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Ecosystem response to increasing hurricane disturbance: Comparing nutrient cycling dynamics associated with early- and late-successional tree species in a wet tropical forest

By Miriam L. Kleit

An Honors Thesis Submitted to the Biology Department at Macalester College, Saint Paul, Minnesota, USA

Advisor: Christine O’Connell, Department of Environmental Studies

Submitted April 28, 2024

Abstract

Puerto Rico has seen changes in the frequency and severity of disturbances in recent years as hurricanes become more frequent and more intense under climate change. In ecosystems experiencing increasing disturbances, we expect that species composition will shift as early successional trees become more common. These changes to species composition and community ecology are likely to affect terrestrial nutrient cycling both directly and indirectly, and it is still not well understood how shifting community composition may alter ecosystem functioning. To address this gap, I measured carbon (C) and nitrogen (N) variables in soils, microbial biomass, roots, leaves, and soil greenhouse gas fluxes within 1 m of individuals from three tree species (5 replicates per species) across a topographic gradient in El Yunque National Forest in Puerto Rico. The three species of interest are likely to be differently affected by changing hurricane regimes: an early successional tree species (*Cecropia schreberiana*), a secondary successional species (*Prestoea montana*), and a late successional species (*Guarea guidonia*). I hypothesized that the soil area surrounding early successional and late successional tree species would exhibit differences in carbon and nitrogen cycling and the resulting soil greenhouse gas emissions. I found that there were significant species-related differences in leaf composition, soil nutrients, and soil gas fluxes. *G. guidonia* had the highest %C and %N in senesced leaves compared to the other two species, having on average 6.39% and 8.38% higher %C compared to *C. schreberiana* and *P. montana* respectively. Senesced *G. guidonia* leaves had on average more than 50% higher %N compared to *P. montana*, and nearly double the %N of *C. schreberiana* at 90.55% more on average. All three species had statistically distinct C:N ratios, with *G. guidonia* having the lowest at 28.859 ± 2.435 (compared to 39.988 ± 2.274 for *P. montana* and 51.522 ± 3.751 for *C. schreberiana*), and thus likely decomposing the fastest. *C. schreberiana* and *G. guidonia* had statistically distinct amounts of extractable C and N associated with the soil at the base of each tree ($p < 0.01$). While the soil CO_2 flux associated with each tree did not differ significantly between species, the CH_4 flux was significantly higher in the soil near *P. montana* compared to the other two species, averaging around -0.052 ± 0.155 compared to -0.608 ± 0.123 and -0.685 ± 0.041 for *C. schreberiana* and *G. guidonia* respectively, suggesting that *P. montana* is associated with lower soil CH_4 uptake. In combination, my results suggest that, as the successional state of the forest shifts to be dominated by early successional species for longer stretches of time due to increasing incidence of large-scale hurricane disturbance, the nutrient cycling of this forest may also be altered drastically.

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Acknowledgements

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Introduction

Hurricanes have both immediate and long-term effects on forest communities and nutrient dynamics, that have significant implications for the biodiversity, water resources, and nutrient cycling of the affected area (Crow 1980, Lodge & McDowell 1991, Ostertag et al. 2003, Gavito et al. 2018, Gutiérrez del Arroyo & Silver 2018). As tropical forests contain large stores of carbon, shifts in carbon (C) dynamics can lead to a reduction in those stores and the associated net carbon emissions of these systems as a whole (Fernández-Alonso et al. 2018). As climate change causes hurricanes to become more frequent and more intense (Elsner 2006, Bender et al. 2010, Holland & Bruyère 2014), it will be important to quantify how changing disturbance regimes might alter the C and nitrogen (N) cycles, both as a direct consequence of disturbance and as an indirect consequence.

Human-caused climate change is altering hurricane regimes in the Caribbean, leading to an increase in the frequency of intense hurricanes (Bender et al. 2010, Holland & Bruyère 2014, Elsner 2006). Hurricane models predict that the number of Category 4 and 5 hurricanes will nearly double by the end of the 21st century (Bender et al. 2010). In recent decades, Puerto Rico experienced Category 5 Hurricanes Hugo and Maria in 1989 and 2017 respectively, as well as the Category 4 Hurricane Georges in 1998. All three of these hurricanes were associated with significant ecological disturbance including shifts in ecosystem structure and biogeochemistry (Lodge & McDowell 1991, Silver 1996, Comita et al. 2009, Heartsill-Scalley et al. 2010, Gutiérrez del Arroyo & Silver 2018, Uriarte et al. 2019).

Hurricanes: litter and soil chemistry

In the immediate aftermath of a hurricane, there is a pulse of nutrients into soils from leaves and branches as a result of wind damage. In the absence of major hurricane disturbance, the year-round leaf litter in an aseasonal tropical forest is generally senesced and the amount of litterfall remains relatively high throughout the year (Ruan et al. 2004, Silver et al. 2014, Liu et al. 2018). The litter pulse from a hurricane is nutritionally distinct from regular litter due to being composed of a higher percentage of branches/woody materials and green (rather than senesced) leaves. As a result, these pulses not only represent an input of nutrients to the system, but the stoichiometry of these nutrients also differs from senesced litter (Lodge et al. 1991, Lodge & McDowell 1991, Whigham et al. 1991). Green leaves generally have a higher concentration of N and lower C:N ratios compared to senesced leaves (Lodge et al. 1991, Fonte & Schowalter 2004). Lower C:N ratios are associated with faster decomposition rates, meaning that the less-senesced, more green leaf litter that falls to the forest floor as a result of a hurricane may decompose faster than regular senesced litter (Hobbie 1992, Xuluc-Tolosa et al. 2003, Fonte & Schowalter 2004, Krishna & Mohan 2017, Gavito et al. 2018). However, woody materials, which contain recalcitrant compounds such as lignin and cellulose, tend to be less nutritionally dense and decompose slower than leaf litter (Zinke 1962, Zhang & Zak 1995). It remains unclear to what extent this large nutrient input from wind-shear driven litter inputs shifts long-term belowground biogeochemistry. Ostertag et al. 2003 found that post-hurricane litter inputs, while substantial, decomposed quickly, with forest litter standing stocks returning to pre-hurricane levels by 2-10 months after Hurricane Georges. Similar resilience to long-term biogeochemical cycling changes were observed in Puerto Rico after Hurricane Hugo (Silver et al. 1996) and in a tropical dry forest system after Hurricane Jova (Gavito et al. 2018). These results suggest that single-event hurricane disturbances may not have long-term effects on soil biogeochemistry due to changing litter inputs alone. In contrast, results from a long-term hurricane manipulation experiment found that soil C, soil N and soil P remained higher in the “debris-addition” treatment 10 years after a simulated hurricane litter input event (Gutiérrez del Arroyo & Silver 2017). It remains unclear how a changing hurricane regime might affect long-term nutrient cycling rates and belowground C and nutrient stocks.

Hurricanes: forest structure and composition

The widespread disturbance caused by hurricanes can drastically change the composition and structure of a forest by removing mature canopy trees, opening up large light gaps that reach the forest floor (Crow 1980, Heartsill-Scalley et al. 2010). Early successional tree species tend to rapidly increase in abundance post-disturbance due to their fast growth rates and high light tolerance which enables them to take advantage of the newly opened gaps in the canopy. Secondary and late successional species, which tend to have slower growth rates and higher shade tolerance, are generally either unaffected or are negatively affected by hurricane disturbance (Bazzaz 1979, Drew et al. 2009, Heartsill-Scalley et al. 2010).

In Puerto Rico, the early successional species *Cecropia schreberiana* had relatively low population density and was not as widespread in the Luquillo Experimental Forest (LEF) just prior to Hurricane Hugo, which hit the island in 1989. However, in the four years following the hurricane, *C. schreberiana* proliferated rapidly, becoming one of the most common tree species in those same plots (Drew et al. 2009, Heartsill-Scalley et al. 2010). Changes of this nature can affect the ecosystem functioning of the forest as a whole, but it is unclear how permanent these changes are. Given enough time without another major disturbance, the forest would likely return to a pre-disturbance state. Canopy light gaps rapidly close within a few years post-hurricane disturbance, suggesting that the forest has a strong ability to recover. One study from the Bisley Experimental Watersheds found that aboveground biomass returned to pre-hurricane levels within 15 years after Hurricane Hugo, though the forest remained altered in other ways (Heartsill-Scalley et al. 2010). On a species level, it appears that changes in tree species abundance may also revert to pre-disturbance levels given enough time. Despite initially becoming widespread post Hurricane Hugo, *C. schreberiana* began to decline noticeably in the following years. The fact that prior to Hugo, the *C. schreberiana* population had declined to near zero also points to this idea (Drew et al. 2009). However, as intense hurricanes become more frequent due to climate change and rising ocean temperatures, there are likely to be fewer extended periods without major disturbances, and the forest/tree species composition is likely to remain in an altered state (Bender et al. 2010, Holland & Bruyère 2014). Disturbance-driven shifts in plant communities can lead to indirect impacts on belowground biogeochemistry via mechanisms including plant-soil feedbacks (van der Putten et al. 2016), altered litter stoichiometry (Hobbie 2015), and other species effects (Hobbie 1992). As each tree species can affect the nutrient cycling of the forest differently, large, potentially long-lasting, changes in tree species composition may alter the nutrient dynamics of the entire forest.

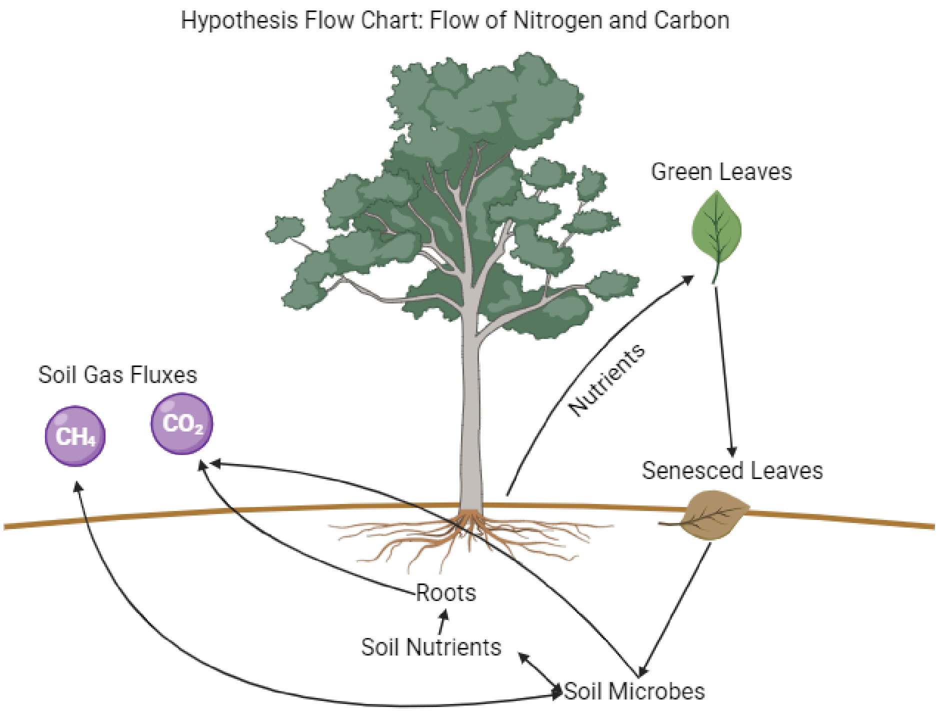

Figure 1. Hypothesis flowchart showing how carbon and nitrogen move through the system. Created in BioRender.

Spheres of influence

Individual trees can exert influence over the soil chemistry of the surrounding ecosystem in a spatial pattern, with the effect being stronger closer to the tree's trunk and weaker further away (Zinke 1962, Hobbie 1992, Reed et al. 2008, Day et al. 2010, Uriarte et al. 2015). Differences between tree species change the nature and extent of this influence (Lin et al. 2022, Jing et al. 2023). A variety of studies have examined the extent of this influence, though the majority were conducted in temperate or otherwise non-tropical ecosystems (Zinke 1962, Lovett et al. 2004, Vivanco & Austin 2008, Runte et al. 2021). Several studies from tropical ecosystems have found similar effects (Reed et al. 2008, Uriarte et al. 2015), though a few studies (such as Powers et al. 2004) found evidence that this trend may not hold true for complex tropical ecosystems. Trees may also affect the soil around them via nutrient uptake, root respiration, and more.

Litterfall from trees is the primary nutrient input for soil in forests, and the quality and composition of that litter is largely determined by the characteristics and abundance of the tree species present (Hobbie 1992, Silver 1994, Aerts & Chapin 1999, Uriarte et al. 2015). The nutrient composition of leaf litter affects the amount of nutrients that re-enter the soil, as well as the speed of that re-entry via decomposition. In particular, the C:N ratio of litter is correlated with the C:N ratio of soil, and the C:N ratio of litter is highly associated with its decomposition rate (Hobbie 1992, Zhang & Zak 1995, Aerts & Chapin 1999, Uriarte et al. 2015). Litter with higher N concentrations and lower C:N ratios is associated with higher microbial activity and, as a result, faster decomposition rates (Zhang & Zak 1995, Xuluc-Tolosa et al. 2003).

Differences in the life history strategies of tree species, specifically between early and late successional strategies, are associated with differences in the nutrient composition of litter. Early successional species tend to produce leaf litter with higher N concentrations and lower C:N ratios. In contrast, the litter produced by late successional species tends to be higher in lignin and lower in %N, meaning that litter from early successional species may have faster decomposition and mineralization rates compared to late successional species (Alder et al. 2014, Uriarte et al. 2015). As a result, successional shifts in tree species composition may have large effects on the nutrient composition and decomposition rates of leaf litter. Additionally, soil nutrients can influence green leaf nutrients, though this effect may only be visible through limiting nutrients (Davidson et al. 2007, Wood et al. 2011).

Microbial community and decomposition

The soil microbial community is vital to nutrient cycling and soil biogeochemistry due to its role in decomposition. Decomposition of plant material (i.e. leaves, bark, etc.) moves nutrients into the soil where they can be taken up by plants or other organisms (Xuluc-Tolosa et al. 2003). When soil conditions are disrupted (such as by fire, drought, or agricultural land use), the litter decomposition rate can slow as the microbial community is still adapted to the previous, pre-disturbance conditions (Zhang & Zak 1995, Prieto-Fernández et al. 1998, Fernández-Alonso et al. 2018). This can interfere with the speed at which nutrients re-enter the soil, potentially affecting the nutrient cycling of the entire ecosystem. The recovery of microbial processes to their baseline rates can vary by type of disturbance (e.g., agricultural land use change vs. drought vs. fire) (Kaschuk et al. 2011, Holden & Treseder 2013, Zhang et al. 2016, Ludwig et al. 2018, Schimel 2018), ecosystem type (Philippot et al. 2021), and multiple other factors (Malik et al. 2018, Philippot et al. 2021).

The microbial community also contributes to nutrient cycling via metabolic processes that either assimilate and/or release various gasses, in particular carbon dioxide (CO_2), methane

(CH_4), and nitrous oxide (N_2O) (Oertel et al. 2016). These gas fluxes have implications for the ecosystem functioning and greenhouse gas emissions of tropical forests, which have historically been considered to be carbon sinks, especially as there is growing evidence of forests potentially shifting to become sources under climate change (Pan et al. 2011, Mitchard 2018, Schimel et al. 2018, Hubau et al. 2020). There are other factors influencing these fluxes, such as root respiration in the case of CO_2, so soil gas fluxes cannot be attributed to the microbial community alone (Oertel et al. 2016, Bezyk et al. 2023, Cui et al. 2024). Due to the relationship between soil microbes and litter quality, and the association between litter quality and tree species, it is possible that there is a relationship between soil microbial communities, soil gas fluxes, and the species of large nearby trees.

My experiment

In this study, I compared how three common tree species in Puerto Rico's wet tropical forest - one early successional (*C. schreberiana*), one secondary (*P. montana*), and one late successional (*G. guidonia*) - influence aspects of belowground biogeochemistry, in order to measure how changes in tree species composition as a result of hurricane disturbance may impact ecosystem-level nutrient cycling. This experiment was conducted at the Sabana Field Research Station in Luquillo, Puerto Rico. I examined the nutrient content (C and N) of green and senesced leaves from five individuals from each of the three tree species. I also examined the nutrient content of each species' live and dead roots, the soil nutrients at the base of each tree (including %C, %N, microbial C, microbial N, and extractable C and N), and the soil gas fluxes (CO_2 and CH_4) of the soil near the base of each tree. I hypothesized that early and late successional species would differ in their leaf chemistry, leading to a difference in litter quality associated with each tree. I further hypothesized that differences in litter composition would in turn affect soil chemistry, potentially altering nutrient availability, microbial community, and gas fluxes associated with the soil near each tree. A hypothesis flow chart is shown in Figure 1. This study contributes to our understanding of the possible consequences of changing hurricane regimes by quantifying the potential effects on multiple, related nutrient stocks and fluxes of changing community composition in a biodiverse, C-rich forest that is likely to experience dramatic changes to its established hurricane disturbance regime.

Methods

Study site

This experiment was conducted at the Sabana Field Research Station in the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico (18.32549656982167, -65.72995159076665). This field site is a wet subtropical forest currently dominated by *Psychotria brachiata* and *Cecropia schreberiana*. It is a secondary forest that has recovered naturally from pasture over the last 60-70 years. The site is located at 100 m elevation and has relatively steep slopes averaging 21°. The soils are classified as red clay soils (Ultisols), with a mean annual temperature of 24°C and a mean annual precipitation of 3,500 mm. The site is also home to the first long-term warming experiment located in a tropical forest (Garcia-Martino et al. 1996, Kimball et al. 2018). The species makeup of the site changed significantly after Hurricane Maria in 2017, with many early successional species, such as *Cecropia*, proliferating.

Three tree species

Three tree species were included in this experiment: the early successional *Cecropia schreberiana*, the mid-successional palm *Prestoea montana,* and the late successional *Guarea guidonia*.

Cecropia schreberiana is a medium-sized pioneer tree species that reaches around 20 meters in height. The spread and ecological success of *C. schreberiana* has been linked to major hurricane disturbances in Puerto Rico, in particular Hurricanes Hugo and Maria (Brokaw 1998, Wood et al., unpublished data). *C. schreberiana* have hollow trunks, making them susceptible to hurricane mortality from wind damage. However, they resprout and reach maturity quickly, allowing them to dominate light gaps much faster than other species and take over the canopy of the forest (Brokaw 1998, Drew et al. 2009).

Prestoea montana is a mid-successional palm species that has come to dominate the understory of many parts of the Luquillo Experimental Forest (Crow 1980, Heartsill-Scalley et al. 2010). *P. montana* grow more slowly than *C. schreberiana*, but they are also more resistant to hurricane/wind damage due to their sturdy trunks and lack of branches. For example, at the El Verde field site, *P. montana* rarely experienced mortality due to Hurricane Hugo unless another tree fell on them, damaging their stem (Zimmerman et al. 1994). They appeared to spread more rapidly post Hurricane Hugo, though their numbers and total basal area had already been on the incline for some time (Drew et al. 2009). Compared to late successional species such as *G. guidonia*, they are still relatively fast growing and light tolerant.

Guarea guidonia is a late successional/non-pioneer tree species that is relatively common at the Sabana field site where this experiment was conducted. Mature trees are large, growing to over 20 meters, with dense wood that makes them very resistant to hurricane-related mortality (Zimmerman et al. 1994, Uriarte et al. 2015).

Experimental design

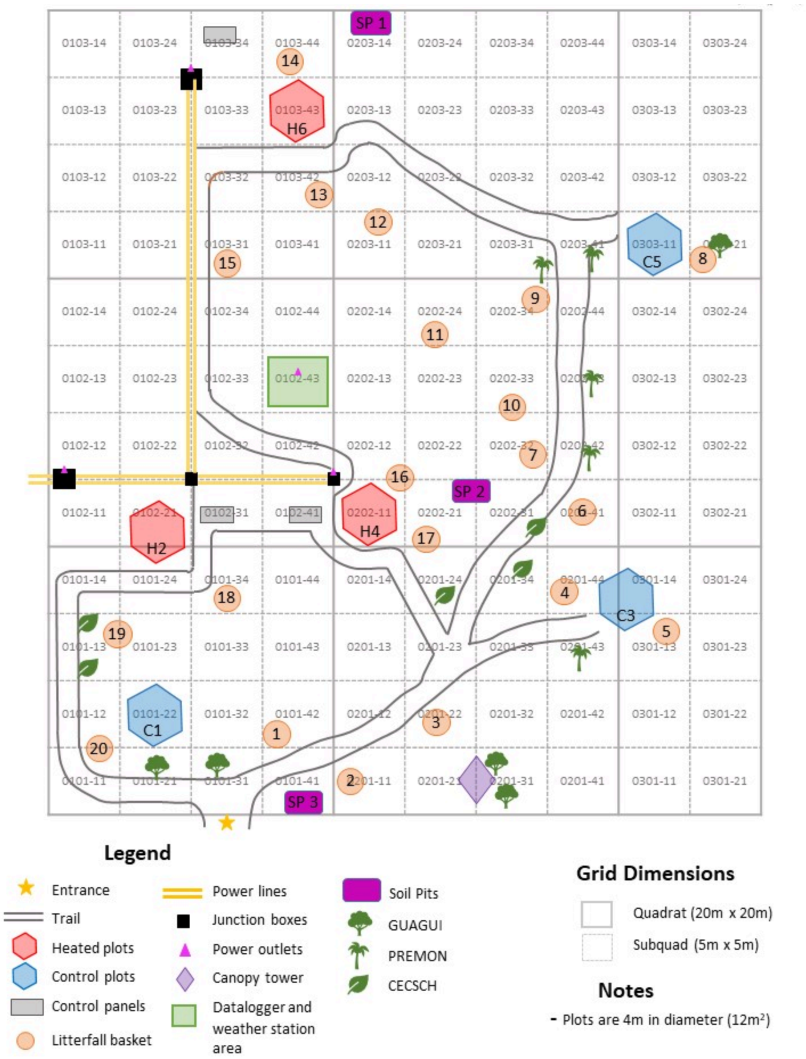

Figure 2. Map of the study site with each experimental tree marked.

In July of 2023, five individuals of each tree species were selected in the study site

(Figure 2). The criteria for tree selection was based on size (above average for their species based on the 2021 tree census) and accessibility (both in terms of ease of access and ease of soil collar installation). For each individual, samples were taken from within 1 m of the tree stem, with the exception of collection of green leaves (see below).

Plant tissue data

Senesced leaves were collected by placing a trash bag near the base of each tree (within a meter) and checking daily for new leaves from that species. When possible, green leaves were additionally collected from each tree using clippers. For trees where green leaves were inaccessible due to the lowest leaves being higher than clipper extenders, green leaves were taken from more accessible trees of the same species, preferably in the vicinity of the original tree. This was done only for three of the *C. schreberiana* individuals as all other individuals had accessible green leaves. For each tree, I collected 3 leaves or leaflets as appropriate. For senesced samples, up to 3 leaves/leaflets were collected depending on how many fell on each trash bag.

The leaf samples were weighed, labeled, and put in the oven at 65°C for at least 48 hours within an hour of collection. They were then weighed again, ground, and analyzed on an elemental analyzer (Elementar Vario Micro Cube) to determine %C and %N.

After gas sampling was complete, soil cores (0-10 cm) were taken from within each collar. The cores were weighed for bulk density and then rootpicked. Each core was rootpicked for at least 40 working minutes, and the roots were then separated into alive and dead samples for each core. These samples were then dried in the oven for a minimum of 48 hours at 65°C before being ground up. Those ground root samples were subsequently analyzed on an elemental analyzer (Elementar Vario Micro Cube) to determine %C and %N.

Soil variables

Three 5g subsamples were taken from each soil core previously collected. The first of these subsamples was used to measure soil moisture. After being weighed, it was dried in the oven for at least 48 hours at 105°C before being weighed again.

The next two 5g subsamples were used to analyze total organic carbon and nitrogen, in addition to microbial biomass. Microbial biomass was measured using the microbial biomass chloroform fumigation extraction method (Jenkinson & Powlson 1976).

One group of these subsamples was placed in Erlenmeyer flasks, weighed, and then 1 ml of chloroform was added. A stopper was placed in each flask, and the flasks were left in a dark, well-ventilated space for at least 24 hours. The stopper was then removed, and the samples sat in a well-ventilated place for another hour before being placed into urine cups for the next step. The other group of 5 g samples was weighed and directly placed in the urine cups.

30 ml of 0.5M K_2SO_4 was added to each sample, and the samples were shaken for one hour at 200 rpm. The samples were left to sit for 10 minutes, and then vacuum filtered. Samples were then frozen before being shipped to the Southwest Biological Science Center, U.S. Geological Survey for analysis. Samples were analyzed on a Shimadzu Total Organic Carbon (TOC) Analyzer with a Total Nitrogen unit (allowing simultaneous TOC and TN measurements; Shimadzu TOC Vcpn with TN-1 module). Two blanks were included in the processing steps. The microbial biomass chloroform fumigation extraction method allows for an estimate of microbial carbon and nitrogen via the difference between chloroform-treated and not-treated samples, in addition to an estimate of extractable soil carbon and nitrogen from the not-chloroform treated samples.

Trace gas data

PVC soil collars (20 cm diameter) were installed to a depth of 2-3 cm within one meter of the base of each tree. Net soil CO_2 and CH_4 fluxes were collected once a week for three weeks in two minute intervals for each recorded flux. Data was collected using a LI-COR 7810 survey trace gas analyzer and LI-COR Smart Chamber (LI-COR 8200-01S) system. All gas measurements were taken within a one-hour time span to ensure that ambient air temperatures didn't differ substantially across daily data. Soil moisture and temperature data (0-5 cm depth) was collected concurrently with soil gas measurements immediately adjacent to the chamber using a connected Stevens HydraProbe soil moisture and temperature probe.

Soil greenhouse gas fluxes were processed in SoilFluxPro (v. 5.3). Fluxes were screened for whether they were in the normal range for the following variables: chamber pressure, initial CO_2 and CH_4 concentrations, and chamber temperature. Flux rates were calculated using an exponential model in SoilFluxPro. Flux fits below an R^2 of 0.95 for CO_2 fluxes and below 0.90 for CH_4 fluxes would have been eliminated from the dataset; however all fluxes met the quality control cut off so none were eliminated.

Statistical analyses

Subsequent quality control/quality assurance and statistical analyses were performed in R (version 4.3.2). One-way ANOVAs were conducted to compare variables between species. Statistically significant ANOVA tests were followed by a Tukey's HSD post-hoc test. Simple linear regressions and Pearson's correlations were performed for relationships hypothesized and shown in the hypothesis flowchart (Figure 1).

Results

Plant tissue results

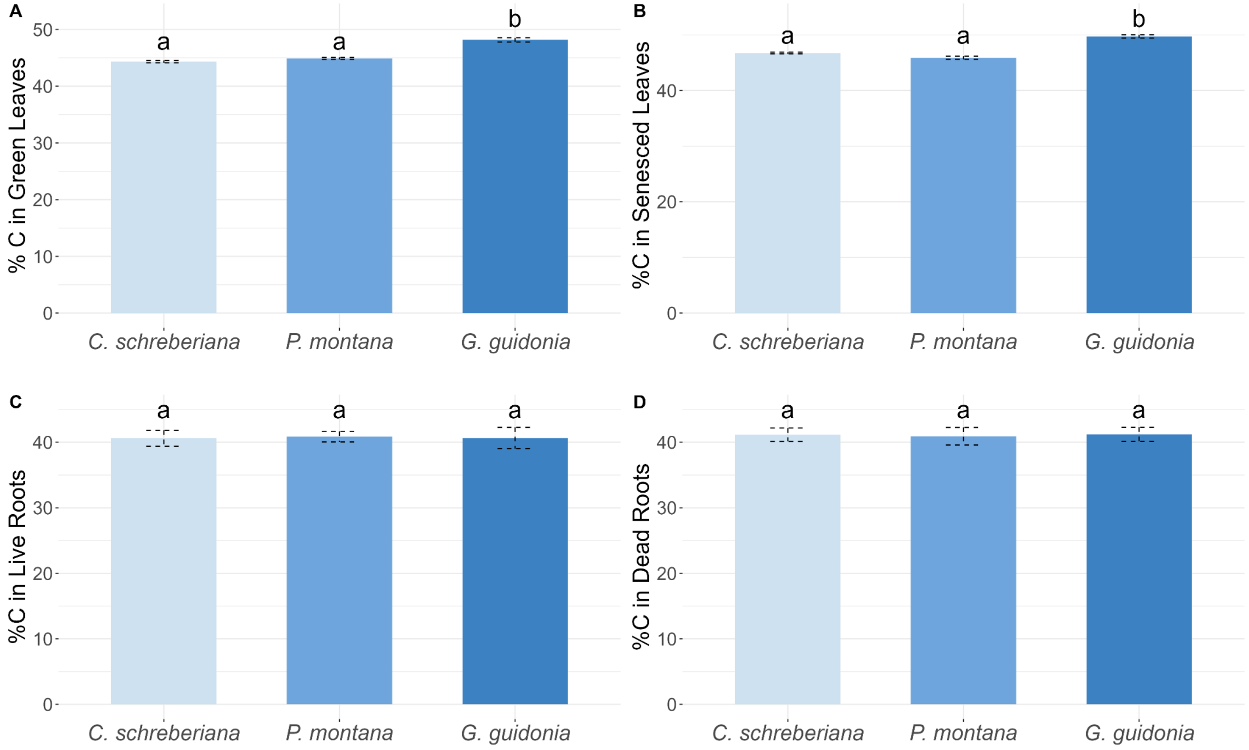

Figure 3. Percent carbon in the roots and leaves of each species based on their status when collected (green or senesced for leaves; live or dead for roots). Error bars indicate standard error.

I found significant differences across species for leaf C, leaf N, and leaf C:N ratios. *G. guidonia* had significantly higher %C for both live and senesced leaves (green: 48.189 ± 0.377%, senesced: 49.722 ± 0.300%) compared to *C. schreberiana* (green: 44.345 ± 0.197%, senesced: 46.736 ± 0.155%) and *P. montana* (green: 44.909 ± 0.177%, senesced: 45.878 ± 0.287%) ($p < 0.00001$) (Figure 3A-B, Table 1).

Percent C in live roots was similar across all species (*C. schreberiana*: 40.608 ± 1.213%, *P. montana*: 40.849 ± 0.809%, *G. guidonia*: 40.637 ± 1.623%, p = 0.989). Percent C in dead roots was the same, with no significant difference (*C. schreberiana*: 41.137 ± 1.02%, *P. montana*: 40.910 ± 1.338%, *G. guidonia*: 41.208 ± 1.068%, p = 0.982) (Figure 3C-D, Table 1).

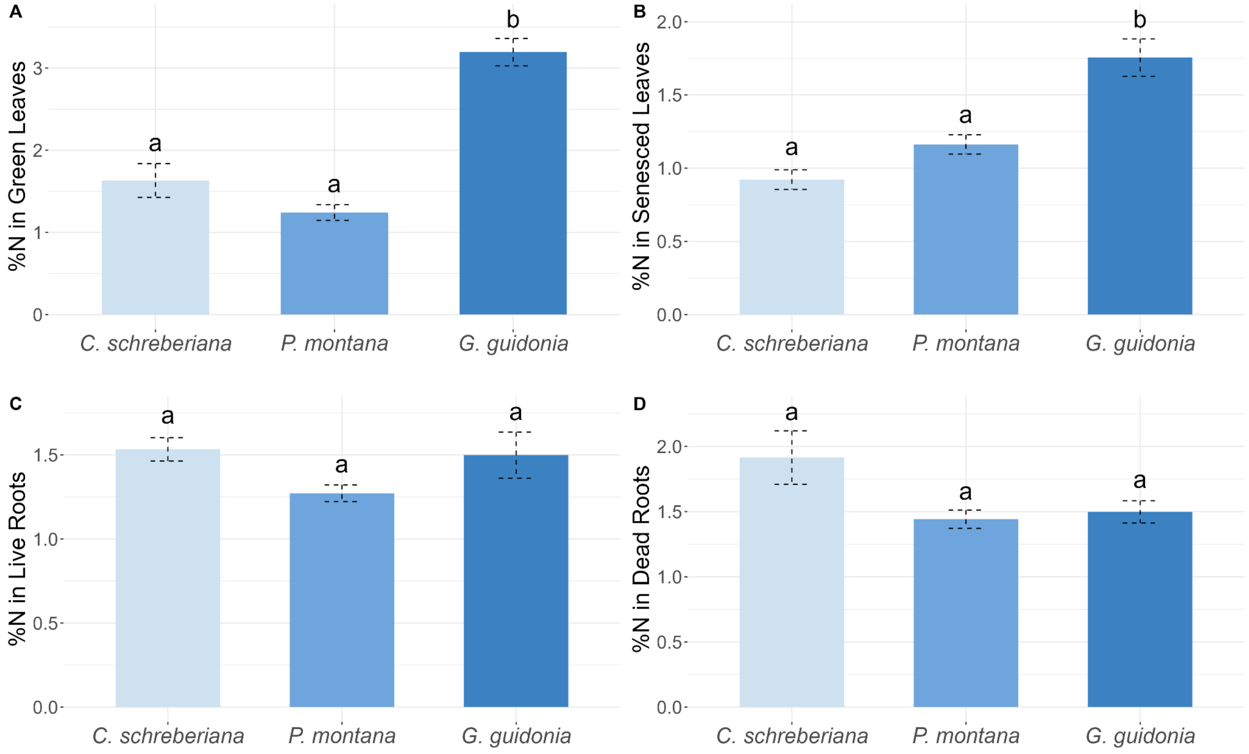

Figure 4. Percent nitrogen in the roots and leaves of each species based on their status when collected (green or senesced for leaves; live or dead for roots). Error bars indicate standard error.

Green leaves had higher %N than senesced leaves across all species. *G. guidonia* green leaves had significantly higher nitrogen content (3.194 ± 0.166%) than both *C. schreberiana* (1.631 ± 0.206%) and *P. montana* (1.243 ± 0.096%) (p < 0.00001). *G. guidonia* senesced leaves also had significantly higher nitrogen content (1.755 ± 0.128%) than both *C. schreberiana* (0.921 ± 0.067%) and *P. montana* (1.162 ± 0.066%) (p < 0.001) (Figure 4A-B, Table 1).

C. schreberiana had the highest %N in both live and dead roots (live: 1.535 ± 0.070%, dead: 1.915 ± 0.206%), followed by *G. guidonia* (live: 1.499 ± 0.138%, dead: 1.498 ± 0.086%), and finally *P. montana* (live: 1.272 ± 0.050%, dead: 1.442 ± 0.07%). There was no significant difference across species in %N for neither live nor dead roots (live: p = 0.143, dead: p = 0.057) (Figure 4C-D, Table 1).

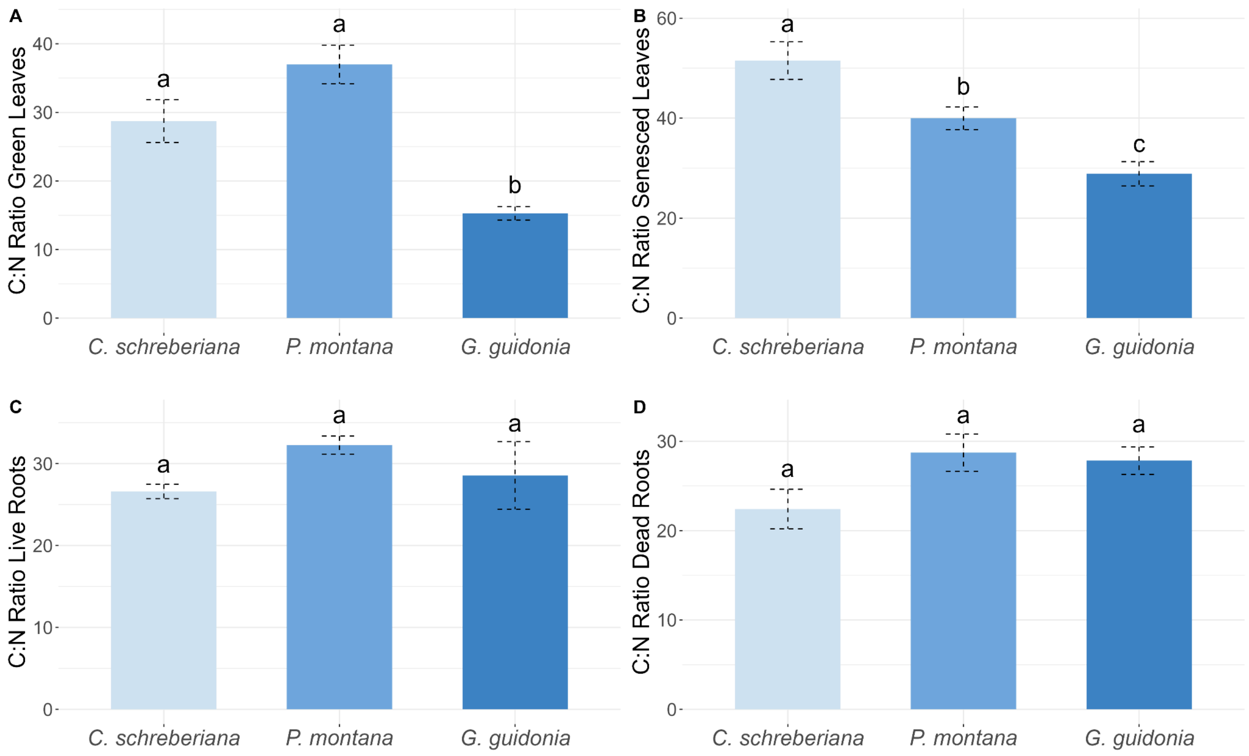

Figure 5. C:N ratio in the roots and leaves of each species based on their status when collected (green or senesced for leaves; live or dead for roots). Error bars indicate standard error.

G. guidonia had a significantly higher C:N ratio in green leaves (15.291 ± 0.984) compared to *C. schreberiana* (28.732 ± 3.133) and *P. montana* (36.990 ± 2.817) ($p < 0.001$). *G. guidonia* also had a significantly higher C:N ratio in senesced leaves (28.859 ± 2.435) compared to *P. montana* (39.988 ± 2.274), and *P. montana* had a significantly higher C:N ratio compared to *C. schreberiana* (51.522 ± 3.751) ($p < 0.001$) (Figure 5A-B, Table 1).

There was no significant difference between the C:N ratios in live roots across species (*C. schreberiana*: 26.604 ± 0.879, *P. montana*: 32.258 ± 1.100, *G. guidonia*: 28.555 ± 4.121, $p = 0.307$), or between dead roots across species (*C. schreberiana*: 22.410 ± 2.213, *P. montana*: 28.727 ± 2.087, *G. guidonia*: 27.836 ± 1.540, $p = 0.087$) (Figure 5C-D, Table 1).

Soil nutrient and microbial biomass results

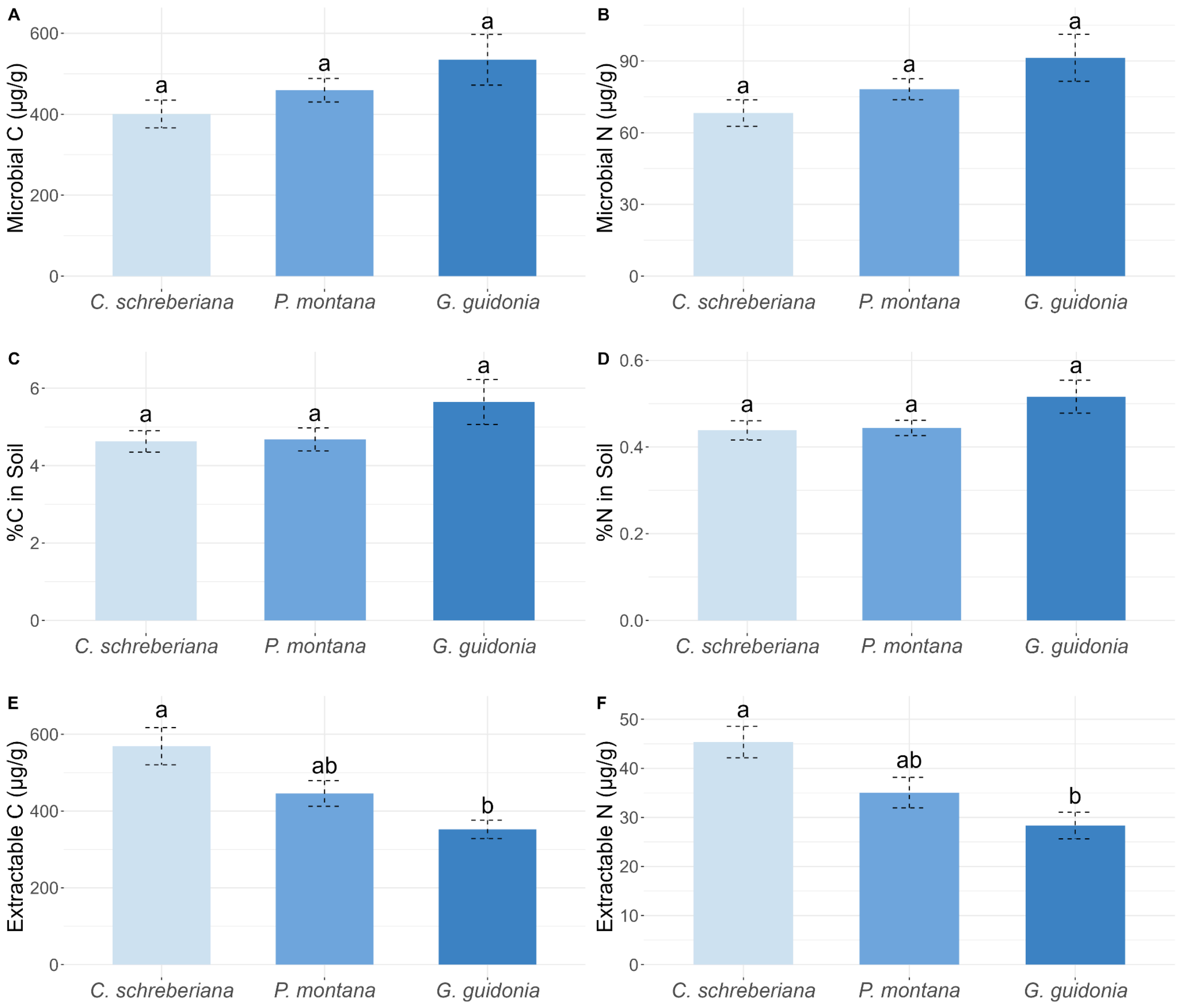

Figure 6. Microbial carbon (A) and nitrogen (B), soil %C (C) and %N (D), and extractable soil carbon (E) and nitrogen (D) from samples collected at the base of each tree. Error bars indicate standard error.

There were no significant differences across species in %C or %N in soil, or in C or N in microbial biomass (Figure 6A-B, Table 1). However, there was a non-significant pattern worth noting: soils around *G. guidonia* individuals consistently reported higher soil %C, soil %N, and C and N in microbial biomass. Specifically, *G. guidonia* had the highest microbial C (534.573 ± 62.688 µg/g dry soil) and N (91.344 ± 9.820 µg/g dry soil), followed by *P. montana* (C: 459.420 ± 29.148 µg/g dry soil; N: 78.181 ± 4.371 µg/g dry soil). *C. schreberiana* had the least microbial C and N (C: 400.506 ± 34.229 µg/g dry soil; N: 68.238 ± 5.550 µg/g dry soil). There was no significant difference in soil %C (*C. schreberiana*: 4.626 ± 0.278%, *P. montana*: 4.678 ± 0.297%, *G. guidonia*: 5.644 ± 0.582%) or in soil %N (*C. schreberiana*: 0.438 ± 0.022%, *P.*

montana: 0.444 ± 0.018%, *G. guidonia*: 0.516 ± 0.038%) between species (Figure 6C-D, Table 1).

G. guidonia exhibited the reverse pattern for soil extractable C and N - there was significantly less soil extractable C and N in the soils adjacent to *G. guidonia* individuals (Figure 6E-F, Table 1). *G. guidonia* had significantly lower extractable C (352.323 ± 23.995 µg/g dry soil) compared to *C. schreberiana* (568.883 ± 48.402 µg/g dry soil) ($p < 0.01$). There was no significant difference between *P. montana* and the other species in the amount of extractable C present (445.758 ± 33.347 µg/g dry soil) (*C. schreberiana*: $p = 0.083$, *G. guidonia*: $p = 0.21$) (Figure 6E, Table 1). *C. schreberiana* also had a significantly higher amount of extractable N (45.353 ± 3.218 µg/g dry soil) compared to *G. guidonia* (28.343 ± 2.724 µg/g dry soil) ($p < 0.01$). There was no significant difference between *P. montana* and the other species in terms of the amount of extractable N present (35.040 ± 3.113 µg/g dry soil) (*C. schreberiana*: $p = 0.078$, *G. guidonia*: $p = 0.297$) (Figure 6F, Table 1).

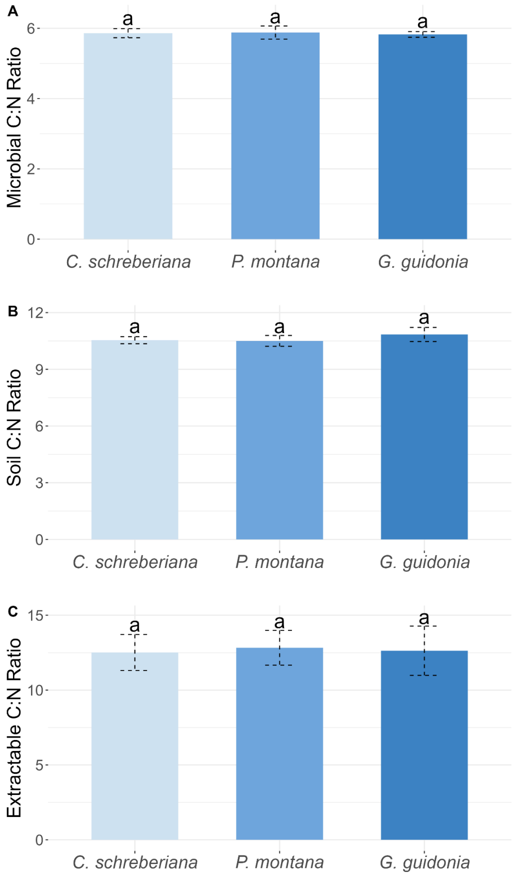

Figure 7. Microbial C:N ratio (A), soil C:N ratio (B), and extractable soil C:N ratio (C) from samples collected at the base of each tree. Error bars indicate standard error.

There was no significant difference in the microbial C:N ratio between species (*C. schreberiana*: 5.862 ± 0.128, *P. montana*: 5.880 ± 0.187, *G. guidonia*: 5.827 ± 0.081, $p = 0.963$). There was also no significant difference in the soil C:N ratio (*C. schreberiana*: 10.539 ± 0.187, *P. montana*: 10.504 ± 0.287, *G. guidonia*: 10.842 ± 0.373, $p = 0.677$) or the extractable soil C:N ratio (*C. schreberiana*: 12.508 ± 1.204, *P. montana*: 12.826 ± 1.164, *G. guidonia*: 12.628 ± 1.645, $p = 0.932$) between species (Figure 7, Table 1).

Trace gas results

There was no significant difference in soil CO_2 fluxes between species (*C. schreberiana*: 5.213 ± 0.671 $\mu mol\ m^{-2}s^{-1}$, *P. montana*: 6.481 ± 0.799 $\mu mol\ m^{-2}s^{-1}$, *G. guidonia*: 5.730 ± 0.426 $\mu mol\ m^{-2}s^{-1}$, $p = 0.391$) (Figure 8A, Table 1), while there were significant differences across species for soil CH_4 flux rates. *P. montana* had the highest soil CH_4 flux of the three species (-0.052 ± 0.155 nmol $m^{-2}s^{-1}$, $p < 0.01$). *C. schreberiana* and *G. guidonia* exhibited similar associated CH_4 fluxes, with no significant difference between the two being found (*C. schreberiana*: -0.608 ± 0.123 nmol $m^{-2}s^{-1}$, *G. guidonia*: -0.685 ± 0.041 nmol $m^{-2}s^{-1}$, $p = 0.887$) (Figure 8B, Table 1).

The relatively low soil CH_4 uptake rate associated with *P. montana* was driven by soil gas flux rates from a single *P. montana* individual. However, even when gas sampling data from that individual was removed from the dataset, *P. montana* still had significantly higher CH_4 flux compared to *G. guidonia* (-0.335 ± 0.032 nmol $m^{-2}s^{-1}$ for *P. montana* without the outlier individual compared to -0.685 ± 0.041 nmol $m^{-2}s^{-1}$ for *G. guidonia*) ($p < 0.05$) (Figure 9, Table 1). However, in the *sans* outlier *P. montana* individual analysis, *C. schreberiana's* CH_4 flux (-0.608 ± 0.123 nmol $m^{-2}s^{-1}$) did not differ significantly from either *G. guidonia* ($p = 0.772$) or *P. montana* ($p = 0.067$). In addition, the flux rates from the outlier *P. montana* do not feature any methodological or data concerns; for that reason, I maintain the full dataset in the analyses below.

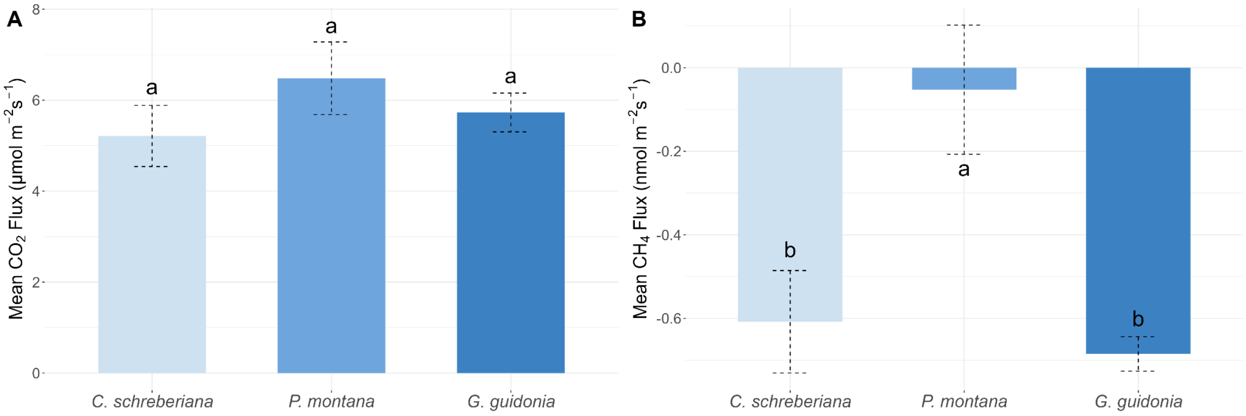

Figure 8. Average (A) CO_2 and (B) CH_4 soil gas fluxes over a two minute collection period for each tree species. Error bars indicate standard error.

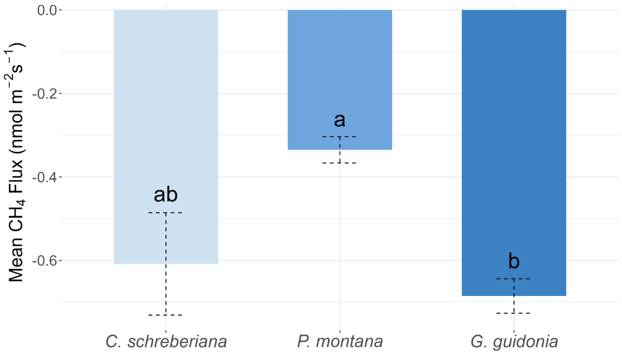

Figure 9. Average CH_4 gas fluxes over a two minute collection period for each tree species, excluding the *P. montana* that was an outlier. Error bars indicate standard error.

Fig.	Mean ± SE	*C. schreberiana*	*P. montana*	*G. guidonia*	ANOVA
3A	**%C green leaves**	**44.345 ± 0.197^{a}**	**44.909 ± 0.177^{a}**	**48.189 ± 0.377^{b}**	**$p < 0.00001$**
3B	**%C senesced leaves**	**46.736 ± 0.155^{a}**	**45.878 ± 0.287^{a}**	**49.722 ± 0.300^{b}**	**$p < 0.00001$**
3C	%C live roots	40.608 ± 1.213	40.849 ± 0.809	40.637 ± 1.623	p = 0.989
3D	%C dead roots	41.137 ± 1.02	40.910 ± 1.338	41.208 ± 1.068	p = 0.982
4A	**%N green leaves**	**1.631 ± 0.206^{a}**	**1.243 ± 0.096^{a}**	**3.194 ± 0.166^{b}**	**$p < 0.00001$**
4B	**%N senesced leaves**	**0.921 ± 0.067^{a}**	**1.162 ± 0.066^{a}**	**1.755 ± 0.128^{b}**	**$p < 0.001$**
4C	%N live roots	1.535 ± 0.070	1.272 ± 0.050	1.499 ± 0.138	p = 0.143
4D	%N dead roots	1.915 ± 0.206	1.442 ± 0.070	1.498 ± 0.086	p = 0.057
5A	**C:N green leaves**	**28.732 ± 3.133^{a}**	**36.990 ± 2.817^{a}**	**15.291 ± 0.984^{b}**	**$p < 0.001$**
5B	**C:N senesced leaves**	**51.522 ± 3.751^{a}**	**39.988 ± 2.274^{b}**	**28.859 ± 2.435^{c}**	**$p < 0.001$**
5C	C:N live roots	26.604 ± 0.879	32.258 ± 1.100	28.555 ± 4.121	p = 0.307
5D	C:N dead roots	22.410 ± 2.213	28.727 ± 2.087	27.836 ± 1.540	p = 0.087
6A	Microbial C	400.506 ± 34.229	459.420 ± 29.148	534.573 ± 62.688	p = 0.145
6B	Microbial N	68.238 ± 5.550	78.181 ± 4.371	91.344 ± 9.820	p = 0.104
6C	%C soil	4.626 ± 0.278	4.678 ± 0.297	5.644 ± 0.582	p = 0.184
6D	%N soil	0.438 ± 0.022	0.444 ± 0.018	0.516 ± 0.038	p = 0..124
6E	**Extractable soil C**	**568.883 ± 48.402^{a}**	**445.758 ± 33.347^{ab}**	**352.323 ± 23.995^{b}**	**$p < 0.01$**
6F	**Extractable soil N**	**45.353 ± 3.218^{a}**	**35.040 ± 3.113^{ab}**	**28.343 ± 2.724^{b}**	**$p < 0.01$**
7A	Microbial C:N	5.862 ± 0.128	5.880 ± 0.187	5.827 ± 0.081	p = 0.963
7B	Soil C:N	10.539 ± 0.187	10.504 ± 0.287	10.842 ± 0.373	p = 0.677
7C	Extractable soil C:N	12.508 ± 1.204	12.826 ± 1.164	12.628 ± 1.645	p = 0.932
8A	CO_2 flux	5.213 ± 0.671	6.481 ± 0.799	5.730 ± 0.426	p = 0.391
8B	**CH_4 flux**	**-0.608 ± 0.123^{b}**	**-0.052 ± 0.155^{a}**	**-0.685 ± 0.041^{b}**	**$p < 0.001$**
9	**CH_4 flux (no outlier)**	**-0.608 ± 0.123^{ab}**	**-0.335 ± 0.032^{a}**	**-0.685 ± 0.041^{b}**	**$p < 0.05$**

Table 1**.** Table containing all ANOVA results. Superscripts indicate results of a TukeyHSD test, which was only conducted if the ANOVA result was significant. ANOVAs where $p < 0.05$ are highlighted and bolded. All values are rounded to three decimal places.

Links between biogeochemical pools and fluxes

Linear regression was used to test the relationships shown in the hypothesis flowchart (Figure 1).

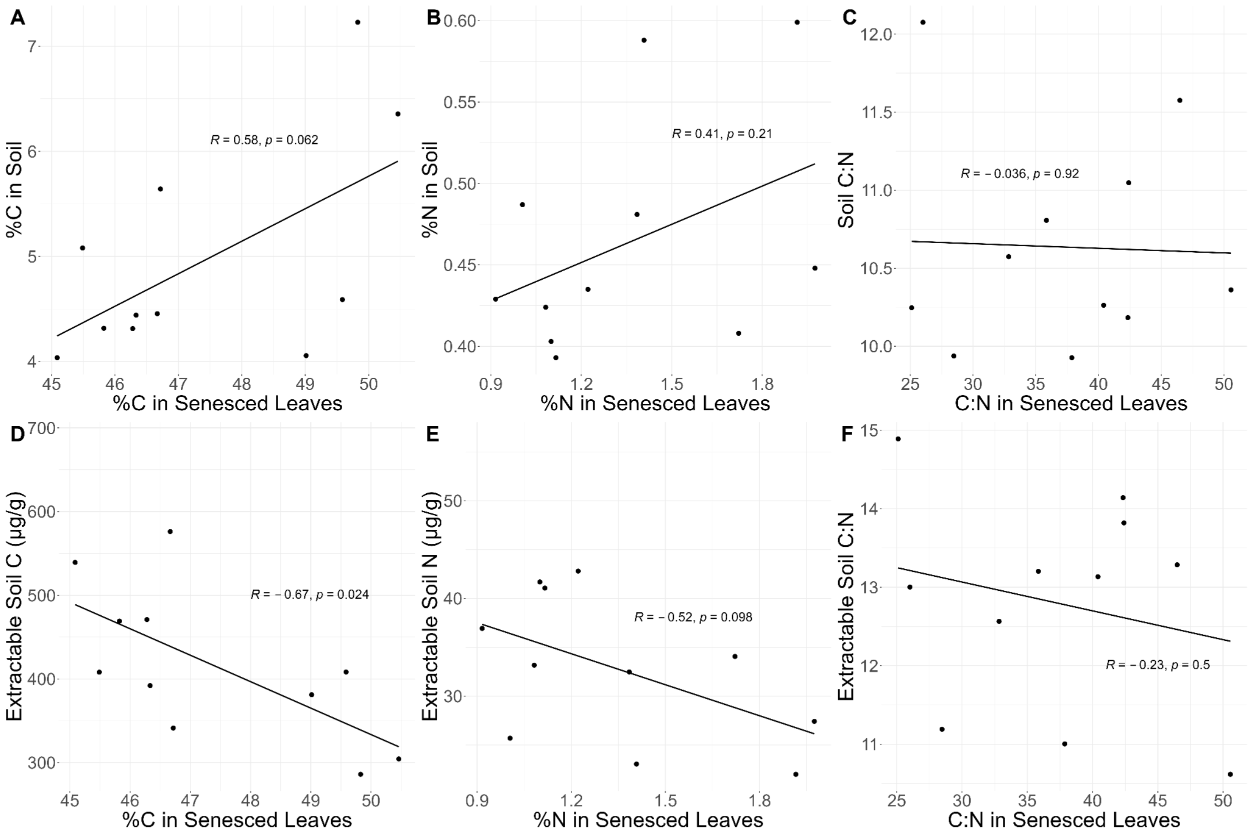

Figure 10. Linear regressions comparing bulk (A-C) and extractable (D-F) soil nutrients to senesced leaf nutrients nearby of the same tree species.

Senesced leaf nutrients is the main source of soil nutrient inputs in forests (Hobbie 1992, Silver 1994, Aerts & Chapin 1999, Uriarte et al. 2015). Percent C in senesced leaves was a significant predictor of extractable soil C ($p < 0.05$, $R^2 = 0.449$), demonstrating a negative relationship between the two (cor = -0.67, slope = -31.60) (Figure 10D, Table 2). Percent N in senesced leaves was negatively correlated with extractable soil N (cor = -0.524, slope = -10.577), but this relationship was not significant ($p = 0.098$, $R^2 = 0.275$) (Figure 10E, Table 2). Though also not significant ($p = 0.504$, $R^2 = 0.051$), the C:N ratio in senesced leaves was also negatively correlated with the extractable soil C:N ratio (cor = -0.226, slope = -0.037) (Figure 10F, Table 2).

Percent C in bulk soil was positively correlated with %C in senesced leaves (cor = 0.579, slope = 0.309) (Figure 10A, Table 2). Similarly, %N in bulk soil was positively correlated with %N in senesced leaves (cor = 0.408, slope = 0.078) (Figure 10B, Table 2). However, neither of these relationships were significant (%C: $p = 0.062$, $R^2 = 0.335$; %N: $p = 0.213$, $R^2 = 0.167$). The C:N ratio of bulk soil was slightly negatively correlated with the C:N ratio of senesced leaves (cor = -0.036, slope = -0.003), though this relationship was also not significant ($p = 0.916$, $R^2 =$

0.001) (Figure 10C, Table 2).

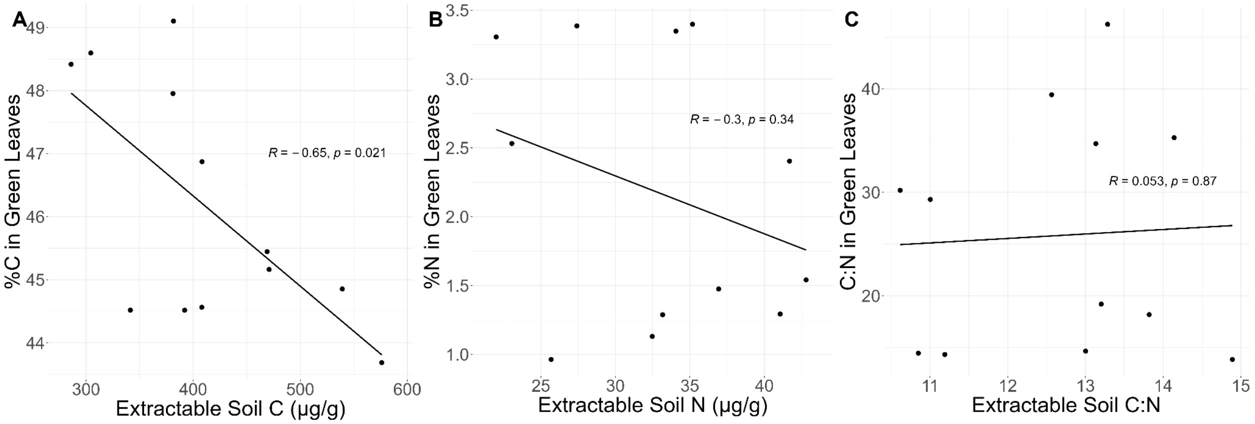

Figure 11. Linear regressions comparing nutrients in green leaves and the extractable soil nutrients nearby.

Regression 11A was significant ($p < 0.05$, $R^2 = 0.426$), showing that extractable soil C significantly predicted the %C in green leaves (cor = -0.652, slope = -0.014) (Table 2). Regression 11B was not significant ($p = 0.337$, $R^2 = 0.092$), but showed that %N in green leaves was negatively correlated with extractable soil N (cor = -0.304, slope = -0.042) (Table 2). Regression 11C was also not significant ($p = 0.869$, $R^2 = 0.003$), but showed that the C:N ratio of green leaves was slightly positively correlated with the C:N ratio of the extractable soil (cor = 0.053, slope = 0.432) (Table 2).

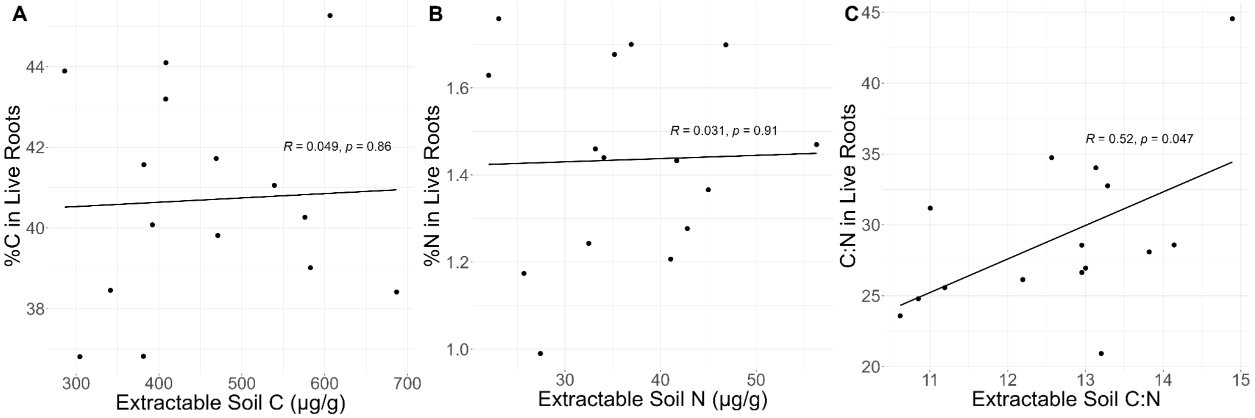

Figure 12. Linear regressions comparing live root nutrients to extractable soil nutrients collected from the same soil core.

%C of live roots was slightly positively correlated with extractable soil C (cor = 0.049, slope = 0.001), though this relationship was not significant ($p = 0.863$, $R^2 = 0.002$) (Figure 12A,

Table 2). Similarly, the regression between %N in live roots and the extractable soil N was not significant ($p = 0.912$, $R^2 < 0.001$), but they were slightly positively correlated (cor = 0.031, slope = 0.0007) (Figure 12B, Table 2). The C:N ratio of extractable soil significantly predicted the C:N ratio of the live roots ($p < 0.05$, $R^2 = 0.270$), demonstrating a positive relationship between the two (cor = 0.520, slope = 2.366) (Figure 12C, Table 2).

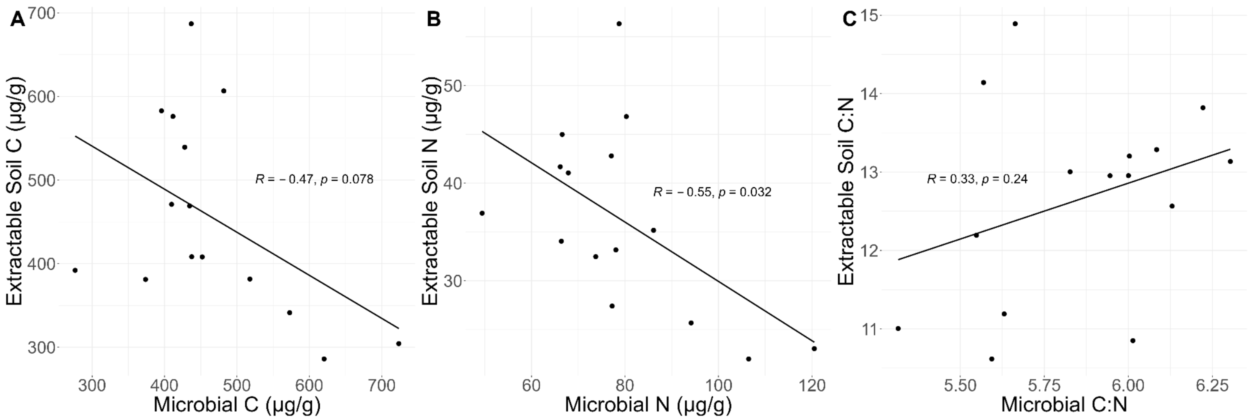

Figure 13. Linear regressions comparing extractable soil nutrients to microbial nutrients. Microbial nutrients were included within the extractable soil nutrients.

Microbial N significantly predicted the extractable soil N ($p < 0.05$, $R^2 = 0.307$), showing a negative relationship between the two variables (cor = -0.554, slope = -0.304) (Figure 13B, Table 2). However, microbial C was not a significant predictor of extractable soil C ($p = 0.078$, $R^2 = 0.219$), though they were also negatively correlated (cor = -0.468, slope = -0.515) (Figure 13A, Table 2). The extractable soil C:N ratio was positively correlated with the microbial C:N ratio (cor = 0.326, slope = 1.425), but this relationship was not significant ($p = 0.236$, $R^2 = 0.106$) (Figure 13C, Table 2).

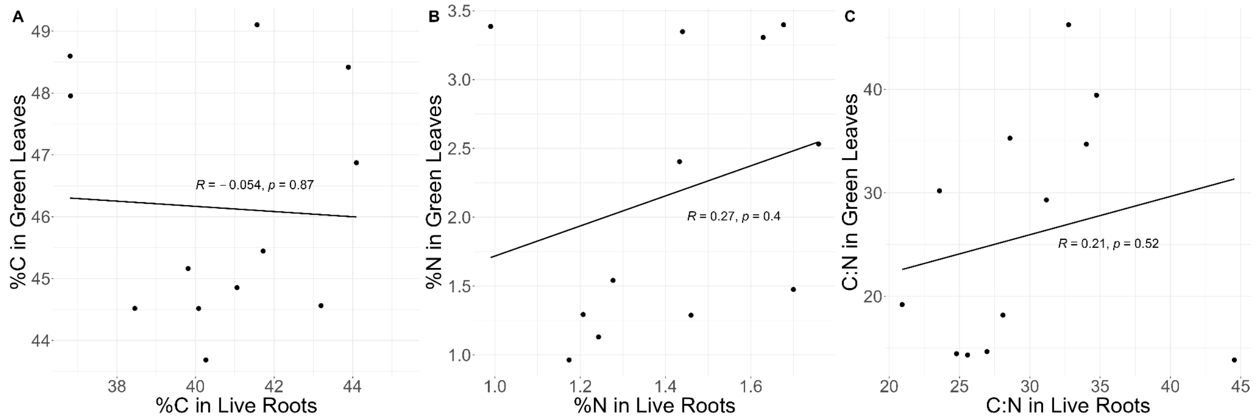

Figure 14. Linear regressions comparing nutrients in green leaves to nutrients in live roots.

Soil nutrients can drive plant tissue stoichiometry (Davidon et al. 2007). Percent C in green leaves was slightly negatively correlated with %C in live roots (cor = -0.054, slope = -0.042), though this relationship was not significant (p = 0.868, R^2 = 0.003) (Figure 14A, Table 2). %N in green leaves was positively correlated with %N in live roots (cor = 0.267, slope = 1.092), though this relationship was also not significant (p = 0.401, R^2 = 0.072) (Figure 14B, Table 2). Similarly, the regression between the C:N ratio of green leaves and the C:N ratio of live roots was not significant (p = 0.521, R^2 = 0.042), though they were positively correlated (cor = 0.206, slope = 0.370) (Figure 14C, Table 2).

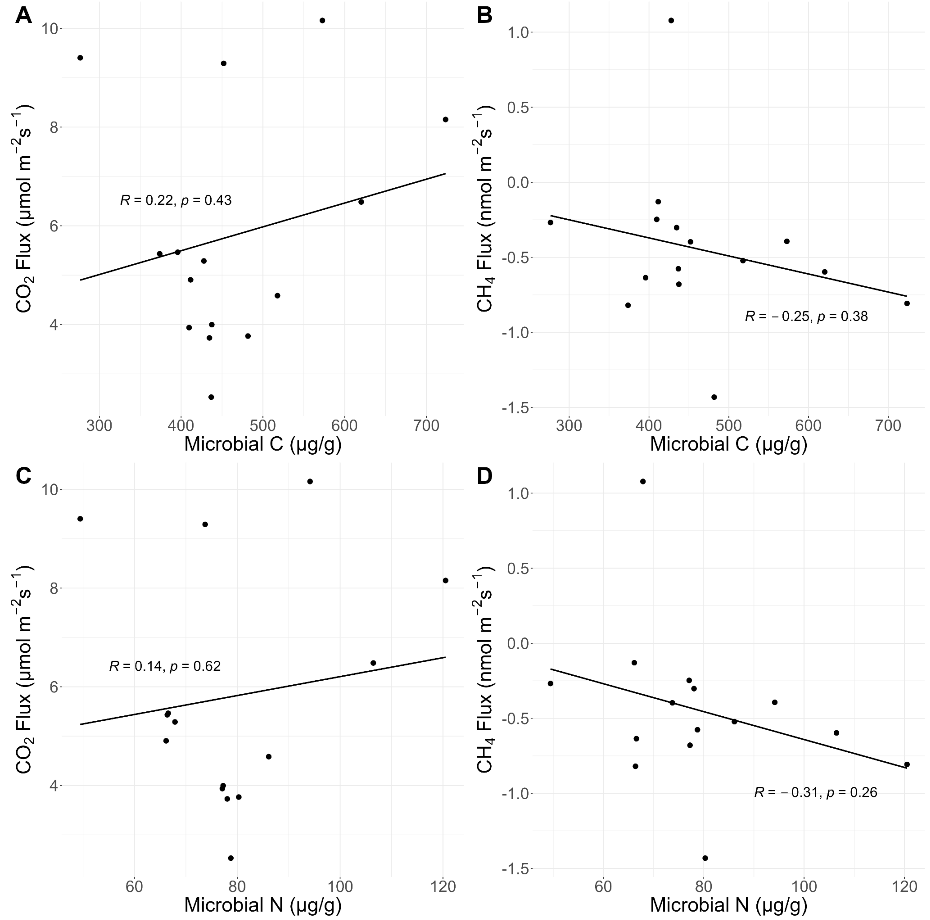

Figure 15. Linear regressions comparing CO_2 and CH_4 fluxes to the amount of microbial C and N found in the soil at that location. Each CO_2 or CH_4 data point is the average of each tree's gas measurements (three measurements per tree).

The soil microbial community is a major contributor to soil gas fluxes through their metabolic activity (Oertel et al. 2016). Microbial C was positively correlated with CO_2 flux (cor = 0.22, slope = 0.005) and negatively correlated with CH_4 flux (cor = -0.247, slope = -0.001), though neither of these relationships were significant (FCO_2: p = 0.43, R^2 = 0.049; FCH_4: p = 0.365, R^2 = 0.061) (Figures 15A-B, Table 2). Similarly, microbial N was positively correlated with CO_2 flux (cor = 0.141, slope = 0.019) and negatively correlated with CH_4 flux (cor = -0.308, slope = -0.009), but these relationships were not significant (FCO_2: p = 0.616, R^2 = 0.012; FCH_4: p = 0.265, R^2 = 0.095) (Figure 15C-D, Table 2).

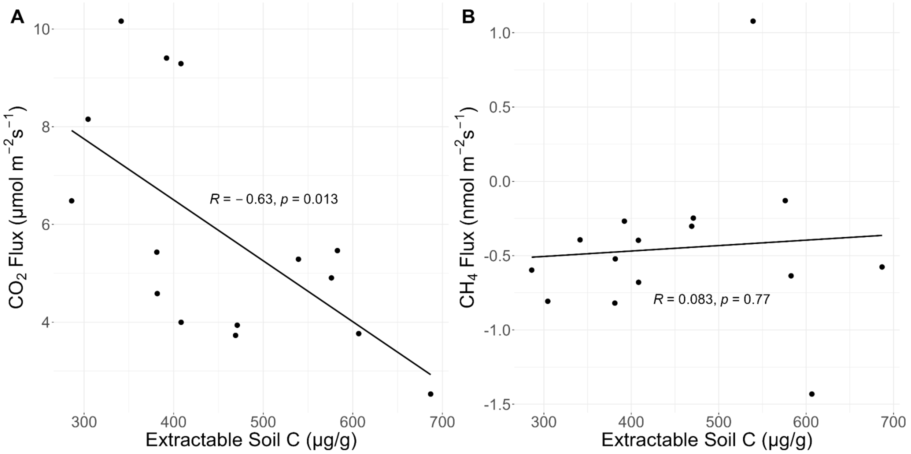

Figure 16. Linear regressions comparing CO_2 (A) and CH_4 (B) fluxes to the amount of extractable C found in the soil at that location. Each CO_2 or CH_4 data point is the average of each tree's gas measurements (three measurements per tree).

There was a significant negative relationship between CO_2 flux and extractable soil C ($p < 0.05$, $R^2 = 0.392$, cor = -0.626, slope = -0.013) (Figure 16A, Table 2). CH_4 flux and extractable soil C were slightly positively correlated (cor = 0.083, slope = 0.0004), though this relationship was not significant ($p = 0.77$, $R^2 = 0.007$) (Figure 16B, Table 2).

The following linear regressions are not part of the hypothesis flowchart, but involve soil moisture, a known factor impacting soil gas fluxes.

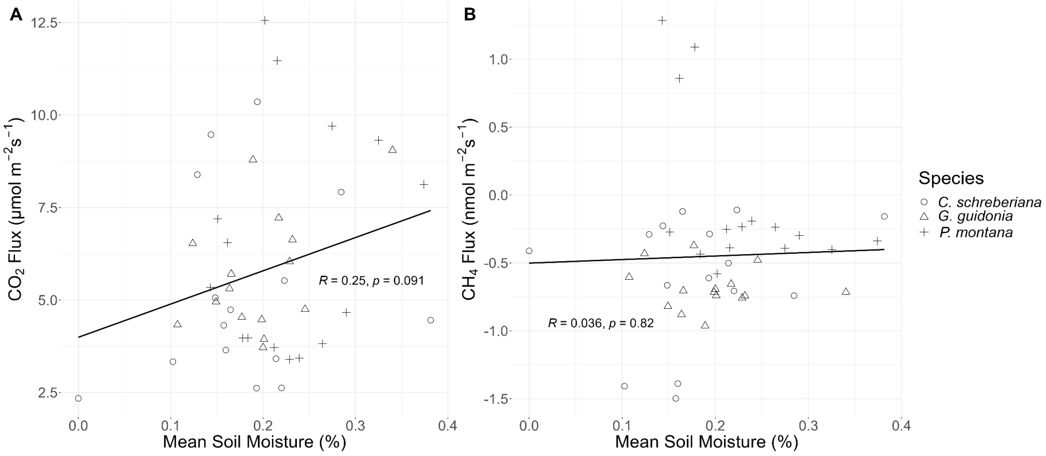

Figure 17. Linear regressions comparing soil CO_2 (A) and CH_4 (B) fluxes to the mean percent soil moisture at that location. Soil moisture data was collected with a Stevens HydraProbe. The species associated with each data point is represented by shape, and each tree is represented by three data points (one for each measurement).

CO_2 flux was positively correlated with percent soil moisture (cor = 0.255, slope =

8.984), though this relationship was not significant ($p = 0.091$, $R^2 = 0.065$) (Figure 17A, Table 2). There was no strong relationship between percent soil moisture and CH_4 flux ($p = 0.817$, $R^2 = 0.001$), though they were slightly positively correlated with one another (cor = 0.036, slope = 0.261) (Figure 17B, Table 2).

Fig.	Linear Regression	Corr.	Slope	R^2	p-value
10A	**%C soil vs. %C senesced leaves**	**0.579**	**0.309**	**0.335**	**0.062**
10B	%N soil vs. %N senesced leaves	0.408	0.078	0.167	0.213
10C	C:N soil vs. C:N senesced leaves	-0.036	-0.003	0.001	0.916
10D	**Extractable soil C vs. %C senesced leaves**	**-0.67**	**-31.60**	**0.449**	**< 0.05**
10E	**Extractable soil N vs. %N senesced leaves**	**-0.524**	**-10.577**	**0.275**	**0.098**
10F	Extractable soil C:N vs. C:N senesced leaves	-0.226	-0.037	0.051	0.504
11A	**%C green leaves vs. extractable soil C**	**-0.652**	**-0.014**	**0.426**	**< 0.05**
11B	%N green leaves vs. extractable soil N	-0.304	-0.042	0.092	0.337
11C	C:N green leaves vs. extractable soil C:N	0.053	0.432	0.003	0.869
12A	%C live roots vs. extractable soil C	0.049	0.001	0.002	0.863
12B	%N live roots vs. extractable soil N	0.031	0.001	0.000	0.912
12C	**C:N live roots vs. extractable soil C:N**	**0.520**	**2.366**	**0.270**	**< 0.05**
13A	**Extractable soil C vs. microbial C**	**-0.468**	**-0.515**	**0.219**	**0.078**
13B	**Extractable soil N vs. microbial N**	**-0.554**	**-0.304**	**0.307**	**< 0.05**
13C	Extractable soil C:N vs. microbial C:N	0.326	1.425	0.106	0.236
14A	%C green leaves vs. %C live roots	-0.054	-0.042	0.003	0.868
14B	%N green leaves vs. %N live roots	0.267	1.092	0.072	0.401
14C	C:N green leaves vs. C:N live roots	0.206	0.370	0.042	0.521
15A	FCO_2 vs. microbial C	0.220	0.005	0.049	0.430
15B	FCH_4 vs. microbial C	-0.247	-0.001	0.061	0.365
15C	FCO_2 vs. microbial N	0.141	0.019	0.012	0.616
15D	FCH_4 vs. microbial N	-0.308	-0.009	0.095	0.265
16A	**FCO_2 vs. extractable soil C**	**-0.626**	**-0.013**	**0.392**	**< 0.05**
16B	FCH_4 vs. extractable soil C	0.083	0.000	0.007	0.770
17A	**FCO_2 vs. soil moisture**	**0.255**	**8.984**	**0.065**	**0.091**
17B	FCH_4 vs. soil moisture	0.036	0.261	0.001	0.817

Table 2. Table containing all linear regression results. Regressions where $p < 0.01$ are highlighted and bolded. All values are rounded to three decimal places.

Discussion

Spheres of influence: litter and soil chemistry

The link between individual trees and nearby soil chemistry is well attested to in the scientific literature (Zinke 1962, Uriarte et al. 2015, Reed et al. 2008), and is supported by my data as well. I found a strong positive correlation between litter (senesced leaves) %C and soil %C (corr = 0.579, $p < 0.10$) (Figure 10A, Table 2). This trend is broadly attributed to litter being the primary nutrient input for soils (Silver 1994, Uriarte et al. 2015). My results demonstrate that there are clear differences in nutrient cycling between tree species exhibiting different successional strategies, especially with regard to litter and soil nutrients. The early successional *C. schreberiana* and secondary *P. montana* both had significantly less %C and %N in their leaves compared to the late successional *G. guidonia* (Figures 3B, 4B, Table 1). These results suggest that a shift in species composition that favors earlier successional species may result in significantly less C and N in leaf litter, and thus likely a noticeable decrease in the rate of C and N re-entering soil. *G. guidonia* leaves also had significantly lower C:N ratios compared to the other two species (Figure 5B, Table 1), suggesting that litter from *G. guidonia* is not only more nutrient rich, but also returns those nutrients to the soil faster via decomposition (Zhang & Zak 1995, Xuluc-Tolosa et al. 2003). However, it is worth noting that I did not find a significant relationship between litter and soil C:N ratios (bulk soil: $p = 0.92$, extractable: $p = 0.504$) (Figure 10C, F), which seems atypical (Uriarte et al. 2015). A shift away from *G. guidonia* and similar species and towards early successional species like *C. schreberiana* could thus impact not only the amount of nutrients being cycled from the canopy back into the soil, but also the rate at which nutrients are able to re-enter the soil.

Factors influencing extractable soil nutrients

Extractable soil nutrients had a stronger negative relationship with senesced leaf nutrients compared to nutrients from green leaves (Figures 10-11), which contradicted my hypothesis that extractable soil nutrients and green leaf nutrients would be highly correlated due to trees extracting nutrients from the soil and incorporating them into their green foliage (Figure 1). I found that %C in green leaves was strongly negatively correlated with extractable soil C (corr = -0.652, $p < 0.05$), however this relationship did not hold true for N ($p = 0.337$) (Figures

11A-B, Table 2). Contrary to my predictions, the relationship between extractable and leaf nutrients was actually stronger for senesced leaves, though it was still negative (C: corr = -0.670, $p < 0.05$. N: corr = -0.524, $p < 0.10$) (Figures 10D-E, Table 2). While I expected there to be a relationship between senesced litter and extractable soil nutrients, I did not expect the relationship to be negative. It is possible that, because this is a tropical ecosystem, N is not a limiting nutrient in this system, which may result in litter and soil N becoming decoupled (Davidson et al. 2007, Wood et al. 2011, Tully et al. 2013, Raich et al. 2014). Another factor in extractable soil nutrients was the live root C:N ratio, which was significantly correlated with the extractable soil C:N ratio (corr = 0.520, $p < 0.05$) (Figure 12C, Table 2). Despite this, neither the %C nor %N in live roots were significantly correlated with extractable C or N, or with any other tested variable for that matter (Figures 12A-B, Table 2).

Despite overall soil %C and %N being the same across all three species, extractable soil C and N significantly differed between the early and late successional species. The early successional *C. schreberiana* had significantly more extractable C and N compared to the late successional *G. guidonia*, while the secondary *P. montana* did not significantly differ from either of the other two (Figure 6E-F, Table 1). This is somewhat surprising as *G. guidonia* had the lowest leaf C:N ratios, suggesting faster decomposition rates, and the highest leaf %C and %N out of the three species. It is generally understood that faster growing, early successional species, such as *C. schreberiana*, must take in larger amounts of nutrients compared to slower growing species, such as *G. guidonia* (Bazzaz 1979, Bazzaz & Pickett 1980, Hobbie 1992, Aerts & Chaplin 1999). Due to this, I expected to find the extractable soil nutrients near *C. schreberiana* to be less than near *G. guidonia*. The senesced leaf C:N ratio results also conflict with much of the current literature, which finds that fast growing species cycle nutrients faster than slower growing ones, though most of these studies compare between high and low nutrient ecosystems rather than between species within the same ecosystem (Hobbie 1992, Aerts & Chaplin 1999). There are several possible explanations, including that trees may be taking in extractable nutrients to build and maintain tissues, including leaves, resulting in less extractable nutrients being left in the soil when more nutrients are present in leaves. Additional factors potentially influencing my results include the age of the individual trees sampled in this study and differences in total litter mass contributed to the forest floor litter mix between species. The *C. schreberiana* included in this study are likely much younger than the *G. guidonia*, as most of them originated at the site post-Hurricane Maria in 2017. As a result, the soil near *C. schreberiana* individuals has had less time to be visibly influenced by its litter stoichiometry compared to soil near *G. guidonia* individuals. There is also a difference between the proportion of N and C in a species' litter and the actual bulk amount of those nutrients present, and the latter is likely more important for soil nutrients. I used leaf samples of roughly equivalent biomass for each species, so I do not actually have a measurement of bulk litter nutrients associated with each tree. It is also worth noting that the litter from *P. montana* (and *C. schreberiana* as well, though to a lesser extent) often persists in the canopy for extended periods of time post-senescence before reaching the ground. This impacts the decomposition rate of the litter and the rate at which litter nutrients can re-enter the soil or be broken down by soil microbes.

Microbial nutrients and greenhouse gas fluxes

Despite the microbial community widely being considered the primary source of soil greenhouse gas fluxes (Oertel et al. 2016), neither microbial C nor N was found to have a significant relationship with either of the measured trace gas fluxes (CO_2 and CH_4) (Figure 15A-D, Table 12). The only variables found to have significant relationships with microbial nutrients were negative relationships with extractable soil C and N (C: corr = -0.468, $p < 0.10$; N: corr = -0.554, $p < 0.05$) (Figure 13A-B, Table 2). When there are more microbes in the soil, they may consume more extractable nutrients, resulting in there being less extractable nutrients left in the soil.

CH_4 is of particular interest for climate change models due to its role as an especially potent greenhouse gas, but there is limited data characterizing the relationship between tree species and nearby soil CH_4 uptake in tropical systems (Quebbeman et al. 2021). My results show that there are significant differences in soil CH_4 uptake associated with different species, and that some species are associated with significantly higher CH_4 fluxes than others (Figure 8B, Table 1). Of particular note was the species *P. montana*, which not only was associated with lower CH_4 uptake across individuals, but also included the only tree in the entire experiment with a positive CH_4 flux (Figures 9, 17, Table 1). Community composition data was collected by identifying the species of all individuals with a diameter at breast height (DBH) greater than 1 cm located within a 1 m radius of each soil collar. There were no trees above 1 cm DBH in the proximity of the outlier tree. Due to the small sample size, it is unclear whether it is common for soil near the base of *P. montana* to be releasing rather than taking in CH_4, or if the consistently positive CH_4 flux in that location was due to other factors. Regardless, even when excluding the outlier, *P. montana* was associated with significantly lower CH_4 intake by soil than the other two species. *P. montana* has proliferated in various parts of the LEF, including in the Luquillo Forest Dynamics Plots where the species makes up 22% of total stems and 23% of the total basal area (Chatzopoulos et al. 2024). My results suggest that areas dominated by *P. montana* in place of other tree species may be significantly less effective at taking in CH_4, a potent greenhouse gas.

There are other known factors influencing CH_4 and CO_2 soil emissions, in particular soil moisture and soil nutrients. I found that CH_4 flux was not significantly impacted by soil moisture ($p = 0.817$) (Figure 17B, Table 2). This is in conflict with much of the existing literature, which strongly links CH_4 flux with soil moisture (Oertel et al. 2016, Bezyk et al. 2023). Despite the results of this experiment, I am still confident that, broadly, soil moisture is a major driving factor behind spatial and temporal dynamics in soil CH_4 emissions. This experiment found only a small range of soil moisture variation at the sampled locations, and as a result soil moisture may not have been a significant factor for soil CH_4 flux on the scale of this particular experiment.

Despite this small range of soil moisture, soil CO_2 emissions were still significantly correlated with soil moisture, though this correlation was not very strong ($p < 0.1$, corr = 0.255) (Figure 17A, Table 2). Soil CO_2 flux was strongly negatively correlated with extractable soil C (corr = -0.626, $p < 0.05$) (Figure 16A, Table 2). Both of these results are in line with existing literature (Pei et al. 2021, Bezyk et al. 2023). One possible explanation for these results is that low soil moisture results in non-optimal conditions for microbial activity, resulting in lower CO_2 flux and less extractable C being utilized as quickly for microbial respiration.

Conclusion

There is significant evidence that hurricane disturbance will increase in intensity under climate change (Bender et al. 2010, Holland & Bruyère 2014, Elsner 2006). Hurricane disturbance is associated with significant community shifts in species composition, favoring early successional species that proliferate with the opening up of the forest canopy (Crow 1980, Brokaw 1998, Drew et al. 2009, Heartsill-Scalley et al. 2010). My results demonstrate clear differences in nutrient cycling between tree species with different successional life history strategies, and found clear links between leaf nutrients and soil chemistry. While this study only looked at three species, the results suggest that hurricane-mediated shifts in community composition may have a significant effect on the nutrient cycling of the entire forest, even after the immediate pulse of nutrients dissipates. As hurricane disturbance regimes shift under climate change, forest species composition will shift in response, and it will be critical to both measure the current and also model the future effects of community ecology and successional dynamics on biogeochemical cycling and ecosystem carbon storage.

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