.263$). Units of gas fluxes are umol m^{-2} s^{-1} for CO_2 and nmol m^{-2} s^{-1} for CH_4 and N_2O.

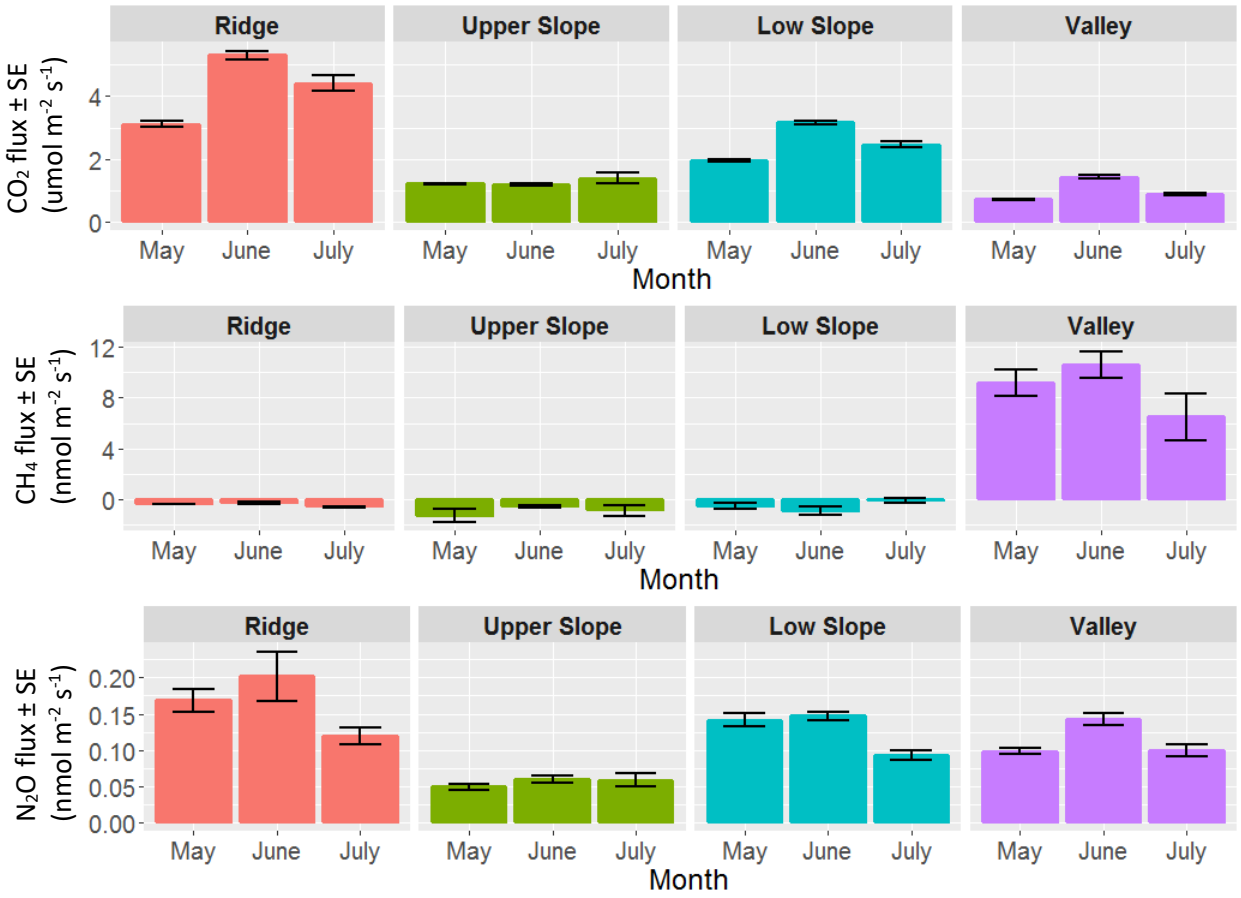

Figure 8. Fluxes for each greenhouse gas along a topographic gradient. (a) CO_2 emissions decrease downslope except for upper slope, which has similar emissions to the valley. (b) CH_4 is only emitted from the valley, while all other topographic locations consume CH_4. (c) N_2O emissions decrease downslope much like the CO_2 flux, but upper slope has the lowest N_2O emissions.

DISCUSSION

Decomposition rates were the lowest in the valley, likely due to the anaerobic micro-environment created by the high soil volumetric water and low soil oxygen in this topographic zone. CH_4, a by-product of anaerobic decomposition, was only emitted from the valley, and CO_2 and N_2O emissions were generally much lower in the valley than anywhere else. These results indicate that anaerobic microbial activity plays a significant role in driving greenhouse gas fluxes, and such activity can be influenced by a subtle environmental gradient.

Decomposition rates along topography

I measured decomposition rates along the topographic gradient to see how they might differ along this gradient. My results showed that there were variations in decomposition rates, which were likely linked to differences in soil moisture and soil oxygen. Decomposition rates were low for the valley in comparison to the other three topographic locations and generally increased upslope. The valleys had the highest soil moisture and lowest soil oxygen, which are indications of an anoxic environment. In less aerated environments, anaerobic decomposition, which is much slower than aerobic decomposition (Acharya 1935), begins to predominate. Therefore, it is reasonable that decomposition rates slowed down in the valley where it was intermittently water-logged. However, the similar decomposition rates between the lower slope and the ridge, even though the lower slope had a much higher soil water content and a lower soil oxygen content than the ridge, suggest that decomposition rates are not as sensitive to the moisture and oxygen gradient in the environment. This is also supported by the lower decomposition rate at the upper slope in comparison to the lower slope and ridge. The variation in decomposition rates do not parallel the gradual topographic gradient of soil moisture and soil oxygen, but instead suggest that there is a threshold effect on decomposition rates. Mo et al. (2008) found that soil moisture below a certain threshold had a significant effect on soil respiration. In other words, in dry soils, soil moisture can be a strong factor in determining soil respiration, or microbial decomposition. Soil moisture and soil oxygen are driving factors at the threshold at which aerobic decomposition switches to anaerobic decomposition, and this study shows that the small-scale environmental changes along a hillslope can be significant enough to influence microbial decomposition.

Overall, the decomposition rates I observed (ranging from 1.17 to 1.49) were consistent with other studies conducted in Puerto Rico. Bloomfield et al. (1993) conducted litter decomposition experiments on specific species, *Prestoea montana* and *Dacryodes excelsa*, and reported the k-values as 1.6 and 1.3, respectively. Ostertag et al. (2008) found that the k-values ranged from roughly 1.2 to 0.6 in older secondary forests and primary forests. Minor deviations can be attributed to differences in length of time leaves were left in the field, yearly fluctuations of abiotic factors such as temperature and precipitation, and specific differences in field sites that may affect soil nutrients and microbial communities. Litter quality can also affect decomposition rates (Riggs et al. 2015; Bloomfield et al. 1993); my study purposefully used a mixture of leaf litter

from various species at the field site to more realistically portray the in-situ conditions, unlike Bloomfield et al. (1993) who looked at decomposition rates of two different species. Ostertag et al. (2008) observed lower decomposition rates, but their study site was roughly 300 m higher in elevation, and the environment can change significantly along an elevational gradient (Silver et al. 1999).

The significant differences in soil volumetric water and oxygen content along a topographic gradient emphasize the spatial variations within tropical forests, even at a 5-m scale. Volumetric water increased from ridge to slope to valley while oxygen decreased from ridge to slope to valley. Basnet (1993) also found that there was a significant difference in soil moisture along topography, increasing from ridge to slope to valley. In contrast, Wang et al. (2002) found that soil moisture increased from ridge to slope then decreased from slope to valley with the valley having a lower moisture content than the ridge tops. However, while Basnet (1993) collected his data year-round, Wang et al. (2002) only conducted their study during a drier winter period. Therefore, Wang et al. (2002) concluded that there is likely a high spatial variance in soil moisture along topography in the dry season. Silver et al. (1999) also made a similar conclusion about temporal variation based on their soil oxygen data. Similar to my results, Silver et al. (1999) found that soil oxygen decreased from ridge to slope to valley. They also observed that longer term rainfall trends influenced soil oxygen on ridges, but previous day's rainfall events had a much stronger impact on soil oxygen in valleys, suggesting that less consistent rainfall patterns in the drier periods would lead to high spatial variations along topography (Silver et al. 1999). I did not find significant difference in temperature along topography which is consistent with other studies (Silver et al. 1999, Kosugi et al. 2007).

Change in C:N ratio along topography

I also looked at C:N ratios in the decomposing litter to see if topography may affect the rate of change in the ratio. There were no significant differences in C:N ratios in the last month. Because the initial leaf litter was taken from a homogenized, random mixture of litter, initial C:N should be relatively similar. Therefore, this indicates that the rate of change of C:N along the topographic gradient did not differ significantly. C:N decreased for all four locations throughout my study, which indicates that the microbes take up organic C from the litter faster than organic

N. This is likely because tropical forest soils are highly abundant in inorganic N, so there is less demand for organic N (Vitousek and Sanford 1986, Chapin et al. 2002). The similar rates of change in C:N at all topographic locations also suggest that N abundance is relatively uniform along the topographic gradient. I initially hypothesized that C:N will be higher in anoxic conditions because the consumption of organic C would slow relative to that of organic N, due to the predominance of anaerobic decomposition. This was not true because although the valley experienced clear anoxic conditions, it did not have a slower rate of change in C:N. As decomposition rates slowed, it is likely that it not only slowed the consumption of organic C but also of organic N. The breakdown of organic N occurs in parallel to the breakdown of organic C and is therefore likely controlled by similar factors as decomposition (Chapin et al. 2002), which would explain this relationship of C:N.

Greenhouse gases and decomposition

Lastly, I examined the relationship between decomposition rates and greenhouse gas fluxes for CO_2, CH_4, and N_2O along the topographic gradient. CO_2 and CH_4 fluxes both had strong linear correlations with k-values, but N_2O fluxes and k-values had a weaker linear correlation. However, only four data points were available for the linear regressions, and hence may not be full representations of the relationships. CO_2 fluxes and k-values had a positive correlation which means that as decomposition rates increased, CO_2 emissions also increased. This was expected because CO_2 is a direct by-product of aerobic decomposition (Chapin et al. 2002). However, this regression may be misleading because the decrease in k-values downslope seemed to follow a threshold effect along the topography rather than a gradual decrease along topography as seen in CO_2 emissions. The relationship may also be misleading for the CH_4 fluxes and k-values. The strong, negative linear correlation between the two indicates that CH_4 emissions decreased as k-values increased, but this relationship is largely driven by the high CH_4 emissions and low decomposition rates in the valley. In fact, CH_4 emissions were only observed from the valley which suggests that CH_4 emissions follow a threshold relationship similar to the decomposition rates. It is more likely that CH_4 emissions and k-values have a non-linear relationship, showing a threshold effect relating to soil moisture and soil oxygen. As CH_4 emissions are largely tied to anaerobic

decomposition (Chapin et al. 2002), these results suggest that the distinction between aerobic and anaerobic microbial activity is a driving force for CH_4 emissions.

Although the relationships between k-values and fluxes for CO_2 and N_2O emissions are inconclusive, I observed that the two gas fluxes were well-coupled along my study site, which has implications for the relationship between C and N cycles. Both CO_2 and N_2O emissions generally decreased from ridge to slope to valley which paralleled the gradient of soil moisture and soil oxygen along topography. However, emissions for upper slope did not fit this trend for either gases; emissions at the upper slope were lower than expected for both CO_2 and N_2O given this trend. The close coupling of CO_2 and N_2O emissions may be due to the link between high nitrification rates and fast C cycling (Venterea et al. 2012). Faster C cycling (ie. decomposition) allows for an accumulation of inorganic N due to high microbial activity which then leads to higher N loss from soils in various gaseous N forms, including N_2O (Vitousek and Sanford 1986, Venterea et al. 2012). The lower emissions at the upper slope may potentially be the result of a low productivity zone along the upper slope caused by specific conditions in that area leading to lower microbial activity.

The greenhouse gas fluxes that I observed were similar to those reported in other studies that conducted their measurements along a topographic gradient. Net C emissions were highest along the ridge and were largely in the form of CO_2. CO_2 emissions generally decreased from ridge to slope to valley which agrees with the findings of Epron et al. (2006), who attributed their results to the increasing soil water content and decreasing root biomass and soil carbon content. They reported an average respiration rate of 4.3 umol m^{-2} s^{-1} which is similar to the rate I observed along the ridge. CH_4 emissions were two orders of magnitude lower than CO_2 emissions and only came from the valleys; the ridges and the slopes acted as CH_4 sinks. Silver et al. (1999) made similar measurements with the valleys emitting 3.32 nmol m^{-2} s^{-1} and the ridges and the slopes consuming 0.56 and 1.89 nmol m^{-2} s^{-1}, respectively. N_2O emissions followed a similar pattern of decreasing from ridge to slope to valley as CO_2. Detailed N_2O fluxes are limited, but my N_2O fluxes were within range of the fluxes that Bowden et al. (1992) observed, which was between 0.01 and 0.27 nmol m^{-2} s^{-1}.

Limitations and future directions

Results from this study showed that tropical forest biogeochemistry varied spatially in a humid tropical forest, and that distinct patterns can be observed along topographic gradients. More research along tropical forest topographic gradients will help determine if these results are generalizable. Tropical forests span the equatorial globe at different latitudes, elevations, precipitation inputs, species composition, soil type and more. Even within Puerto Rico, the rainforests are distinguished into three distinct forest types at different elevations: a subtropical, wet tabonuco forest (300 – 600 masl); a lower montane, wet colorado forest (600 – 750 masl); and lower montane cloud forest (750 – 1050 masl) (Brown et al. 1983). With unique biotic and abiotic factors characterizing each of these forest types, it would be interesting to see if the data from the tabonuco forest could be extrapolated to the other two forest types. Therefore, conducting similar decomposition experiments and greenhouse gas monitoring at the colorado forest and cloud forest with an in-depth analysis of both biotic and abiotic soil characteristics for all forest types will greatly increase our understanding of how variables interact to influence both decomposition and greenhouse gas fluxes. Furthermore, it would be beneficial to expand the experiment into broader, continental rainforests such as those in the Amazon. There may be unforeseen differences based on island and continental biogeography which is crucial to understand, especially because the Amazon plays a much larger role in global effects (Metcalfe et al. 2010).

Conclusion

As dominant players in the global greenhouse gas fluxes, understanding how subtle changes in the environment could affect the ecosystem dynamics of tropical forests is important in combatting current and future changes in global climate. Climate change is already affecting rainfall patterns in tropical forests. For example, regions of the Amazon rainforest are already facing more severe dry events and concentrated rainfalls, increasing seasonality (Malhi et al. 2008), and the forest in the LEF experienced a rare, severe drought in 2015 (Ramirez et al. 2017). The small-scale topographic gradient measured here created differences in soil moisture and soil oxygen that had noticeable impacts on decomposition, nutrient recycling, and greenhouse gas fluxes. This implies that changes in precipitation patterns associated with increased seasonality in

the tropics can cause major global perturbations in the carbon and nitrogen cycles. Prolonged dry periods may hinder decomposition while increased precipitation may lead to anaerobic conditions with slower decomposition and increased CH_4 emissions. The more frequent fluctuations of soil conditions may lead to higher loss of N. Such events not only result in higher emissions of more potent greenhouse gases, but also have impacts on the ecosystem—slower nutrient recycling and the imbalance of nutrient availability could damage plant productivity, decreasing carbon sequestration and disturbing food chains. Furthering our knowledge of the biological processes and the interactions of abiotic factors is crucial in understanding the impacts of climate change.

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