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The missing linkages between mineral soil organic carbon and litter decomposition

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Abstract

Mineral soil carbon is an important terrestrial carbon stock, however, the pathway between leaf litter decomposition and mineral soil organic carbon is still undefined. To gain an understanding of this carbon stabilization pathway and the other drivers of mineral soil carbon I addressed the question: (1) is leaf litter decomposition correlated with soil mineral carbon pools within and across forest ecosystems? And more broadly, (2) what are the drivers of mineral soil carbon stabilization at a global and biome specific scale? I answered the first question by conducting a meta-analysis of previously collected litter decomposition data and soil organic carbon (SOC) content in the mineral layer. The data was extracted from data depositories and primary literature. My results showed that mineral SOC was not correlated with litter decomposition rates, or the amount of carbon remaining when the decomposition rate is zero (asymptotic limit value (A)), determined through linear regression. For the second question, I found different drivers of mineral SOC in temperate, tropical, and boreal biomes using structural equation modeling. Including actual evapotranspiration (AET), soil microbial carbon, soil nitrogen, soil clay content, gross primary productivity, litter decomposition rate, and the asymptotic limit value (A), I was able to explain 24.8% of the variation in SOC in the mineral layer globally. This varied in the different biomes; in the temperate biome, 69.2% of the variation in SOC in the mineral layer was explained by the same variables as above, in the boreal system 48.1% of the variation was explained excluding soil N, and in the tropics, 48.5% of the variation was explained excluding AET. Some of the most important drivers of mineral SOC include soil N and AET. However, I found no relationship between mineral SOC and litter decomposition, therefore pushing the scientific community to look at other inputs of stabilized SOC in the mineral layer, such as root inputs.

1 | Introduction

For decades, ecosystem ecologists have been fascinated with mineral soil carbon accrual and its drivers, such as leaf litter decomposition (Wiesmeier et al., 2019). As ecosystem properties or processes, soil carbon storage and decomposition are controlled by the five state factors: climate, biota (the plant species present), topography (e.g. physiographic setting), the soil parent material, and time since disturbance (Guo, Gong, Amundson, & Yu, 2006). While these large-scale drivers are well studied, the often-assumed link between leaf litter decomposition and mineral soil carbon pools is surprisingly poorly defined. This leads us to the question investigated in this study: is soil mineral carbon a function of leaf litter decomposition rates within and across ecosystems and, if not, what are the drivers of mineral soil carbon stabilization at a global and biome specific scales?

At a global scale, climate regulates mineral soil carbon content. Warmer and wetter ecosystems are characterized by high productivity and species richness. This greater species richness and plant growth allows for greater litter (and thus also carbon) input to soils (Lajtha, Bowden, & Nadelhoffer, 2014). However, there is also rapid litter decomposition as the increased temperature and wetness create an environment that allows microbes and soil fauna to thrive, while also fostering increased below and above ground growth (Kirschbaum, 1995; Zhang, Hui, Luo, & Zhou, 2008). For example, in tropical ecosystems, there is high productivity and high decomposition, so less carbon accrues in the soil; in the boreal forest, cool temperatures limit decomposition and allow carbon to build up within soils (Malhi, Baldocchi, & Jarvis, 1999). Thus, soil organic stocks are highest where the climate is cool and humid, and lowest in areas that are hot and dry (Wiesmeier et al., 2019). Yet, at more local scales, there are other known

regulators of mineral soil carbon content, such as the biotic influences of leaf litter decomposition (Liski, Perruchoud, & Karjalainen, 2002).

Plant leaves/needles and wood are deposited on the forest floor where they are mineralized by soil organisms. Some of this material is converted into microbial biomass, soil organic carbon, and humus while some is lost via respiration and leaching (Prescott, 2010). Leaf litter decomposition has been extensively studied across multiple sites and in many regions around the world (Adair et al., 2008; Cornwell et al., 2008; Powers et al., 2009; Trofymow & CIDET Working Group, 1998) and much of this work assumes that forest floor C, via decomposition processes, has a large influence on the accumulation of mineral soil C (Liski et al., 2002).

Importantly, litter quality and plant characteristics have a large influence on decomposition rates (Prescott, 2010; Zhang et al., 2008). A large study of 110 global sites found that the litter nutrient concentrations and the C:N ratio accounted for 70.2% of litter decomposition rates (Zhang et al., 2008). Illustrating the importance of litter characteristics, another study found that naturally occurring litter decomposes more quickly than transplanted, non-naturally occurring litter (Prescott, 2010). Gross primary productivity (GPP) is another metric used to quantify biotic forest characteristics and the amount of C inputs to soil C. GPP increases are considered to increase soil carbon decomposition partially due to increased temperature (Piao, Friedlingstein, Ciais, Viovy, & Demarty, 2007) and increased respiration (Litton, Raich, & Ryan, 2007).

Contrary to previously assumed relationships between litter decomposition and mineral soil carbon content, new research which explores connections between doubled litter input and resulting mineral soil carbon response, suggests that litter and soil pools of carbon may not be tightly coupled (Crow et al., 2009; Lajtha et al., 2018). In one example, doubled litter inputs over

five years did not increase bulk soil C concentrations relative to controls (Crow et al., 2009). Therefore, other variables are also important to investigate as drivers of mineral soil organic carbon content.

Soil characteristics, both biotic and biogeochemical, impact forest floor C and mineral soil C. One such characteristic is the microbial community of any particular forest. There is increasing evidence that there are large microbial carbon inputs to the stable organic matter in soils as microbial-specific compounds are found in stabilized carbon within the soil (Lützow et al., 2006). A meta-analysis working to quantify the global importance of prokaryotes identified these organisms as an important element of terrestrial soil decomposition and determined that there were a comparable number of prokaryotes in the soil as there are in the ocean (Whitman, Coleman, & Wiebe, 1998). Mineralogy also has a large influence on soil carbon storage. Clay presence in soils can influence the amount of carbon that can be sorbed due to the negative charge that clay particles have (Mayes, Heal, Brandt, Phillips, & Jardine, 2012). Indeed, across a wide array of soil types, the sorption of organic matter onto mineral surfaces is the largest determinant of soil organic carbon stock as it protects organic carbon from microbial decomposition (Wiesmeier et al., 2019). Soil nitrogen (N) also has a large influence on carbon dynamics within the soil and increased soil N tends to increase soil carbon storage (Whittinghill, Currie, Zak, Burton, & Pregitzer, 2012) and overall stabilization (Prescott, 2010).

Here, I used an extensive decomposition dataset that spans biomes from the tropics to the boreal and tundra (Figure 1) and represents 61 data points across the globe. I coupled this data with mineral soil carbon data, actual evapotranspiration (AET), soil microbial carbon biomass, soil

nitrogen, soil clay content, and gross primary productivity (GPP) to explore the relationship between forest floor C and mineral soil C and the drivers of carbon stabilization in the mineral layer of soil. I worked towards answering the question, is leaf litter decomposition correlated with soil mineral carbon pools within and across forest ecosystems? Furthermore, what are the drivers of mineral soil carbon stabilization at a global and biome specific scale? Answering this question helps to determine to what extent two pools of carbon, forest floor carbon, and mineral soil carbon, are connected to one another. To investigate the first question, I ran two regressions: one between litter decomposition rate (k) and mineral soil organic carbon, and the other between the amount of carbon remaining when the decomposition rate is zero (the limit value, A) and mineral soil organic carbon. Then, to see how other variables influence mineral soil carbon stabilization, I constructed structural equation models (SEMs) for different biomes to explore how the drivers differ in areas with varying biotic and abiotic factors. I hypothesized that there was a non-significant link between forest floor C and mineral soil C due to the increasing evidence that these two carbon pools are not correlated.

2 | Methods

2.1 Decomposition data

I combined three unique decomposition datasets: LIDET (Adair et al., 2008), CIDET (Trofymow & CIDET Working Group, 1998), and GT DEC (Powers et al., 2009), to create a global decomposition dataset. The Long-term Intersite Decomposition Experiment Team (LIDET) data set contains ten years of North and Central America decomposition data. This data was gathered from a reciprocal litterbag study that transplanted leaf litter from 26 species across 27 sites across a range of ecosystems (Figure 1). At each site, nine standard litters that cover a range of

lignin to N ratios, as well as a wildcard litter, were transplanted. Their weight was measured every year for temperate and boreal sites, and every 3-6 months in tropical locations (Adair et al., 2008). The Canadian Intersite Decomposition Experiment (CIDET) is a cross- Canadian decomposition experiment for which six years of data will be analyzed for this study. This experiment examined relationships between decay rates, substrate quality, and climate using data collected from litterbags spread across 21 Canadian sites (Figure 1). For this project, 12 different litter types were used at the different sites. For each litter type, there were multiple replicated bags of litter, and every year of data collection, one bag would be removed and weighed (Trofymow & CIDET Working Group, 1998). Representing tropical data, Global Tropical (GT Dec), is a dataset with approximately one year of data gathered from 23 tropical forests in 14 countries that measured litter decomposition (Figure 1). This work measured litter decomposition of two standardized substrates, bay leaves, and raffia, to keep the methods standardized across the globe. The litterbags were collected and weighed 1, 3, 5, 7, and 9 months after placement to determine the rate of decomposition (Powers et al., 2009). The compiled experiments from the three decomposition datasets were conducted on five different continents; however, they were spread unevenly, with 57 of 61 locations in North and South America (Figure 1). Ultimately, I used 25 sites from LIDET, 17 sites from CIDET and 19 sites from GT Dec as those were the sites I was able to compile additional data characteristics for, such as soil carbon content.

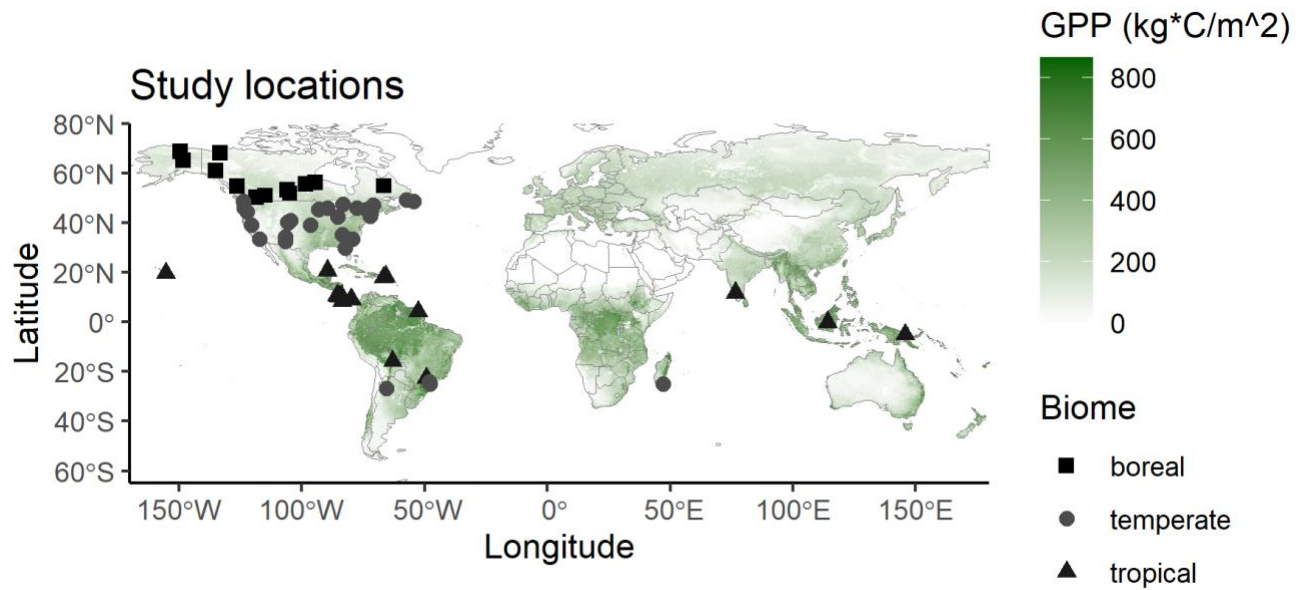


Figure 1. Map of sites indicating the locations of decomposition experiments in the CIDET, GT Dec, and LIDET datasets. Different biomes are indicated by different shapes on the map.

2.2 Soil carbon data

I paired the decomposition data from LIDET, CIDET, GT Dec (Figure 1) with mineral soil carbon data. I found soil carbon data that had the same geographical characteristics (elevation, precipitation, vegetation type, etc.) as the decomposition data and was within ± 2 latitude and longitude coordinate points from the decomposition locations. I gathered soil carbon values for each site by compiling existing data from online data archives (e.g., Oak Ridge National Laboratory’s Distributed Active Archive Center for Biogeochemical Dynamics, ORNL DAAC, <https://daac.ornl.gov/> or online Long Term Ecological Research, LTER, databases). Online databases were accessed over the internet, using google to search “location x soil carbon” to see if the data was available. If data was not available in online repositories, I compiled data from the literature using values in tables, or by requesting data from authors. To obtain data from the

literature, I began with a search in Web of Science, searching for both the location of interest and soil carbon. For papers that had data in the correct location, I extracted mineral soil carbon data as well as bulk density, soil texture information, and depth increment (if available). In datasets that had multiple soil carbon values, I extracted percent mineral soil carbon in order to be most consistent amongst sites. For sites where I couldn't find data from databases or the literature, I contacted principal investigators that manage each database, asking for soil carbon data. For one site, Port McNeill (PMC) in the CIDET dataset the soil carbon was obtained but had to be removed. It was a percent carbon outlier and I determined that it was obtained from the organic layers instead of the mineral soil, which uses different methods from my other sites.

2.2 Climatic Variables, Plant Productivity, and Soil Microbial Biomass

I extracted soil total nitrogen (gkg^{-1} , 0-15 cm) and soil clay content (0-15 cm, proportion of clay particles (<0.002 mm) in the fine earth fraction) values from SoilGrids (Hengl et al., 2017). SoilGrids has a resolution of 250m and represents recent conditions. SoilGrids uses machine learning based on global models and available soil data to make global maps of soil properties. I obtained Gross Primary Productivity (GPP) values ($\text{kg}^*\text{C}/\text{m}^2$) from MODIS's Terra Gross Primary Productivity 8-day Global dataset (Running, Mu, & Zhao, 2015). I averaged GPP values by year to obtain the mean annual GPP for 2000-2020. I used Google Earth Engine (Gorelick et al., 2017) to pull data from SoilGrids and MODIS. For climate data, I used the CHELSA (Climatologies at high resolution for the earth's land surface areas) dataset and extracted annual precipitation and temperature data from 1979 to 2013 using the 'raster' package in R (Hijams & van Etten, 2012). This data has a resolution of about 1 km (Karger et al., 2017). I then calculated actual evapotranspiration (AET) using Turc's formula (Turc, 1954):

$$\text{AET} = P / [0.09 + (P/L)^2]^{1/2}$$

where P is MAP (mm yr⁻¹), $L = 300 + 25T + 0.05T^3$, and T used to define L is MAT (°C).

Lastly, I extracted soil microbial carbon (g C/m², 0-30 cm) using ArcGIS from a compiled global dataset with 0.05-degree by 0.5-degree spatial resolution (Xu, Thornton, & Potapov, 2015).

2.3 Data Management and Analysis

To standardize the soil carbon data, I converted (when necessary) the values to percent soil organic carbon in the mineral soil layer. To convert concentration data into a percentage, the soil carbon values were multiplied by the depth increment they were taken from and the bulk density for the site. I used a dataset (ORNL DAAC) to obtain modeled bulk density values for sites that did not have that data collected. Many sites also had multiple decomposition rates, each correlated to different types of leaf litter. I used nonlinear regression with all the mass loss data at a site to fit the following decomposition model:

$$M(t) = A + (1-A)e^{-k*t}$$

Where $M(t)$ is the litter mass remaining at time, t , k is the decomposition rate per unit time and A is the asymptotic limit value, which represents an estimate of the remaining litter mass carbon that exists at each site after the fast carbon pool is decomposed. Thus, the A value represents the slow litter carbon pool, or the amount of carbon remaining when the decomposition rate is zero and k represents initial, relatively fast decomposition. I then paired the decomposition rate and limit value with the soil carbon value to construct a data frame with decomposition rate, limit value, and soil carbon value per site.

I explored the relationship between decomposition rate and soil carbon storage across ecosystem types using a regression analysis (Figure 2). To then calculate one k value for each site within each project, I used a nonlinear regression (*nlin* in R; R Core Team 2018) and fit the exponential decay equation to the proportion of initial litter mass remaining for all litter types at each of the 61 sites over time. Next, I explored the relationship between soil organic carbon in the mineral layer and litter decomposition rate by regressing the k -values obtained from the exponential decay equation (using *lm* in R) against percent mineral soil organic carbon values obtained from the literature and online data repositories. Then, to explore the relationship between the slow pool of stable carbon on the forest floor and the mineral soil organic carbon pool, I regressed A and mineral soil carbon. I used the limit value (A) to test if the relationships between stabilized mineral soil organic carbon pool and the fast (k) or the slow (A) pools of forest floor carbon differed.

Next, to examine how other variables, actual evapotranspiration (AET), soil microbial carbon (SMC30), soil nitrogen, soil clay content, gross primary productivity (GPP), litter decomposition rate (k), and the fraction of the initial litter mass with a decomposition rate of zero (the limit value, A) influenced soil organic carbon in the mineral layer, I created structural equation models (SEM) using the '*Lavaan*' package in R (Rosseel, 2012). Climate was represented by actual evapotranspiration (AET), which was calculated using site mean annual temperature (MAT) and mean annual precipitation (MAP). AET was used as the climate variable because it incorporates both precipitation and temperature, two important variables that influence decomposition and soil carbon dynamics. Soil properties included soil microbial carbon (SMC30), soil nitrogen, and soil clay content. These soil characteristics were included to incorporate an element of

mineralogy (clay content), as well as the biogeochemical characteristics of the soil (soil nitrogen). I include the microbial carbon because it might be an important contributor to the mineral soil carbon pool (Lützow et al., 2006). Gross primary productivity (GPP) was included as a forest characteristic, and the decomposition asymptotic estimate (A), or the limit value, and k was also tested. GPP represents the productivity of an ecosystem, which can include the growth of the plants and the amount of litter in the system. This can have a large influence on decomposition (Piao et al., 2007). The relationship between decomposition and mineral soil carbon is one main thing I was investigating in this study to better understand if leaf litter is one of the pathways of stabilization for mineral soil carbon. That is also why I included k and A in the models.

The overall model structure included the A value and mineral SOC as endogenous variables and soil microbial carbon, soil nitrogen, soil clay, GPP, AET, and the A value as exogenous variables. I found that A was better at explaining variance in mineral soil carbon than k based on AIC scores. Interestingly, k was never a significant link in my models. After creating eight different model structures that had a significant p-value and fit the data, I chose my model structure based on AIC score comparisons and biological importance. I was only able to fit two endogenous variables while keeping a comparatively low AIC score, so I decided to use the A -value and mineral soil carbon as the two important variables of this study. While creating eight significant models, I also created 12 non-significant models that did not fit the data. I then used the model structure with four different sets of data, the total dataset, temperate, tropical, and boreal specific biome data. In the boreal model, I had to remove soil N to attain model fit, and in the tropical biome, I removed AET to attain model fit while keeping the best predictive model. I

included the biome specific data of the temperature, boreal, and tropical ecosystems to see if there were different drivers of mineral soil organic carbon in regions of the world that had very different abiotic and biotic factors.

3 | Results

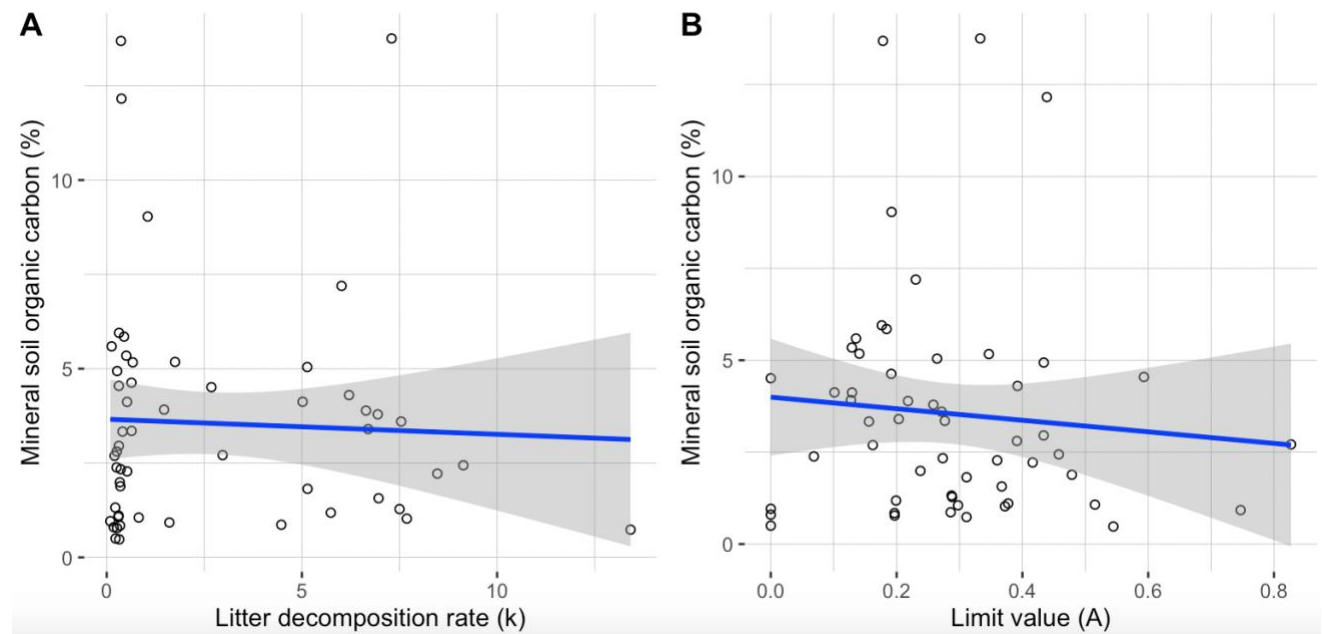


Figure 2. The relationship between mineral soil organic carbon percent and (A) litter decomposition rates (k), and (B) limit value (A). Neither show significant relationships ($R^2 = -0.01693$, -0.01075 , $P = 0.7522$, 0.5169 , respectively, $n=61$).

3.1 Linear Regression Results

Overall, I found that percent soil organic carbon in the mineral soil layer and the litter decomposition rate (k) or the limit value (A) were not correlated (p -value > 0.05 and R^2 value < 1) (Figure 2), indicating that changes in litter decomposition rates and limit values did not have a significant effect on percent SOC in the mineral soil layer at the global scale. To understand

whether the litter decomposition rate (k) or the limit value (A) were correlated with mineral soil carbon on the global scale, I ran two regressions: one between litter decomposition rate (k) and mineral soil organic carbon, and the other between the amount of carbon remaining when the decomposition rate is zero (the limit value, A) and mineral soil organic carbon.

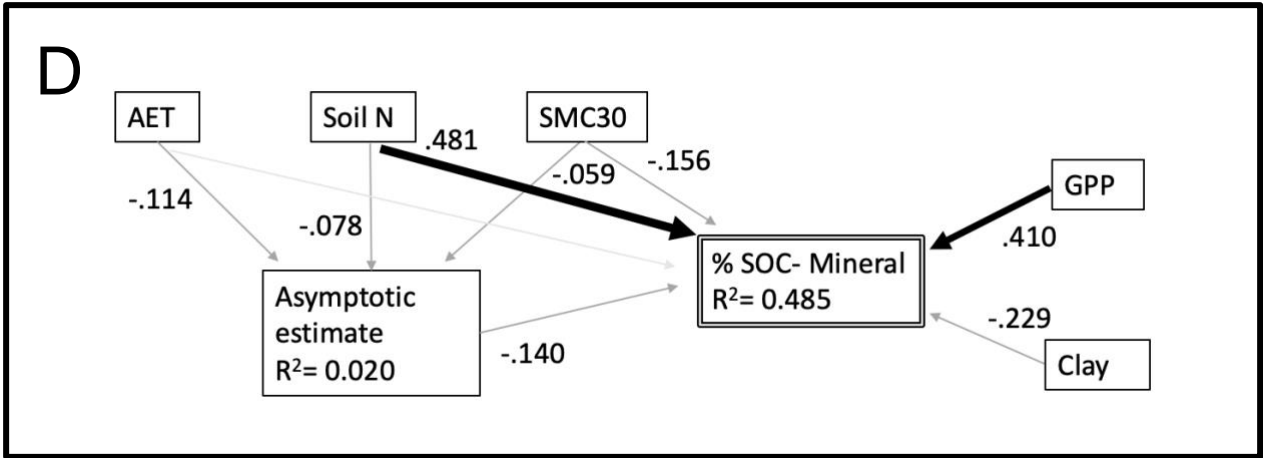
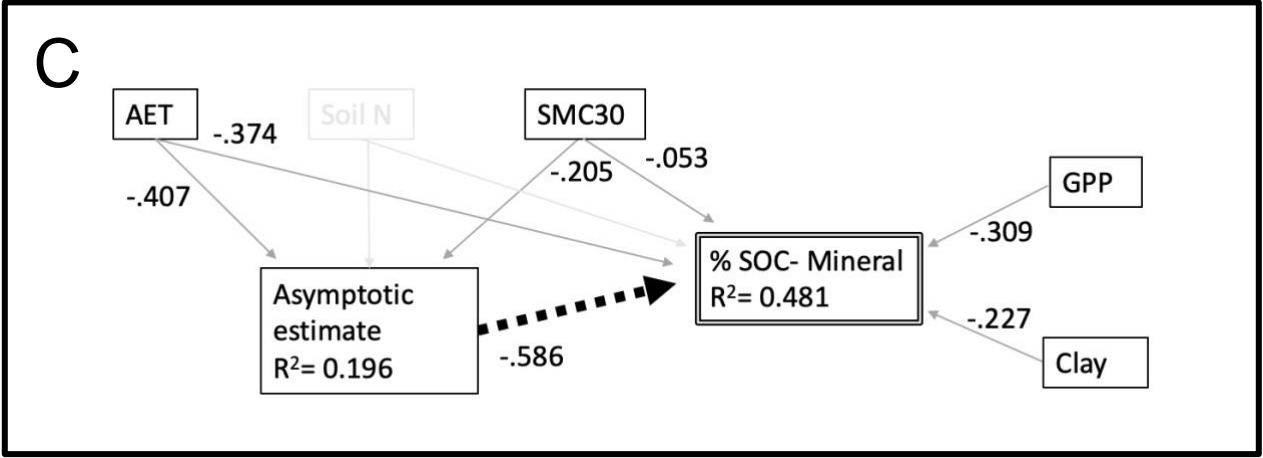
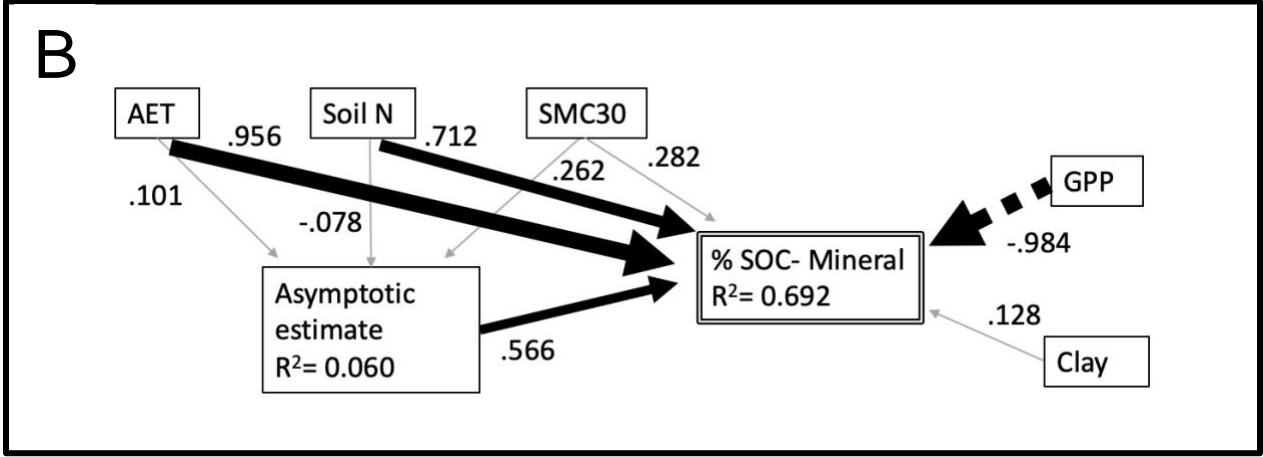
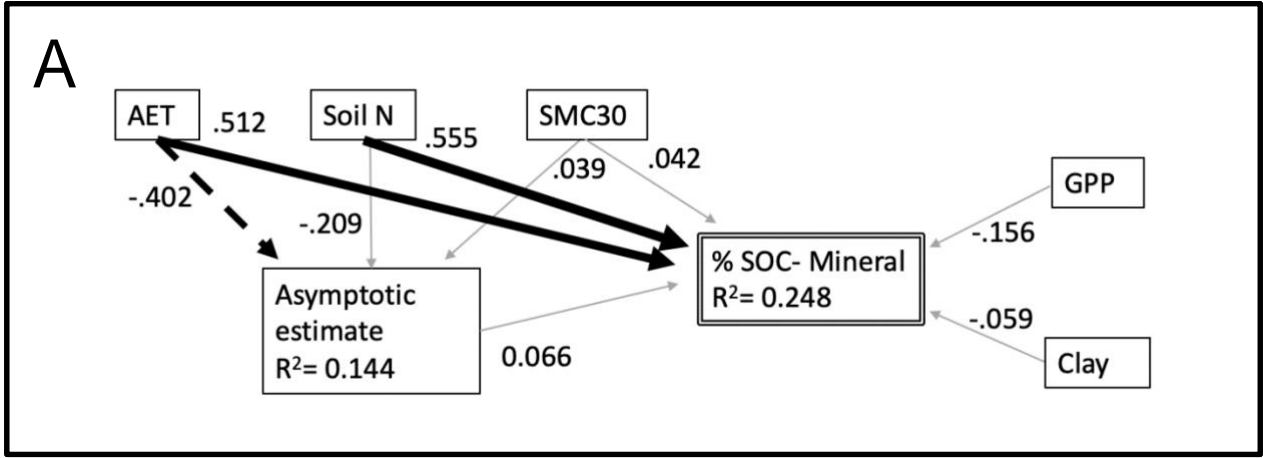


Figure 3: Results of the SEM analysis for all locations (A), temperate biome (B), boreal biome (C), and tropical biome (D). Arrows represent causal paths; greyed out arrows are nonsignificant, black arrows are significant ($P < 0.05$), solid arrows represent positive effects and dashed arrows represent negative effects. Light grey arrows/boxes (C & D) are variables that were removed from analysis to attain model fit. The standardized coefficients are shown on the arrows, and the arrows are scaled to that weight.

3.2 Structural Equation Model Results

To better understand the global drivers of mineral soil carbon beyond k and A , I created structural equation models (SEMs) that included mineral soil carbon, actual evapotranspiration (AET), soil microbial carbon biomass, soil nitrogen, soil clay content, gross primary productivity (GPP), and limit value (A). I found that neither litter decomposition nor the limit value was a significant predictor of mineral SOC (like I found with the regression), however, I found that soil N and AET were significant predictors of mineral SOC at a global scale. Increases in soil N and AET at a global scale increased mineral SOC. Other variables included in the model were GPP, soil clay, and soil microbial biomass, but they had no significant relationship with mineral SOC. AET also had a significant negative effect on the limit value, indicating that as AET increased, the amount of carbon left behind when litter decomposition equals zero decreased. Overall, the model explained 24.8% of the variance in percent SOC in the mineral soil carbon layer and fit the data well ($\chi^2=1.780$, CFI=1.0, $P = 0.411$) (Figure 3).

To see if the controls on mineral soil carbon differed by biomes with vastly different abiotic and biotic conditions, I separated the data into three different biomes for analysis: temperate, boreal, and tropical. I split the data using the latitude values, temperate ecosystems were those locations with a latitude between 23.5 and 50, and -23.5 and -50, tropical sites were greater than -23.5 and

less than 23.5, and boreal sites were greater than a latitude of 50. In the temperate biome, I used the same model structure as the global model and found different controls on mineral soil carbon. In the temperate biome, AET, and soil N and still had a significant effect on mineral SOC, but GPP had a negative significant effect and the limit value had a significant direct effect. The model explained 69.2% of the variance in percent SOC in the mineral soil carbon layer. However, it didn't fit the data very well ($\chi^2=5.851$, CFI=0.783, $P = 0.054$). AET, soil N, and the limit value had a significant direct effect on percent SOC while GPP had a significant negative effect: when AET, soil N, and the limit value increased so did percent SOC. However, when GPP increased, percent SOC decreased.

In the boreal biome, my model was able to explain only 48.1% of mineral soil organic carbon. This model was similar to the previous two models but did not include soil N in order to maintain model fit. This model only had one significant link, a negative link from A to mineral soil carbon. This link indicated that as there was more non-decomposing carbon on the forest floor (what the A value represents), the amount of mineral soil carbon decreased. This model fit the data well ($\chi^2=1.251$, CFI=1.0, $P = 0.535$).

In the tropical biome, my model was able to explain 48.5% of the variance in percent SOC in the mineral soil carbon layer. The tropical model I used was also similar to the global model but did not include a link between AET and mineral soil carbon to maintain model significance. This model did not fit the data very well ($\chi^2=9.494$, CFI=0.455, $P = 0.050$). Similar to the global model and the temperate model, soil N was a significant link, showing that as soil N increased, mineral soil carbon did as well. In the tropics, GPP was also a significant predictor of mineral

soil carbon and as GPP increased (indicating greater ecosystem productivity), mineral soil carbon also increased.

4 | Discussion

At a global scale, I found that neither the decomposition rates nor the limit values were significant predictors of mineral soil organic carbon. Interestingly though, I found that the limit value was a significant predictor of soil mineral carbon within the temperate and boreal biomes, although it had contrasting impacts in each biome (i.e., increasing SOC in temperate but decreasing SOC in boreal biomes). I also found the climate was a significant driver of soil mineral carbon at the global scale and within the temperate biome, and that soil characteristics also were important in determining soil carbon, soil N was a significant predictor of soil mineral carbon on the global scale and within the temperate and tropical biomes.

One of my most unexpected findings was that litter decomposition rates were not significant predictors of mineral soil carbon content at a global scale (Figure 2). This indicates that the pathway of soil carbon from the forest floor carbon pool to the mineral soil carbon pool is not as tightly coupled through litter decomposition as previous research has suggested (Liski et al., 2002). This also suggests that litter decomposition rates might not be a very powerful metric in predicting mineral soil carbon. However, it is worth noting that the limit value, which is the quantity of carbon that remains in the forest floor layer when the decomposition rate is zero, did significantly predict mineral soil carbon content in two biomes, temperate and boreal. In the temperate forest, an increase in the limit value resulted in great soil mineral carbon, and in the boreal biome, an increase in limit value resulted in a decrease in mineral soil carbon. Though the

limit value is less commonly used for ecological research, it might have a more relevant role when considering mineral soil carbon storage. Indeed, a meta-analysis focused on modeling C and N cycling in Michigan forests found that limit values were negatively correlated with exogenous N, leading to a smaller amount of decomposed litter and ultimately a larger proportion of stabilized organic matter and increased carbon storage (Whittinghill et al., 2012). My findings could indicate that this is the case, but only in temperate systems like where this study was conducted. This could be because there is higher GPP than a boreal forest, but lower k than a tropical forest, allowing greater accumulation over time. In the global dataset, as well as boreal and tropical specific biomes, the pattern of an increasing limit value resulting in greater mineral soil carbon content was not found (Figure 3).

If aboveground forest floor carbon pools are not a large contributor to stabilized mineral soil carbon, it could support the growing body of literature suggesting that belowground root inputs are more important to stabilized mineral carbon inputs than aboveground inputs (Jackson et al., 2017; Lajtha et al., 2018; Rasse, Rumpel, & Dignac, 2005). Jackson et al. (2017) found that root inputs with the same mass as leaf litter inputs are five times more likely to be stabilized as soil organic matter. Consistent with my results, an above and belowground litter input manipulation experiment, which both excluded roots, doubled above ground litter inputs, and removed litter input found that soil organic matter quantities did not respond significantly to the continual doubling of leaf litter input (Lajtha et al., 2018). Beyond that, there was also slight evidence that the belowground litter inputs contributed more substantially to soil organic matter pools than aboveground litter inputs (Lajtha et al., 2018). My results indicated that there is not a strong influence of aboveground litter dynamics on soil mineral carbon storage, suggesting that there is

a larger effect of belowground litter dynamics, including root decomposition, on mineral soil carbon content.

Though litter decomposition was not a significant predictor of mineral soil carbon at any scale, I was able to determine a number of other variables that did have significant relationships with mineral soil carbon at both global and biome specific scales (Figure 3). These included AET, GPP, soil N, and limit value (discussed previously). Interestingly, the literature suggests that one of the main ways climate influences soil carbon is as the overarching controller of net primary productivity (NPP) and litter decomposition. It is then assumed that the balance between those two processes is the resulting quantity of soil organic carbon (Gottschalk et al., 2012; Kirschbaum, 1995). However, I found that AET (at the global scale and in the temperate biome) and GPP (in the temperate biome) were significant drivers of mineral soil carbon content while litter decomposition was not. This suggests that there could be unexplained pathways between climate, GPP, and litter decomposition, with climate and GPP influencing mineral soil carbon stocks, but not through litter decomposition pathways. In three out of my four models (global model, temperate and tropical), soil N was a significant predictor of mineral soil carbon content. There have been many proposed mechanisms behind increasing soil N resulting in increased soil carbon content. One N enrichment experiment in Michigan found that increased N reduced lignolytic fungi, which could be part of the reason for the relationship (Entwistle, Zak, & Argiroff, 2018). An earlier study at that same location and study site found that under experimental N conditions, lignin decomposition rates decreased, thus influencing the amount of carbon that enters the soil carbon pool and increasing soil C storage (Whittinghill et al., 2012).

I found that my structural equation models were able to predict soil mineral carbon in temperate forests quite well ($R^2 = 0.692$), while in the boreal and tropical forests they were able to predict much less variation in mineral soil carbon ($R^2 = 0.481$ and 0.485 , respectively). Additionally, in the temperate forest, four significant links predicted mineral soil carbon, while in the boreal and tropical forest there were one and two, respectively. This could signify that I have a greater understanding of temperate forests and what controls mineral soil carbon in that biome, but also likely, it signifies that the variables I used in this study and had access to might help explain the temperate forest more than the tropical or boreal one. For example, a meta-analysis that investigated three different biomes, temperate, tropical, or boreal, found that the most important environmental variable in the tropics for soil carbon dynamic was soil moisture (Malhi et al., 1999), and phosphorus could also be an important variable to consider in the tropics (Malhi et al., 1999); both variables were not included in my analysis. However, there is room for future analysis of boreal and tropical biomes with additional variables.

Further understanding of mineral soil carbon is a vital step in understanding the climate crisis and creating viable management solutions to combat it (Gottschalk et al., 2012). Future directions that would expand my knowledge of the controls of mineral soil carbon, as well as the specific effect that litter decomposition has on that carbon pool, would be focusing on the influence of wood decomposition. Much work, including this project, has been done identifying the influence of leaf litter decomposition on soil carbon dynamics, but there are gaps in the literature related to the influence of wood decomposition on soil carbon dynamics. Root decomposition (and other belowground carbon inputs), should also be studied to understand how this important carbon input is influencing soil carbon dynamics. Lastly, the biome specific

drivers of mineral soil carbon in boreal and tropical biomes could be modeled to better understand how biome specific influences are shaping mineral soil carbon stocks.

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