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## Changes in Ecosystem Processes and Functional Traits over an Elevational Gradient

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# Changes in Ecosystem Processes and Functional Traits over an Elevational Gradient

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A thesis presented to the Faculty of the Department of

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with honors in Environmental Studies

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## **ABSTRACT**

Elevation gradients have been used to understand how climate change impacts various ecosystems processes by substituting distance across elevation with time, reflecting a previous, colder climate. To monitor the changes in soil organic carbon (SOC), plant community, and functional traits across time in the face of climate change, this study used space-for-time substitution to emulate a long-term study with elevational gradients and revisited the same gradient for nearly two decades to monitor elevational effects across time. With this research, I aim to answer the following questions: (1) How does elevation impact ecosystem processes and alpine plant traits? (2) How does each site's plant leaf traits and soil organic carbon content change over time? (3) Does elevation affect how plant traits and ecosystem processes change over time? Our results show that elevation shows a s-curve relationship in carbon cycling and causes a variety of responses in alpine plant traits, of particular note is a significant increase in specific leaf area (SLA) for several species with elevation. Overtime, SOC content had slight variations, but was unchanged. Plant communities could not be accurately predicted to change given the nature of the data set. As the s-curve for SOC and the increase in interspecific plant SLA were consistent across time, elevation's effect on plant communities and ecosystem processes did not change over the study period. Improving our knowledge on the climate-carbon feedback would allow more accurate models for predicted ecosystem effects due to climate change.



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Finally, I would like to acknowledge that my field sites and my college campus are the ancestral and unceded territory of the Ute and Wabanaki People respectively. I express my respect to the indigenous communities who have lived on these ancestral lands and to the future generations.



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## LITERATURE REVIEW

Throughout the history of ecology, scientists have sought to understand how processes impact ecosystems in the long-term, more recently, how climate variation and species movement due to climate change could impact ecosystems. Using an elevational gradient allows ecologists to monitor these types of long-term effects within a short time by assuming that spatial and temporal variation are equivalent (Pickett, 1989). As space increases when moving up in altitude, the assumption is that time also changes, thus higher elevation sites reflect a previous, colder climate compared to lower elevation sites. Many previous models for predicting ecosystem feedbacks to climate change have focused on net primary production (NPP) and heterotrophic respiration (HR) (Stuart Chapin III et al. 2009). Yet, there is lesser-known feedback of the carbon cycle of plants and soils that can result in enhanced concentrations of CO<sub>2</sub> in the atmosphere (Lashof et al. 1997, Schlesinger and Andrews 2000). As temperature increases, soil carbon sequestration has been found to decrease (Jasoni et al. 2005, Crowther et al. 2016, Soong et al. 2021). In some cases, there is even the possibility of carbon being released into the atmosphere, especially with permafrost (Tarnocai et al. 2009, Grosse et al. 2011). This increase in atmospheric carbon concentration results in warmer temperatures, ultimately creating this climate-carbon feedback loop.

In this regard, alpine systems with elevational gradients are of particular importance as they may provide a major source of atmospheric carbon if released due to its large soil carbon stock (Whittaker 1970, Schlesinger and Bernhardt 2013, Hoffmann et al. 2014). Additionally, the sensitivity of alpine plant communities to climatic variables (Bjorkman et al. 2018, Li et al. 2019), such as snowmelt date and length of growing season (Goulden et al. 1998), could exacerbate this climate-carbon feedback. Already, studies have found both fauna and flora shifting upwards (Dullinger et al. 2012, Gómez et al. 2015, Urban 2018) in search for the climate environment they are accustomed to (Dullinger et al. 2012, Urban 2018), an increased rate of warming would also increase their risk of extinction. With the differences in climate, human impact, vegetative biodiversity, and soil mineralogy, elevation had been found to be an effective predictor of organic carbon concentrations (Tsui et al. 2013).

Many studies measure soil organic carbon (SOC) as an indicator of soil carbon, which includes inorganic carbon, in ecosystems as it plays a central role in various soil functions,

including fertility and productivity (Andrews et al. 2004, Blanco-Canqui et al. 2013, Stockmann et al. 2015). With soils as the largest stock of terrestrial organic carbon, even small changes in these pools caused by climate or anthropogenic activity could have an impact on the global carbon cycle (Stuart Chapin III et al. 2009, Crowther et al. 2016, Chen et al. 2017, Griscom et al. 2017). Net primary productivity (NPP), quality and type of organic matter decomposed into the soil, and soil microbial activity are all important drivers of SOC (Stockmann et al. 2013).

As the primary flux of carbon into terrestrial ecosystems, plant-soil interactions modulate the impact of climate change and regulate greenhouse gas feedback for carbon, nitrogen, and water cycles (Ostle et al. 2009). Previous research has found that alpine plants rely on phenotypic plasticity of various leaf traits, such as area, thickness, dry matter content, and nutrients, to better tolerate experimental warming and cooling climate conditions (Henn et al. 2018). These changes in plant functional traits affect the carbon cycle as the rate of plant productivity is correlated (Wright et al. 2004, Hsu et al. 2018).

Due to its carbon rich soils, alpine systems are of particular importance as they may provide a major source of atmospheric carbon as decomposition rates increase, which would further cause warming of temperatures and create a feedback loop exacerbating climate change (Whittaker 1970, Schlesinger and Bernhardt 2013, Hoffmann et al. 2014). A shift in species composition due to climate change can also impact SOC concentration as it was found to reduce carbon inputs by reducing the decomposability of leaf litter (Saleska et al. 2002). Additionally, abiotic factors such as temperature and precipitation, which are expected to change with climate change, limit decomposition from microbes (Schlesinger and Andrews 2000, Nemergut et al. 2005, Stockmann et al. 2013, Hsu et al. 2018). This review intends to synthesize the various drivers of climate change, elevation (Tsui et al. 2013, Tsozué et al. 2019), temperature (Stockmann et al. 2013), precipitation (Tarnocai et al. 2009) and land-use change (Stockmann et al. 2015), and its effect on SOC and plant traits across an elevation gradient. Understanding how and to what extent SOC could change will further increase our limited knowledge of the climate-carbon feedback and how changes in plant traits could exacerbate that feedback.

## **Elevation**

Elevation gradients have been used to understand how climate change impacts various ecosystems processes by substituting the climate changes with elevation for the predicted climate

changes expected over time. In fact, a study has found that SOC increases along the gradient due to the changes in temperature and moisture, which are influenced by changes in elevation (Tsozué et al. 2019). SOC compositions can be similar across sites with different landscape positions or vastly different between sites of similar vegetation types due to slightly different abiotic conditions along elevations affecting microbe communities (Hsu et al. 2018). Through varying molecular techniques, studies have found that microbe communities were most active in snow-free or subnival soils (Nemergut et al. 2005), decreasing in diversity as elevation increases (Bryant et al. 2008).

A shift in species composition was found to reduce carbon inputs to soil carbon both in the short and long term by reducing the decomposability of leaf litter (Saleska et al. 2002), though it takes decades for a shift in composition to occur. 65 years after the initial study, a resampling of 121 sites in Crested Butte, Colorado found significant changes in species richness, diversity, relative abundance, and the distribution matches with patterns expected of a warmer, drier climate (Zorio et al. 2016). Alpine plants typically favor resource conservation due to severe abiotic constraints at high elevation, including protection from UV radiation and low temperature (Lambers and Oliveira 2019, Midolo et al. 2019, Cruz-Maldonado et al. 2021). In a larger meta-analysis of 104 species across 71 studies, interspecific specific leaf area (SLA,  $\text{cm}^2\text{g}^{-1}$ ) decreases with elevation, resulting in thicker leaves and denser tissues (Midolo et al. 2019). Some studies, however, have found SLA to be variable. Plant traits on an elevation gradient in China (3000-4100 m) showed SLA to have a s-curve relationship with elevation (Henn et al. 2018). A study on community-level means found SLA to have a convex relationship to elevation (Kergunteuil et al. 2018), while another study found that for 11 species representing 4 different growth forms (rosette, tussock grass, shrub, and tree), interspecific SLA and leaf area decreased while leaf dry mass content (LDMC) and leaf thickness increased (Cruz-Maldonado et al. 2021). Investigating variability within species found that SLA decreased for six species, was stable for four, and increased for one species at higher elevations (Cruz-Maldonado et al. 2021). With the variety of responses in plant leaf traits (both intraspecific and interspecific), elevation likely is but one factor influencing trait variation.

## **Temperature**

A large proportion of the world's soil carbon is stored in arctic and boreal ecosystems of the northern hemisphere (Tarnocai et al. 2009, Grosse et al. 2011), but, just like its vegetation, SOC is vulnerable to environmental changes (Sulman et al. 2018, Prager et al. 2021, Happonen et al. 2022). Through monitoring of carbon stocks in vegetation, research has found an increase in stocks from 1865, amounting to 30.8 Mg C ha<sup>-1</sup> to 37.2 Mg C ha<sup>-1</sup> in 2003 in the Stubai Valley, Austria (Tappeiner et al. 2008), matching similar results in a survey of alpine grasslands across the Tibetan Plateau (Chen et al. 2017). And yet, if even a small fraction of permafrost carbon is released into the atmosphere, significant climate-carbon feedback could occur (Tarnocai et al. 2009, Grosse et al. 2011).

Previous research has found that under elevated CO<sub>2</sub> environments, there was a decrease in carbon sequestration (Jasoni et al. 2005). More specifically, another study found a 33% loss in subsoil carbon in five years of experimental warming (Soong et al. 2021). Even under conservative assumptions of soil carbon's response to warming, within a year, climate change would drive 55 (+/- 50) petagrams of carbon from the upper soil to the atmosphere by 2050 (Crowther et al. 2016). In one study in the southern Appalachian Mountains, they predicted that low (235-335 m), mid (940-1000 m), and high (1650-1670 m) elevation forests might surrender 40-45% of their SOC if mean annual temperature increased by 4°C (Garten et al. 1999).

Dynamic global vegetation models (DGVMs) use plant function type classifications to better predict impacts of global climate change on terrestrial ecosystems, relying heavily on plant-soil interactions to improve the model's predictive ability (Ostle et al. 2009). Shifts in the microbial community of the soil due to climate change can have effects on plant productivity and establishment, shifting species composition (Classen et al. 2015). Additionally, plants are leafing out and flowering earlier in the growing season (Inouye 2020, Vitasse et al. 2022), resulting in an alteration of functional trait expression (Hudson et al. 2011, Verheijen et al. 2015). Variety in plant traits, leaf area, plant height, SLA, and LDMC, at the individual or population level is related to growing environment, mainly temperature (Bjorkman et al. 2018). Warming has resulted in shrubification, replacing grasses and forbs, in several regions of the arctic and affecting primary productivity (Classen et al. 2015). Plant height, however, is increasing for woody and non-woody species as well, which can result in 8-16% greater photosynthesis and 6-11% greater ecosystem respiration (plant and microbe respiration) (Happonen et al. 2022).

## Precipitation

Climate projections predict a shift in moisture regimes (Seidl et al. 2017) and that seasonal shifts in precipitation are expected to severely alter future water availability in alpine regions (Alpert et al. 2008). Soil organic carbon reflects two processes: adding carbon through plant productivity and removing the carbon through respiration, both are influenced by water availability. Among plant traits, SLA is one key trait reflecting species resource acquisition strategies (Wright et al. 2004). Increased precipitation and nutrient additions significantly shifted plant traits to more resource-acquisitive or fast leaf economics and increased plant abundance (Wu et al. 2022). In fact, a study on *Potentilla anserine* in an alpine system, found that water conditions may affect whether phosphorus is the limiting factor of the ecosystem (Wu et al. 2022). In a comparative study between dry and wet treatments, wetter sites had both larger leaves and more growth as leaf traits were selected in dry environments to prevent evapotranspiration from stomata (Dudley 1996).

Soil respiration is defined as the release of carbon from a combined activity of root (autotrophic) respiration and decomposition of soil organic matter through micro- and microorganisms (heterotrophic respiration) (Stockmann et al. 2013). Though it is difficult to measure the relative contribution to SOC, some studies argue that large accumulation of soil organic matter is dependent not on plant productivity, but due to other factors (e.g., temperature, humidity) which limit decomposition from microbes (Schlesinger and Andrews 2000, Nemergut et al. 2005, Stockmann et al. 2013, Hsu et al. 2018). Moisture content in soils may have a strong influence on soil respiration (Maier et al. 2011, Carey et al. 2016), though it is dependent on the region. In Subarctic and Northern Boreal regions, predicted climate change might alter precipitation patterns and make soils water-saturated, which can cause accelerated anaerobic decomposition and release of CH<sub>4</sub> to the atmosphere (Tarnocai 2009, Grosse et al. 2011). Meanwhile, in the southern part of the Boreal region, drought conditions caused by higher summer temperatures and evaporation rates would lead to highly oxygenated conditions, which can cause accelerated aerobic decomposition and release of CO<sub>2</sub> to the atmosphere (Tarnocai 2009). In one study, SOC distribution in high-latitude North America soils showed strong correlation with decreased mineralization and substantial carbon accumulation in colder, wetter soils (Grosse et al. 2011). For permafrost soils, SOC storage in the upper meter can vary by at

least tenfold due to variations in soil types, drainage status, climate, and disturbance histories (Grosse et al. 2011).

There is predicted to be an increase in disturbances including drought, storms, and fires due to climate change (Seidl et al. 2017). Increase in storms would increase erosion of coastal soils, which will expose permafrost soils to the environment, resulting in increased soil-to-ocean flux (Grosse et al. 2011). Wildfires cause immediate release of carbon through combustion and have long-term effects by reducing autotrophic respiration and altering heterotrophic respiration through changes in microbe community and substrate quality. (Harden et al. 2000, Grosse et al. 2011). Though it depends on the biome, as fire regimes in the savannah, where woody plants threaten biodiversity, have been found to increase SOC (Ansley et al. 2006).

### **Land-use change**

The conversion of natural landscapes to agricultural systems can cause as much as 60% reduction of the SOC pool (Guo and Gifford 2002, Lal 2004), which can be further reduced if the release of carbon is greater than carbon inputs or when soil degradation is severe (Post and Kwon 2000, Lal 2004). A meta-analysis showed that soil carbon declined after land conversion from pasture (-10%) and native forest (-13%) to plantation and (-59%) and (-42%) reduction respectively to crop land (Guo and Gifford 2002). This process is reversible, as abandoned farmland that reverted to woodland had SOC increase by 64 t C ha<sup>-1</sup> in one site, and 44 t C ha<sup>-1</sup> due to increased plant productivity (Hillel and Rosenzweig 2010). So, while increased temperature could exacerbate climate change, soil carbon sequestration could have the potential to remove 5-15% of global emissions from the atmosphere and improve soil quality, achieving food security (Lal 2004). In a long-term manipulation of soil resource availability and grazing intensity causes consistent shifts in grassland functional composition and diversity, which causes greater above-ground net primary productivity (NPP) (Laliberté and Tylianakis 2012) caused by greater plant resource uptake from fast leaf economic plants (Wright et al. 2004).

One interesting case of land use change is from a study on the island of Java, Indonesia. From 1930-1970, there was a decline in SOC values due to conversion of primary forests to cultivated lands and plantations (Minasny et al. 2011). Since 1970, however, there has been an increase of SOC content which has been attributed to human influence and improved agricultural practices (Minasny et al. 2011). Overall, declines in SOC from cultivation are partly due to

tillage or mixing of the soil which exposes organic material otherwise inaccessible to decomposers (Post and Kwon 2000, Lal 2004). Although different biomes may react differently, the important factors for increasing SOC storage are increasing input of organic matter, changing the decomposability of organic matter, and burying organic matter deeper below-ground (Post and Kwon 2000, Lal 2004).

## **Conclusion**

Climate change is predicted to have impacts on different ecosystem processes. The terrestrial carbon cycle, influenced by plant-soil interactions, was found to be influenced by elevation (Tsui et al. 2013, Tsozué et al. 2019), temperature (Stockmann et al. 2013), precipitation (Tarnocai et al. 2009) and land-use change (Stockmann et al. 2015). Abiotic variables, such as temperature and moisture, are influenced by changes in elevation (Tsozué et al. 2019) which can impact species composition (Zorio et al. 2016), plant productivity (Saleska et al. 2002), microbial diversity (Bryant et al. 2008) and respiration (Hsu et al. 2018). Warming temperatures has caused shifts in microbial community, plant leaf traits and productivity, and shifts in species composition (Classen et al. 2015). Precipitation can influence soil respiration by saturating the soils with moisture and limiting aerobic respiration or causing increased evaporation rates leading to accelerated aerobic respiration depending on the region (Tarnocai 2009). Climate change is also expected to increase the frequency and intensity of disturbances, which may overall have a negative effect on SOC in soils of the Boreal region (Grosse et al. 2011). Soil carbon has been found to decline after land conversion from pasture (-10%) and native forest (-13%) to plantation and (-59%) and (-42%) reduction respectively to crop land (Guo and Gifford 2002). The process is reversible (Hillel and Rosenzweig 2010) and a study suggests that with warming temperatures, carbon fertilization may improve soil quality with increased carbon sequestration from enhanced productivity (Lal 2004, Laliberté and Tylianakis 2012). Improving our knowledge on the climate-carbon feedback would allow more accurate models for predicted ecosystem effects due to climate change.

## INTRODUCTION

With soils as the largest stock of organic carbon, even small changes in these pools caused by climate or anthropogenic activity could have an impact on the global carbon cycle (Stuart Chapin III et al. 2009, Crowther et al. 2016, Chen et al. 2017, Griscom et al. 2017). Although the direct effects of climate change have been thoroughly studied, there is a lesser-known impact on the carbon cycle of plants and soils that can result in feedback that enhances anthropogenic CO<sub>2</sub> in the atmosphere (Lashof et al. 1997, Schlesinger and Andrews 2000). Climate change is expected not only to alter plant communities (Hudson et al. 2011, Zorio et al. 2016), but affect plant growth rate (Inouye 2020, Vitasse et al. 2022) and microbial activity (Crowther et al. 2016, Nottingham et al. 2019), thus affecting soil carbon inputs and outputs respectively.

Due to their relatively carbon rich soils, alpine systems are of particular importance as they may provide a major source of atmospheric carbon as decomposition rates increase with increased temperatures, which would further cause warming of temperatures and create a feedback loop exacerbating climate change (Whittaker 1970, Schlesinger and Bernhardt 2013, Hoffmann et al. 2014). A large proportion of the world's soil carbon is stored in arctic and boreal ecosystems of the northern hemisphere (Tarnocai et al. 2009, Grosse et al. 2011). Even under conservative assumptions of soil carbon's response to warming, within a year, climate change would drive 55 (+/- 50) petagrams of carbon from the upper soil to the atmosphere by 2050 (Crowther et al. 2016). Additionally, alpine vegetation is sensitive to climatic variables, such as snowmelt date and growing season (Goulden et al. 1998, Bjorkman et al. 2018, Li et al. 2019), which could disrupt plant productivity and reduce carbon inputs into the soil, further exacerbating this feedback. This further impacts animals (Inouye 2020) with changing vegetation phenology due to warming temperatures (Vitasse et al. 2022), which already face dangers of extinction as organisms shift upwards with warming temperatures (Dullinger et al. 2012, Gómez et al. 2015, Urban 2018).

Many studies measure soil organic carbon (SOC) as an indicator of total soil carbon in ecosystems as it plays a central role in various soil functions, including soil fertility and productivity (Andrews et al. 2004, Blanco-Canqui et al. 2013, Stockmann et al. 2015). Net primary productivity (NPP), quality and type of organic matter decomposed into the soil, and



microbial activity are all important drivers of SOC fluxes (Stockmann et al. 2013). Thus, evaluating carbon cycling, both above- and below-ground processes, is an effective indicator of the ecosystem's response to climate change (Stuart Chapin III et al. 2009, Sørensen et al. 2019, Happonen et al. 2022).

Previous research has found that alpine plants are phenotypic plastic of various leaf traits, such as area, thickness, dry matter content, and nutrients, to better tolerate experimental warming and cooling climate conditions (Henn et al. 2018). These changes in plant functional traits affect the carbon cycle as the rate of plant productivity is correlated (Wright et al. 2004, Hsu et al. 2018). Though a few studies have found that community-level specific leaf area (SLA) decreases with elevation due to resource-acquisitive strategies (Midolo et al. 2019, Cruz-Maldonado et al. 2021), some studies have shown intraspecific SLA to have variable relationships with elevation including convex (Kergunteuil et al. 2018), s-curve (Henn et al. 2018), and even increasing with elevation (Cruz-Maldonado et al. 2021). Aside from attributing these patterns to adaptations to the environment, there are no proposed mechanisms for the variety in intra- and interspecific changes in SLA with elevation. A shift in species composition can also impact SOC concentration as it was found to reduce carbon inputs by reducing the decomposability of leaf litter (Saleska et al. 2002). The more easily carbon decomposes in leaf litter, the more carbon gets returned to the atmosphere and the more rapidly microbes can grow (Ågren and Bosatta 1996). Some studies even argue the soil microenvironment may play a larger role in SOC concentrations than previously thought as soil organic matter is dependent not on plant productivity, but rather due to other factors (e.g., temperature, humidity) which limit decomposition from microbes (Schlesinger and Andrews 2000, Nemergut et al. 2005, Stockmann et al. 2013, Hsu et al. 2018).

With the differences in climate, human impact, plant community composition, and soil mineralogy, elevation had been found to be an effective predictor of SOC concentrations (Tsui et al. 2013). In fact, a study found the factors influencing SOC (NPP, organic matter decomposition, and microbial activity) are also influenced by changes in elevation (Tsozué et al. 2019). Another study found that plant leaves tend to be thicker and denser in response to colder temperatures and greater abiotic stress at higher elevations (Midolo et al. 2019, Cruz-Maldonado et al. 2021). Low temperatures and high water saturation leads to oxygen-limited conditions, thus

lowering aerobic decomposition and leading to greater accumulation of soil carbon (Grosse et al. 2011).

To monitor the changes in SOC across time in the face of climate change and understand its connection to the local plant functional composition, this study looked across an elevation gradient over nearly two decades to monitor elevational effects across time. With this research, I aim to answer the following questions: (1) How does elevation impact ecosystem processes and alpine plant traits? (2) How does each site's plant leaf traits and soil organic carbon content change over time? (3) Does elevation affect how plant traits and ecosystem processes change over time?

Based on previous evidence, I expected SOC should increase with elevation as warmer temperatures decrease carbon stores (Soong et al. 2021; Hsu et al. 2018; Crowther et al. 2016; Saleska et al. 2002) since traveling up an elevation gradient simulates traveling back in time to a previously colder climate. Plant traits would be expected to exhibit changes in SLA as elevation as habitat is changing from an arid environment to a moist one and inter- and intraspecific SLA has been reported to change with elevation (Midolo et al. 2019, Cruz-Maldonado et al. 2021). As an increase in SLA was found to lead to an increase in plant productivity (Gunn et al. 1999, Cornelissen et al. 2003, Cheng et al. 2016), I expect plant productivity to change with elevation. I expect similar trends to be seen across all years as plant composition should be mostly consistent across time as it takes several decades for significant change to occur (Zorio et al. 2016). Finally, I expect for there to be a higher impact on ecosystem processes at higher elevations due to alpine ecosystems high sensitivity (Li et al. 2019; Bjorkman et al. 2018; Schlesinger and Bernhardt 2013; Cannone, Sgorbati, and Guglielmin 2007; Goulden et al. 1998; Groisman, Karl, and Knight 1994; Whittaker 1970), meaning there would be a greater change in SOC and SLA as I move up in elevation as time passes. Insight into the changes of ecosystem processes, like carbon cycling and functional trait composition, due to warming temperatures will improve climate change models and may inspire management policies to prevent accelerating global warming.

## **METHODS**

### **Study Site**

This study was conducted in field sites associated with the research lab of Dr. Brian J. Enquist at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado (30°57'N, 106°59'W, 2900 m elevation). RMBL was chosen based on its well-studied elevational gradient and previous research by Dr. Enquist on plant traits and communities across an elevational gradient (Sloat et al. 2015, Henn et al. 2018). Six sites were chosen along the East River Valley of RMBL, ranging from 2475 and 3463m above sea level. The sites ranged from sagebrush communities in Almont, CO, USA at the lowest elevation to subalpine meadows in Crested Butte, CO, and alpine plant communities at higher elevations. ArcGIS was used to map and analyze elevation of the six sites (Figure 1). All sites consisted of a mixture of shrubs, grasses, and forbs with substantial turnover in plant species between sites with very few of the species occurring in more than two of the sites (Sloat et al. 2015).

### **Field Methods**

Every year, at each site, five 1.3m x 1.3m subplots were selected randomly within a 30-plot grid every year. To create independent measures, plots were distanced at least 5m apart from one another. Each site was visited twice for soil data collection, once during the early season before flowers were in full bloom and once at peak vegetation biomass, except for the highest and lowest elevation sites. Due to the start date, the lowest site, Almont, was already at peak season. The highest site, Cinnamon, had snow blocking the road, which prevented access until later in the summer during its peak season. The data on plant communities was collected only once per site.

### *Soil*

To measure SOC and soil moisture, two soil cores from an open-tube sampler of approximately 10 cm in depth were collected outside, but near the boundary, of each of the five plots at each site. They were labeled A for upslope and B for downslope. The ten samples were stored in a cooler to retain the soil moisture until laboratory processing. The samples serve as

independent data points due to the distance between and across the plots. A total of 100 samples were collected from all sites.

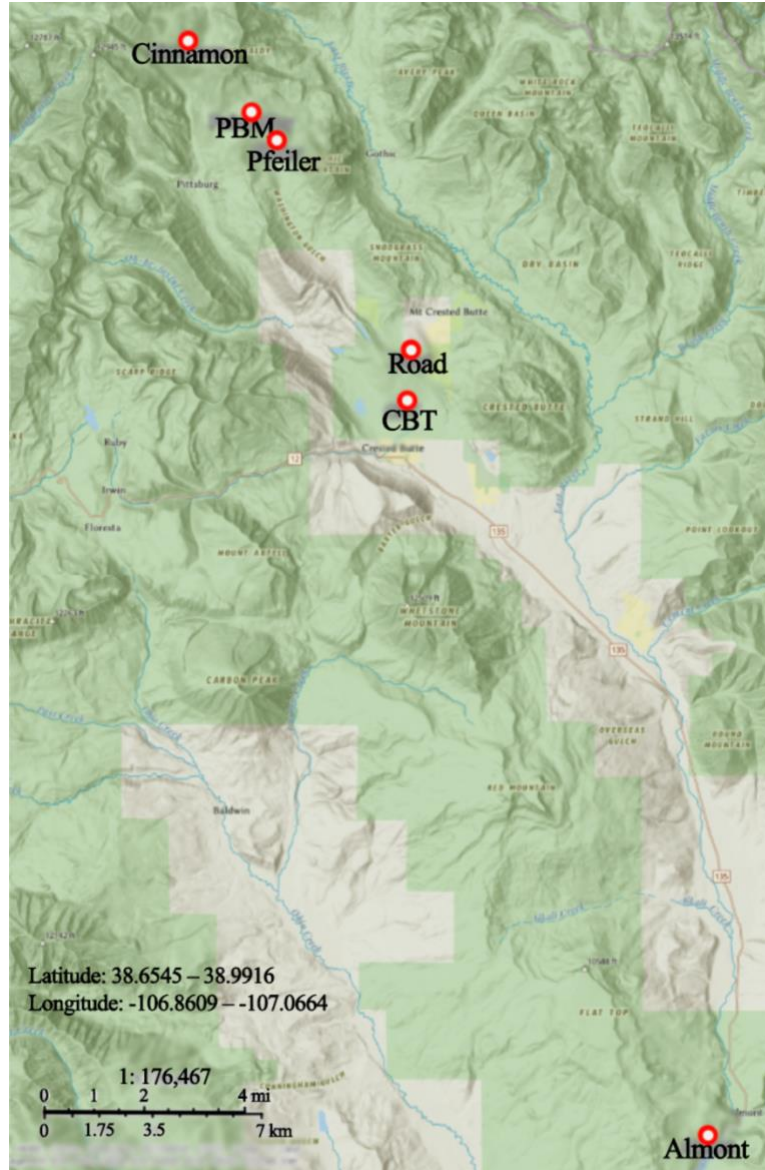


Figure 1: Map of gradient sites in increasing order, Almont (38.6545, -106.8609, 2476m), CBT (Crested Butte Land Trust; 38.8818, -106.9802, 2710m), Road (38.8972, -106.9787, 2815m), Pfeiler (38.9610, -107.0313, 3155m), PBM (Painter Boy Mine; 38.9697, -107.0412, 3380m), Cinnamson (38.9916, -107.0664, 3463m)

### *Species Composition and Leaf Traits*

Species identification was based on a compiled field guide of abundant species found at the same sites in previous years (2004-2022). Depending on the year, one plot per site was completely and destructively sampled for leaf trait measurements (Sloat 2015). Another method included only taking three samples from each species representative of each site for analysis. Trait measurement protocol followed the plant function trait handbook (Cornelissen et al. 2003). All leaves were collected and stored in plastic bags and placed in coolers in the field before transport to the lab.

## **Lab Methods**

### *Soil Processing*

Once back at the lab, the soil samples were crushed to break up any soil clumps. A representative sample of the core was weighed to ensure it is under 20 g, then placed in a tin to be dried in an oven set at 105°C for 24-48 hours to remove moisture. Afterwards, the samples were weighed again. Rocks and biomaterial were removed from the samples using a 2 mm sieve and measured independently before discarding. Biomaterial was picked out for a 5-minute period only for efficiency. The separated soil was then weighed again in its original tin, before being placed back into the drying oven for another hour to remove the moisture it may have accumulated during the process. Soil moisture was calculated by the difference between the wet soil and the dry soil, including for the weight of the rocks and biomaterial, then divided by the dry soil's weight (Nelson and Sommers 1996). Removing soil from the tins till only 6-9 g remain, the samples were placed on a preheated oven at 200°C. The oven ran on a program to combust the carbon in the soil by increasing the temperature by 19°C every minute till it reached 430°C. Once the samples were cool to the touch, their final weight was measured and recorded. Soil organic carbon is calculated as the difference between pre-burn and post-burn weight, divided by two (Nelson and Sommers 1996). Since soil moisture was calculated along with soil carbon, results from soil moisture content may not be representative of the trends at each site.

### *Leaf Trait Measurements*

Once at the lab, leaves were scanned via Canon LiDE scanners then using programs such as ImageJ and the LeafArea package to calculate leaf area (Henn et al. 2018) and measured for leaf thickness by taking the average measurement from using calipers at three random locations on each leaf. Fresh mass was measured by weighing on a balance within 24 h of collection before drying for at least 72 h at 65°C before dry mass, or leaf dry matter content (LDMC), was measured. Leaf area and dry mass was used to calculate specific leaf area (SLA) which is the ratio of area over dry mass. Leaf water content (LWC) was calculated using the differences in weights from fresh mass to dry mass. A subset of the leaves in the dataset were grounded into powder for isotope analysis, including N, C done off-site at the University of Arizona (Henn et al. 2018). Ratios between C:N were calculated and analyzed.

## **Historical Data**

### *Soil*

Historical data of organic soil carbon were gathered from Enquist Lab's RMBL Long Term Soil data which contains soil observation data from sites ranging from Almont, CO, USA up to the base of Cinnamon Mountain. The data holds 1,549 observations of soil samples from 2003 to 2022 with some years missing (2005, 2007, 2014). Soil observations include variables such as tin weight, soil dry weight, rock and biomatter weight, percent of soil moisture, pre-burn weight, post-burn weight, percent organic carbon and more. These variables were necessary to estimate SOC as mentioned above.

Sites were restricted to Almont, Crested Butte Land Trust (CBT), Road to Gothic (Road), Pfeiler, Painter Boy Mountain (PBM), and Cinnamon Mountain (Cinnamon). Variation in elevation was standardized to 2475m for Almont, 2710m for CBT, 2815 for Road, 3155 for Pfeiler, 3380 for PBM, and 3463 for Cinnamon. Additional sites and plots were excluded for consistency. Unexplained errors in data were removed as they were likely due to systematic errors, such as measurement error or input errors, rather than random occurrences.

### *Plant Traits*

Historical data of plant traits were gathered from the RMBL Trait Database, which contains high quality georeferenced vascular plant trait observation data from sites ranging from

Almont, CO, USA up to various mountains including Cinnamon, Gothic, and Baldy. It is a compilation of past and ongoing studies, most of which comes from the Enquist Lab's work from 2003 to present. The data holds 11,561 trait observations of vascular plants from nearly 240 plant species. The data has been taxonomically standardized to the TNRS (<http://tnrs.iplantcollaborative.org/>). Leaf trait variables in this database include individual leaf area, leaf mass, LDMC, leaf thickness, leaf nutrient content (carbon, nitrogen, phosphorus), and more. Errors and missing values were eliminated in a systematic way. The dataset has observations of leaf trait and species composition at various sites from 2004 to 2018 with some years missing (2006, 2007, 2009, 2013, 2014).

To standardize data, sites were restricted to Almont, CBT, Road, Pfeiler, PBM, Cinnamon. Variation in naming in the dataset was cross-referenced to the names above by similarities in plot coordinates. Variation in elevation was also standardized to match the elevations of the soil dataset: 2475, 2710, 2815, 3155, 3380, and 3463 respectively. Any data inputs without identifying the species were removed despite having leaf area and other variables. Similarly, general species identification (e.g., *Taraxacum* sp.) were removed, filtering the total number of species to 182. Leaf trait variables were filtered to only include SLA, LDMC, LWC, leaf thickness, leaf area, and the ratio of carbon to nitrogen. Because of unexplained data inconsistencies, all data from 2010 was removed because these inconsistencies were likely not due to random occurrences but systematic errors. Since I was unable to rectify or identify the cause, the data was excluded from analysis.

## **Data Analysis**

Boxplots were used to visualize the distribution of soil organic carbon (SOC) across elevation and across time. An analysis of variance (ANOVA) was done on soil carbon to determine if there was a significant difference between soil samples across sites and across time. A post-hoc paired Tukey test was performed to compare the sites for statistical differences. A Bonferroni adjustment was performed on all statistics to ensure repeated sampling did not impact significance in the data.

Similarly, scatterplots were used for plant trait distribution, specifically SLA, across elevation and time. Since it is common practice to log transform SLA (Cornelissen et al. 2003, Midolo et al. 2019, Cruz-Maldonado et al. 2021), all graphs and analyses regarding SLA of plant

traits were done on a logarithmic scale. Finally, linear regression was used on SLA across elevation, then the same regression separated by year and a Bonferroni adjustment was made on all p-values.

All statistical and graphical analyses were performed in RStudio (R Core Team 2021). All geographical figures were made in ArcGIS geospatial software (ESRI Inc., Redlands, CA, USA, [www.esri.com](http://www.esri.com)).



## RESULTS

### Species Composition

Of the top 50 more reoccurring species, most (96%) were native to the lower 48 states, while a few (4%) have subspecies that may have been introduced. Across the 15 years of data, few species were shared across sites (Table 1). In Almont (2476m), 19 unique species were found, while CBT (2710m) had 16 species, Road (2815m) had 21, Pfeiler (3155m) had 16 unique species, PBM (3380m) had 18, and Cinnamon (3463m) had 14. Pairwise comparisons of sites found the Road and CBT shared the most species (Table 1). Only Virginia strawberry (*Fragaria virginiana*) and slender cinquefoil (*Potentilla gracilis*) were found in all sites except for Almont. Across the period, there was no pattern in species occurrences across elevation.

Table 1: Unique species shared pairwise between all six sites across elevation and across time.

	Almont	CBT	Road	Pfeiler	PBM	Cinn.
Almont	19	———	———	———	———	———
CBT	0	16	———	———	———	———
Road	3	13	21	———	———	———
Pfeiler	0	1	4	16	———	———
PBM	0	0	3	11	18	———
Cinn.	1	1	1	0	2	14

Summary of leaf trait variables were averaged across all species in the study period (Table 2). Leaf area had a range of 0.01 to 1276.78 cm<sup>2</sup> while SLA ranged from 5.98 to 1991.73 cm<sup>2</sup>/g, LDMC ranged from 14.09 to 4329.80 g/cm<sup>2</sup>, and thickness ranged from 0.01 to 0.64 cm.

Table 2: Summary of plant leaf trait variables of observations of various plant species at all six sites along the elevational gradient in East River Valley, Colorado from 2003 to 2018.

Variable	Min	1st Q	Median	Mean	3rd Q	Max
Leaf Area (cm <sup>2</sup> )	0.0135	1.2400	3.7713	18.8543	16.7243	1276.7788
SLA (cm <sup>2</sup> /g)	5.982	101.438	149.181	168.134	203.316	1991.733
LWC	-3.3298	0.6161	0.7234	0.6850	0.7845	0.9859
LDMC (g/cm <sup>2</sup> )	14.09	215.52	276.64	315.01	383.90	4329.80
Thickness (cm)	0.011	0.154	0.208	0.219	0.272	0.641
C/N Ratio	3.518	12.118	15.121	17.349	19.108	230.779

## Ecosystem Processes

### *Soil Organic Carbon*

SOC across elevation averaged across nearly 20 years showed a significant difference between sites, resembling a s-curve (p-value <  $2 \times 10^{-16}$ , Figure 2). Almont had significantly lower carbon content than all other sites. CBT and Cinnamon had significantly higher carbon content (p-value <  $1 \times 10^{-7}$ ) but were not significantly different from each other (p-value = 0.35). Pfeiler and PBM were not significantly different from each other (p-value = 0.50) but had a greater carbon content than Almont. Road was significantly different from all other sites (p-value <  $1 \times 10^{-7}$ ) and had organic carbon content between CBT-Cinnamon and Pfeiler-PBM pairs. Even with Bonferroni adjustment to account for multiple sampling, these values were found to be significant.

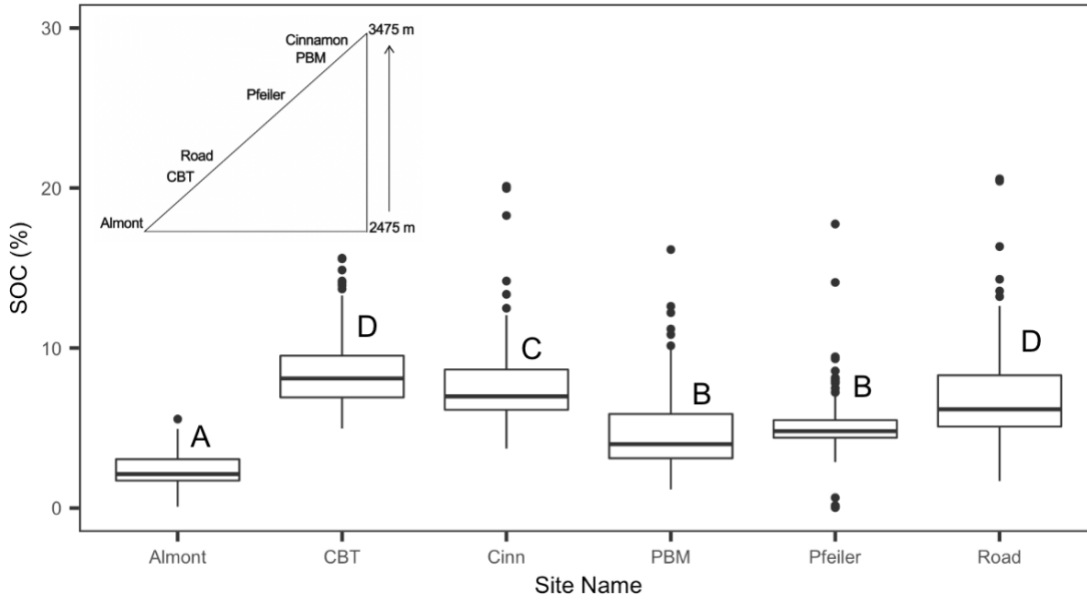


Figure 2: Distribution of soil organic carbon across elevation averaged across time representing a s-curve. Almont and Road are significantly different from each other and other sites ( $p < 2 \times 10^{-16}$ ). CBT and Cinnamon ( $p = 0.345$ ), and Pfeiler and PBM ( $p = 0.501$ ) pairs are similar to each other but significantly different from the other sites ( $p < 2 \times 10^{-16}$ ). In increasing order of soil organic carbon content, Almont, Pfeiler-PBM pair, Road, CBT-Cinnamon pair.

Averaging SOC of all the sites across time, there was no significant difference in average SOC and variability was the same except for 2004, which had higher average SOC and less variability (Figure 3A). Comparing SOC across time individually for each site, we see a similar pattern when averaging across the elevational gradient (Figure 3B).

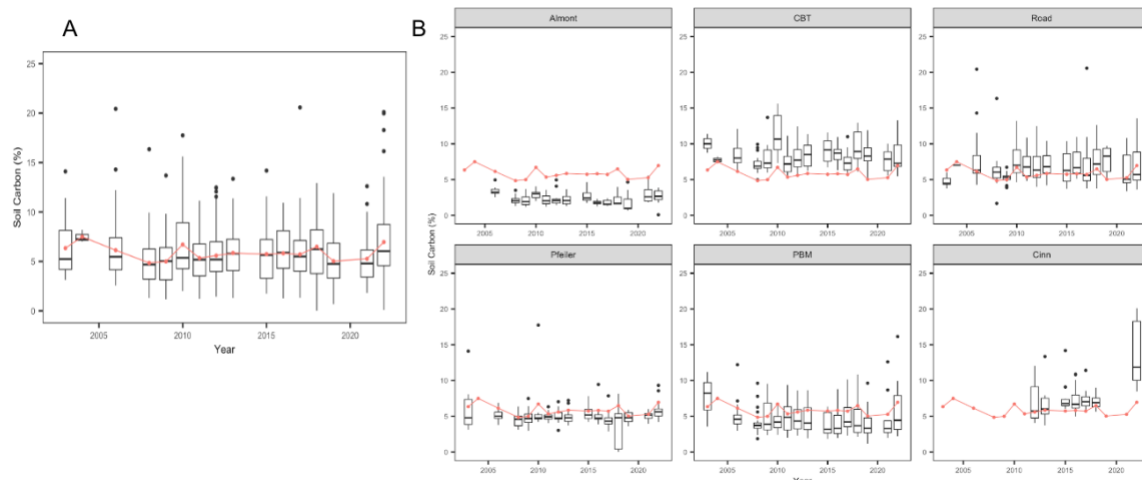


Figure 3: Distribution of soil organic carbon across time. 3A: Soil organic carbon across time and averaged by elevation. Individual years show changes in variation, but overall mean carbon content is consistent. 3B: Soil organic carbon of individual sites across time. The red line shows the average from 3A. Almont is consistently below the average while CBT is consistent above average. Road, Pfeiler, and PBM are near the average and are either above or below similarly to results found in Figure 2. Cinnamon has similar carbon content as Road for most years except for 2022 which showed a significant increase.

Almont consistently has a lower SOC content than the average while CBT nearly has an above average SOC content. Road, Pfeiler, and PBM hover slightly above or slightly below the average, consistent with the pattern across elevation alone. Cinnamon, which has only been a study site since 2012, hovered near the average then had a significantly higher SOC content in 2022. Looking at SOC content at each site and each year, we see a consistent s-curve pattern of Almont, PBM, Pfeiler, Road, CBT in increasing order of SOC content with Cinnamon varying year to year (Figure 4).

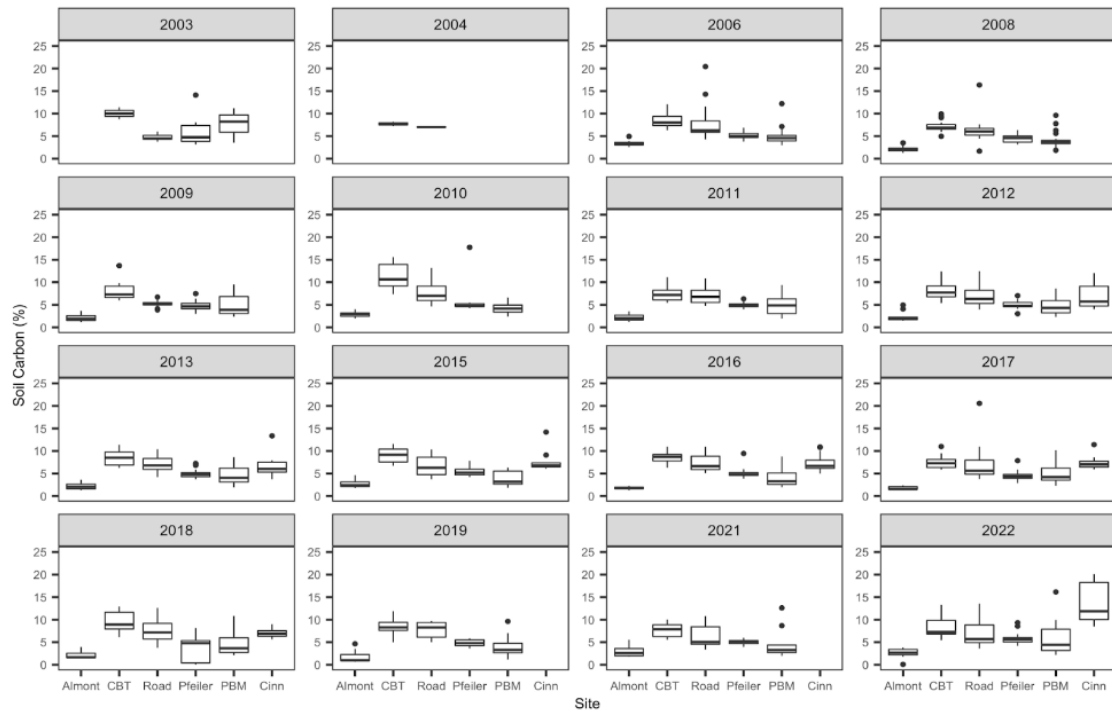


Figure 4: Distribution of soil organic carbon across elevation and across time individually by year. A repetitive s-pattern shows across time with Almont being the lowest in carbon content and CBT being the highest. When years include Cinnamon, it is either similar to Road or similar to CBT. Only 2022 shows a significantly higher carbon content for Cinnamon that makes it larger than CBT.

### *Other Variables*

Average soil moisture content across time along the elevational gradient showed a similar s-curve relationship as SOC (Figure 5), but when investigating moisture of each year found no discernible pattern (Figure 6). Some years had an increasing moisture content with elevation while others had a s-curve or convex relationship.

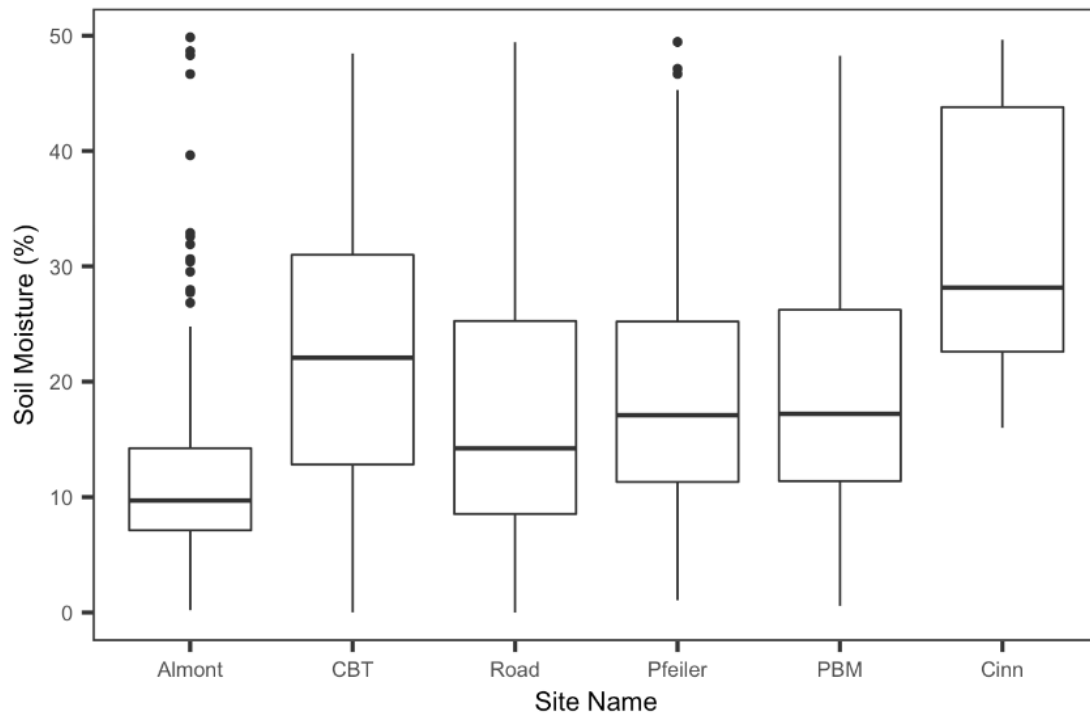


Figure 5: Distribution of soil moisture across elevation and averaged across time. Road, Pfeiler and PBM are all similar to each other. Almont has the lowest soil moisture. Cinnamon has the highest soil moisture.

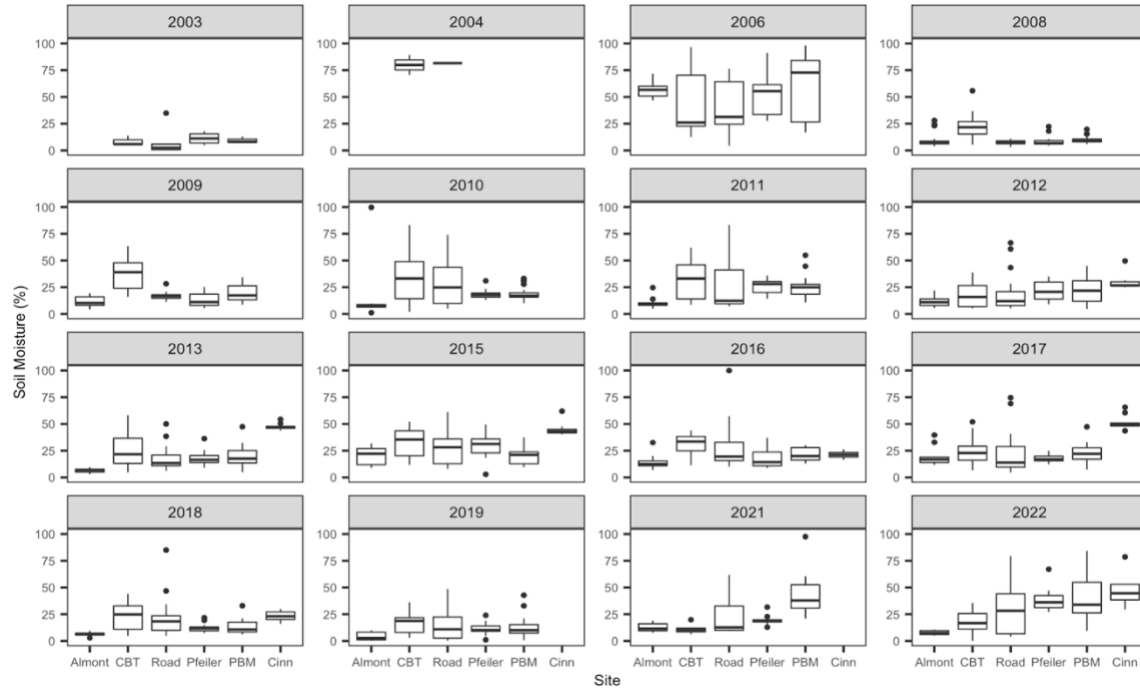


Figure 6: Distribution of soil moisture across elevation and across time individually per year. There is little consistency in the moisture patterns with the sites either being very similar to each other or moisture increasing with elevation. The increase in moisture with elevation becomes most apparent in 2021 and 2022.

## Plant Traits

SLA for all 182 plant species showed a positive correlation to elevation across the study period ( $p\text{-value} < 2.2 \times 10^{-16}$ ) in which 18.76% of the variability in SLA can be explained by changes in elevation with a simple logarithmic model (Figure 7).

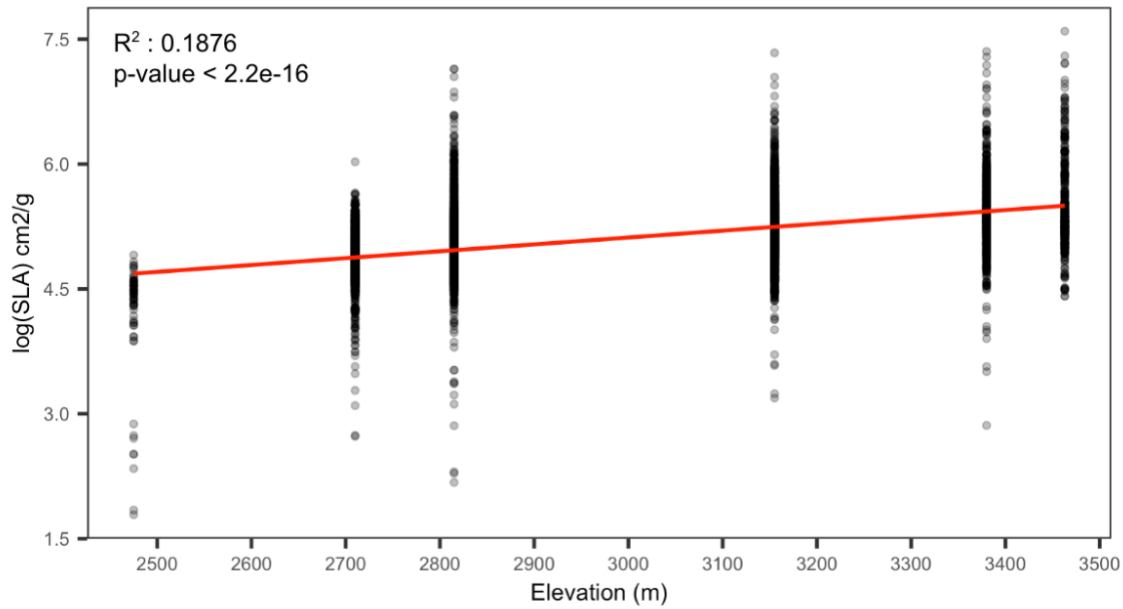


Figure 7: Simple logarithmic model between SLA and elevation across time. SLA has a significant positive relationship with elevation ( $p\text{-value} < 2.2\text{e-}16$ ) and 18.76% of the variation in SLA can be explained by changes in elevation.

Investigating this trend by individual year,  $\log(\text{SLA})$  continues to have a significant positive correlation with elevation for all years (Figure 8). With Bonferroni adjustment, all years still have a significant positive relationship except for 2018 (unadjusted  $p\text{-value} = 4.5 \times 10^{-4}$ ). In 2005, elevation could explain nearly 40% of the variation in  $\log(\text{SLA})$ .



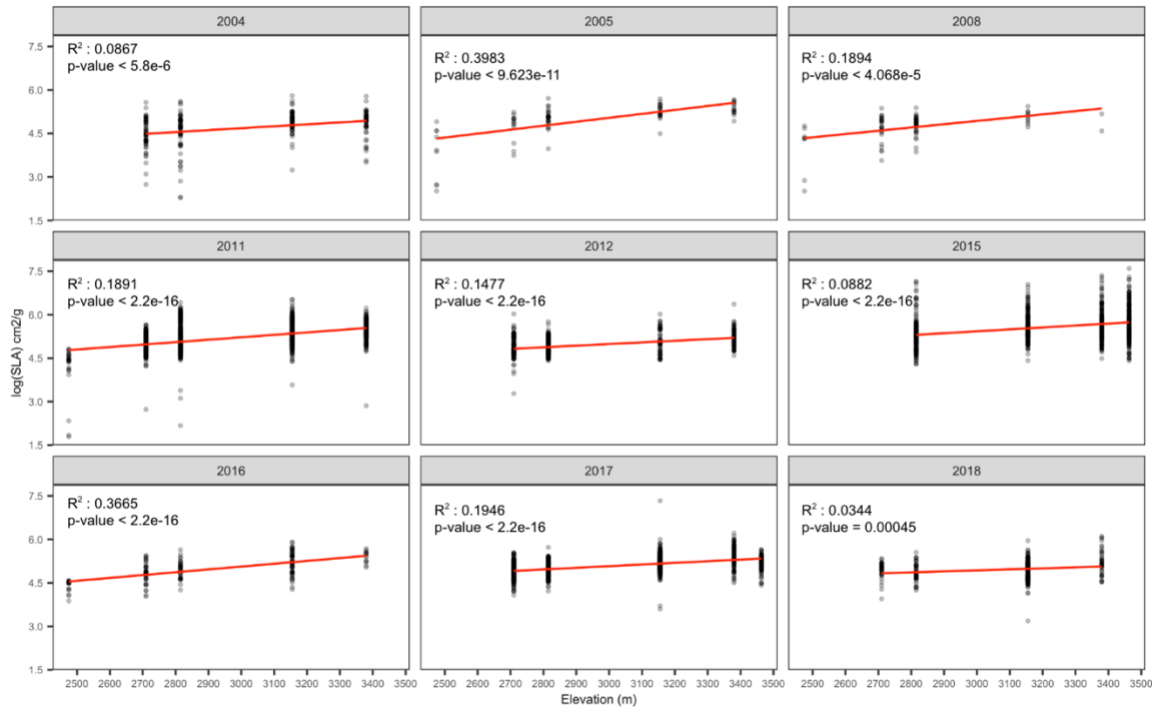


Figure 8: Simple logarithmic model between SLA and elevation across time individually per year. SLA continues to have a significant positive relationship with elevation for all years except for 2018 after Bonferroni adjustment. The greatest predictor of interspecific SLA was in 2005 where 39.83% of the variation in SLA can be explained by change in elevation.

Intraspecific SLA across elevation showed varying relationships (Figure 9). Of the top 25 occurring species in the dataset, most plants showed an increase in SLA. Other plants showed no relationship or even a convex relationship with elevation. The top 25 species were used as it was more likely for them to occur at several sites within the period. The plants were from a variety of families and had different leaf shapes including linear, pedate, pinnate, and spatulate and acicular to name a few.

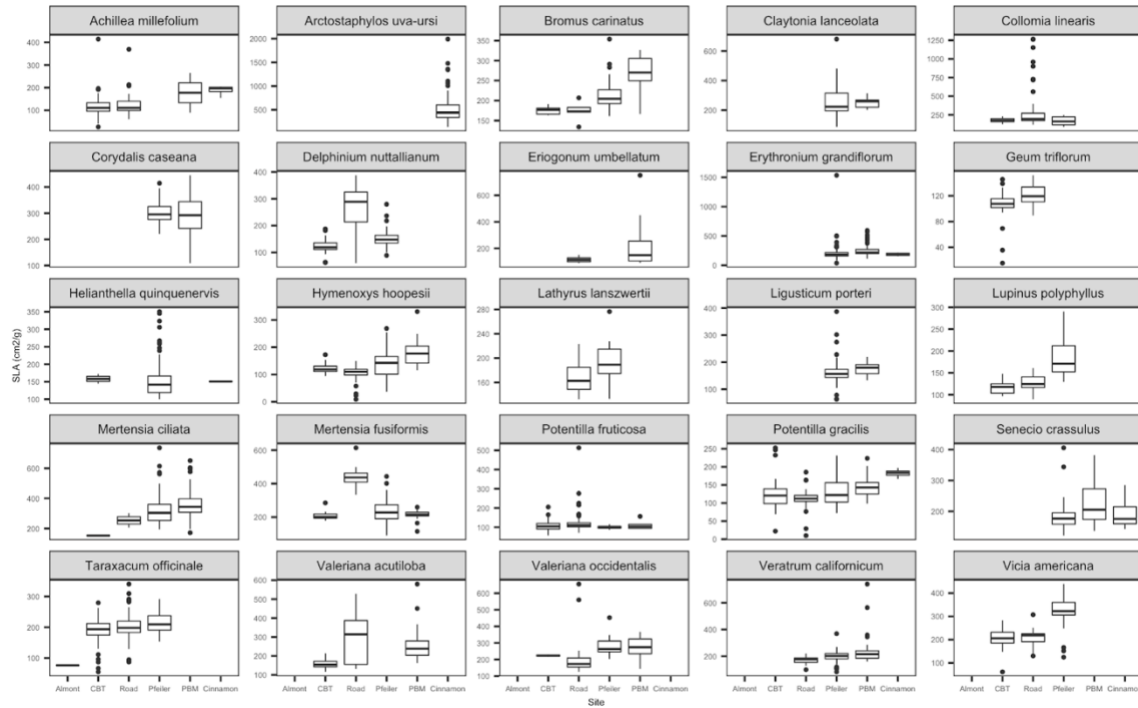


Figure 9: SLA of the top 25 occurring plant species in the data set across elevation. Trends include no relationship, convex relationship, and increasing relationship to elevation.

Since SLA is a measure of leaf area divided by dry mass (Cheng et al. 2016), leaf area, leaf thickness, and LDMC were all examined across the top 25 species. Given the variability in completeness for each observation, only a few species had enough data in leaf area, leaf thickness, and LDMC to make a comparison. Of those species, leaf area seemed to match the trend in SLA and increase with elevation. Leaf thickness tended to have a convex or decreasing relationship with elevation for species that had an increase in SLA. For species with other trends in SLA, leaf thickness tended to increase or had no relationship with elevation. LDMC generally decreased across all 25 species.

A more rigorous investigation of SLA across elevation was done by filtering the dataset to only include plant species that occurred in more than two sites. Of the 37 plant species after filtering, 17 of them showed a significant positive correlation of  $\log(\text{SLA})$  with elevation (Table 3). A few of the plants had elevation explaining a high percentage of the variation in  $\log(\text{SLA})$ . For example, *Geranium richardsonii*, a native to American Southwest mountainous regions with

cleft leaves, had 67.4% of the variation in SLA explained by increase of elevation (p-value <  $1.8 \times 10^{-5}$ ). With Bonferroni adjustment to account for multiple sampling, 11 species out of the 37 were found to have a significant relationship.

Table 3: Summary statistics between SLA and elevation of 37 species that occur in two or more sites. The 11 species bolded show a significant relationship after Bonferroni adjustment.

Species	Adj. R <sup>2</sup>	p-value	Species	Adj. R <sup>2</sup>	p-value	Species	Adj. R <sup>2</sup>	p-value	Species	Adj. R <sup>2</sup>	p-value
<i>Achillea millefolium</i>	0.079	0.001586	<i>Delphinium nuttallianum</i>	-0.005	0.469579	<b><i>Lupinus polyphyllus</i></b>	<b>0.571</b>	<b>0</b>	<b><i>Valeriana acutiloba</i></b>	<b>0.106</b>	<b>4.5e-5</b>
<i>Aconitum columbianum</i>	0.444	0.061214	<i>Erigeron speciosus</i>	-0.022	0.943857	<b><i>Mertensia ciliata</i></b>	<b>0.104</b>	<b>0.000176</b>	<b><i>Valeriana capitata</i></b>	<b>0.318</b>	<b>0.000247</b>
<i>Agoseris aurantiaca</i>	0.826	0.059845	<i>Erythronium grandiflorum</i>	0.024	0.058599	<i>Mertensia fusiformis</i>	0.097	0.000808	<b><i>Valeriana edulis</i></b>	<b>0.589</b>	<b>4.8e-5</b>
<i>Androsace septentrionalis</i>	0.043	0.965458	<i>Fragaria virginiana</i>	0.036	0.103254	<i>Poa reflexa</i>	0.009	0.298817	<i>Valeriana occidentalis</i>	0.18	0.000538
<i>Artemisia tridentata</i>	0.195	0.004064	<b><i>Geranium richardsonii</i></b>	<b>0.674</b>	<b>1.8e-5</b>	<i>Potentilla fruticosa</i>	-0.005	0.554535	<b><i>Veratrum californicum</i></b>	<b>0.141</b>	<b>8e-06</b>
<b><i>Bromus carinatus</i></b>	<b>0.43</b>	<b>0</b>	<i>Helianthella quinquenervis</i>	-0.011	0.822157	<b><i>Potentilla gracilis</i></b>	<b>0.098</b>	<b>1e-6</b>	<i>Veratrum tenuipetalum</i>	0.272	0.047255
<i>Bromus inermis</i>	0.327	0.062677	<b><i>Hymenoxys hoopesii</i></b>	<b>0.23</b>	<b>0</b>	<i>Pseudocymopterus montanus</i>	0.032	0.262099	<b><i>Vicia americana</i></b>	<b>0.371</b>	<b>0</b>
<i>Castilleja sulphurea</i>	-0.005	0.362569	<i>Lathyrus leucanthus</i>	0.226	0.003515	<i>Senecio crassulus</i>	-0.004	0.389437			
<i>Collomia linearis</i>	-0.01	0.80692	<i>Linum lewisii</i>	0.479	0.010964	<i>Taraxacum officinale</i>	0.042	0.003512			
<i>Viola nuttallii</i>	-0.111	0.958061	<i>Lupinus bakeri</i>	0.064	0.107445	<i>Thalictrum fendleri</i>	0	.327449			

## DISCUSSION

This study monitored nearly two decades of data on plant traits and soil organic carbon (SOC) across an elevational gradient in the East River Valley of Gothic, Colorado. SOC was found to have a s-curve pattern as elevation increased (Figure 2). This pattern did not change with time as this s-curve pattern was consistent year after year (Figure 4), though with some variation across time (Figure 3).

A simple logarithmic model showed that community-wide SLA has a significantly positive relationship with elevation and that 19% of the variation was explained by changes in elevation (Figure 7). As this is a logarithmic model, interspecific SLA has a saturating increase pattern with elevation. This patterning is consistent across time with only the recent data from 2018 not being significant after Bonferroni adjustment (Figure 8). Intraspecific SLA was more varied, showing increasing patterns, convex, or no relationship with elevation (Figure 9). Of the 37 species that occurred in more than 2 sites across the 15 years of data, 11 were found to have a significant relationship with elevation after Bonferroni adjustment (Table 3).

### Soil Organic Carbon

SOC content in soils is a balance between inputs (plant productivity) and outputs (autotrophic and heterotrophic respiration) (Tsui et al. 2013, Tsozué et al. 2019). A previous study found that communities with the highest average SLA and lowest average LDMC had about 80% gross primary productivity (GPP) and higher ecosystem respiration (ER), where the effects were intensified with more variation in SLA among communities, resulting in increased soil organic carbon (Happonen et al. 2022).

High SOC doesn't necessarily correlate with high plant productivity as demonstrated by Almont having the second highest number of plant species found uniquely at that site, yet the lowest SOC content. A potential explanation for why Almont has the lowest SOC content may be due to its climate of an arid, sagebrush community which increased respiration rates and the plants have adopted resource-conservative strategies to minimize evapotranspiration.

For CBT to have the highest SOC content in its soil consistently over the nearly 20 years of data must be a result of a tipping toward high plant productivity or low microbe respiration. Plant biodiversity has been found to have a convex relationship with elevation while microbe diversity has been found to decrease as elevation increases. Since CBT is a mid-elevation site, it is more likely that its high SOC content is due to increased plant productivity. Additionally, CBT has a relatively high moisture content (Figure 5), which may have caused a decrease in microbe respiration due to water saturating the soil and creating a hypoxic environment.

In decreasing order, Road, Pfeiler, and PBM had intermediate SOC content. As stated previously, SLA was found to increase with elevation and the highest elevation site plant species were found at were PBM or Pfeiler. Increase in SLA may lead to increase in plant productivity as it improves the rate of photosynthesis (Gunn et al. 1999, Cornelissen et al. 2003, Cheng et al. 2016). For these mid-elevation sites to have intermediate SOC content despite increase in plant productivity, biodiversity, and decrease in microbial diversity, there may have been an increase in respiration rate due to moisture content. All three of those sites were found to have similar soil moisture content compared to each other and intermediate moisture compared to Almont with low SOC content and CBT and Cinnamon, both with high SOC.

A similar reasoning to CBT's high SOC could explain why Cinnamon also has significantly high carbon content. Across the twenty years, it seems Cinnamon has only recently increased from the average SOC for all sites in 2022 (Figure 3). Intraspecific SLA showed that, for some species, SLA increased with elevation, sometimes significantly so (Table 3). Observing the soil moisture content, Cinnamon had relatively higher moisture content compared to all other sites in 2022 (Figure 6). Though it is difficult to make the claim that this increased moisture led to increased SOC content as Cinnamon has not been visited during the few years leading up to 2022, likely due to the COVID-19 pandemic. So, it is difficult to ascertain whether the high carbon and moisture content from 2022 are outliers or evidence of change. Additionally, moisture content results would be more representative of the moisture taken at the time of soil sampling. Higher or lower moisture content of sites of certain years may represent a particularly dry or wet season. For example, in 2022, there were many rainy days in Cinnamon which may explain the higher soil moisture content. It may not be accurate to relate these trends of moisture at each site to an entire year.

## Plant SLA

Alpine plants typically favor resource conservation due to severe abiotic constraints at high elevation, including protection from UV radiation and low temperature (Lambers and Oliveira 2019, Midolo et al. 2019, Cruz-Maldonado et al. 2021). SLA is a measure of leaf area divided by dry mass and is tied to a plant's growth (Cheng et al. 2016) as well as plant productivity and SOC input (Happonen et al. 2022). For the top 25 occurring species that showed an increase in SLA with elevation, leaf area typically was similar and increased with elevation. Meanwhile, leaf thickness tended to have a convex or decreasing relationship with elevation and LDMC decreased. So, for some plants, it was a decrease in mass and an increase in leaf area that caused the increase in intraspecific SLA. For example, *Bromus carinatus* had a significantly positive relationship with elevation ( $p\text{-value} < 1 \times 10^{-6}$ ) and 43% of variation in SLA could be explained (Table 3). *B. carinatus* had only a slight increase in leaf area across the elevational gradient, while leaf thickness showed a convex relationship and LDMC decreased. Thus, the largest contributing factor for the increase in SLA was the decrease in LDMC to better conserve resources and protect against abiotic stresses at higher elevations.

Previous studies have found a variety of relationships in SLA with elevation, both interspecific and intraspecific. One study found that for 11 species representing 4 different growth forms (rosette, tussock grass, shrub, and tree), interspecific SLA and leaf area decreased while LDMC and leaf thickness increased (Cruz-Maldonado et al. 2021). In a larger meta-analysis of 104 species across 71 studies, interspecific SLA decreases with elevation, resulting in thicker leaves and denser tissues (Midolo et al. 2019). Another study, however, found that bootstrapped means of plant traits on an elevation gradient in China (3000-4100 m) showed SLA to have a s-curve relationship with elevation (Henn et al. 2018). A study on community-level means found SLA to have a convex relationship to elevation (Kergunteuil et al. 2018). Investigating species individually, SLA decreased for six species, was stable for four, and increased for one species at higher elevations (Cruz-Maldonado et al. 2021). These studies, however, relied on functional groups or vegetation classifications to describe functional properties of vegetation which is difficult to compare across studies as classifications may differ across biomes (Happonen et al. 2022). Standardizing plant functional trait measurements could

be the key to demonstrating the variation in leaf properties and its relationship to ecosystem processes such as carbon cycling. Further studies should be conducted to investigate the mechanism between plants varying changes in SLA with elevation.

A study on tundra communities found that taller plants increase photosynthesis and above-ground carbon while changes in plant traits (higher SLA and lower LDMC) increases soil organic carbon and decreases above-ground carbon (Happonen et al. 2022). Thus, plant size and leaf economic traits have separate effects on carbon cycling. Faster economic traits (higher SLA and lower LDMC) have a well-established strong positive relationship with greater photosynthesis (Wright et al. 2004, Stuart Chapin III et al. 2009), but have also been found to have higher ecosystem respiration through production of more nutrient-rich litter easily broken down by microbes and increasing of root exudates which facilitates root respiration (Happonen et al. 2022). Slower leaf economics (lower SLA and higher LDMC) produce relatively small carbon inputs to the soil as they tend to retain their leaves (Wright et al. 2004) and might have ecto- and ericoid mycorrhiza which decompose organic matter faster unlike faster economics whose arbuscular mycorrhizae retain more carbon in the soil (Happonen et al. 2022). With the variety of responses in plant leaf traits (both intraspecific and interspecific), elevation likely is but one factor influencing trait variation as supported by our results and those of previous studies.

## **Further Research**

As tools to monitor long-term change in a localized environment, elevational gradients provide insight to how climate change could impact ecosystem processes and plant communities. Consistent with previous studies, SOC did increase with elevation, but to a certain extent. Comparing Almont, our lowest site, to Cinnamon, our highest elevation site, we can clearly see SOC significantly increased with elevation, consistent with previous findings of SOC decreasing with increasing temperature (Soong et al. 2021; Hsu et al. 2018; Crowther et al. 2016; Saleska et al. 2002). The results from our mid-elevation sites, however, suggests there is more than one underlying driver behind changes in SOC. Possible mechanisms behind our results included microbial and plant diversity, soil moisture content affecting respiration, and plant traits that could affect plant productivity. All of which likely worked in concert to produce the SOC results

we got. This study only focused on SOC content in soil samples and observations of plant traits observed at each site. A more thorough study is required, investigating organic and inorganic stores in soil, a consistent record of plant composition and traits, and a measure of microbial diversity. More details as to the mechanism behind SOC deposition in soil and how it changes across an elevational gradient would provide better information on the intensity of the climate-carbon feedback loop in this area.

The sampling methodology of plant species composition was not consistent throughout the study period as data was collected by several different people. This collaborative effort introduced errors in data, incomplete data, and overall inconsistencies across the study. For example, some years seemed to gather only 3 samples of each plant species observed at each site and used those samples as a representative of the entire species leaf traits, while other years destructively sampled one plot per site for leaf trait measurements. This inconsistency prevented us from accurately monitoring any species composition changes across the period. Any differences we noticed in species composition could be attributed to sampling bias due to the methodology of the study. Despite this, the simple logarithmic model of community-wide SLA significantly increasing with elevation across time suggests a veritable trend. SLA increasing with elevation may suggest a greater need to conserve nutrients at lower elevations due to increased temperature, which can be causing drought, or from other unidentified sources of abiotic stress. Though it is important to note that there are species-specific responses to the environment and elevational gradients (Albert et al. 2010, Cruz-Maldonado et al. 2021). Ultimately, more research should be done on the comparison of inter- and intraspecific leaf traits on an elevational gradient.

Finally, there could be other changes influencing SOC such as herbivory destroying specific plants or altering functional traits, thus influencing carbon input to the system. Human trampling while sampling at the site was avoided as best as possible, but some sites were located near trails and camping sites. Destruction of plants or compaction of soil could impact plant productivity or microbial environmental conditions, restricting respiration and the removal of carbon from the system. Overall, this study only focused on changes in plant productivity and abiotic conditions related to changes in elevation as explanations for changes in SOC and more studies should be done to further investigate all the various influences.



## **Conclusion**

Elevation causes a s-curve relationship in carbon cycling and causes a variety of responses in alpine plant traits, of note is a significant increase in SLA for several species. Overtime, SOC content had slight variations, but was overall consistent. Plant communities could not be accurately predicted to change given the nature of the data set. As the s-curve for SOC and the increase in interspecific plant SLA were consistent across time, elevation's effect on plant communities and ecosystem processes did not change over the study period. Investigating trends in ecosystem processes, like carbon cycling, and plant communities in vulnerable biomes such as alpine environments will improve our understanding of climate change and better models and management strategies for both flora and responding fauna.

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