

# SOIL BIOGEOCHEMICAL AND VEGETATIVE RESPONSE TO SLASH PILE BURNING IN LODGEPOLE PINE FOREST

A Thesis

Presented to

The Faculty of the Environmental Program

The Colorado College

In Partial Fulfillment of the Requirements for the Degree

Bachelor of Arts in Environmental Science

By

Cosette A. Turvold

May 2021



---

Dr. Rebecca T. Barnes  
Associate Professor of Environmental Science, Colorado College



---

Dr. Michael J. Wilkins  
Associate Professor of Soil and Crop Science, Colorado State University

## **Table of Contents**

<b>Abstract</b>	3
<b>Acknowledgements</b>	4
<b>Introduction</b>	5
Shifting Fire Regime	5
Lodgepole Pine Ecology	8
Interval Squeeze Hypothesis	8
Forest Management Implications	10
Research Questions	11
<b>Methods</b>	12
Study Area	12
Soil Collection	13
Vegetation Characterization	14
Soil Analysis	14
Data Processing	16
<b>Results</b>	17
Soil Characterization	17
Soil Respiration and Bioavailability Time Series	17
<b>Discussion</b>	20
Soil Response to Disturbance	20
Vegetation Succession	22
Conclusions	25
<b>References</b>	27
<b>Figures</b>	31

## **Abstract**

Climate change is shifting fire regimes and changing localized conditions in forests around the globe. Forest vegetation and soils act as major global carbon sinks, and this carbon storage is threatened by increasing fire frequency and severity, especially if altered disturbance regimes result in a shift in vegetation. The effects of slash burn piles on soil biogeochemistry and revegetation contribute valuable information on forest fire ecology and the feedbacks between the soil, vegetation, and microbiome after severe fire events. Clear cut and burn pile soils collected in the Medicine Bow-Routt National Forests in northern Colorado were analyzed for microbial activity and elemental composition over a 60 year chronosequence. Soils in burn pile scars had less organic matter and generally lower microbial activity compared to soils from their clear cut harvest counterparts. Revegetation trends in a similar chronosequence and location confirmed that effects of burn piles influenced soil biogeochemistry for decades if not longer. Ultimately, pile burning impacts the resilience of the forest to future severe fire events. In combination with expected warmer, drier climatic trends, results suggest that a more severe fire could lead to a shift away from forests and towards shrublands. Rehabilitation of burn scars is essential to maintain forest ecosystems in Colorado.

## **Acknowledgements**

First and foremost I would like to thank my amazing advisor, Dr. Rebecca Barnes. Over the course of forming this thesis she supported me to pursue research work and catalyzed my enthusiasm for soil biogeochemistry. Becca will always be a female scientist I look up to for inspiration and advice. She took me under her wing in the middle of a pandemic and taught me how to navigate being a woman in STEM; connecting me to her network, sending endless resources and always encouraging me to keep working and digging for answers in my hardest times. I am forever grateful for her invested time and effort, and I will always work to become the female scientist to others as she was to me.

This research would not have been possible without the collaboration of Dr. Charles Rhoades and Tim Fegel of the United States Forest Service, Amelia Nelson and Dr. Mike Wilkins of Colorado State University. They generously collected the soil samples for this thesis and allowed me to engage with their vegetation data so that I could dive further into my forest ecology interests. I am so excited to be following their path after graduation and am thankful for their collaboration on this research.

My appreciation also extends to my lab partners Michelle Wolford and Oliver Dunn. They were always there for me, any hour of the day or night, and because of their friendship I was able to accomplish writing this thesis. I loved working in the lab, talking R code, and especially editing our papers collaboratively. It has truly been a pleasure to work with them and I look forward to seeing their achievements in the future.

Lastly, I would like to thank the people who have always supported my path to becoming a scientist. My friends and family kept me aligned towards my goals through four years of undergraduate studies, and while forming this research, they played a massive part in my personal growth. I especially thank my parents for being my biggest supporters and motivators.

## **Introduction**

Fire is a dominant disturbance regime in many terrestrial landscapes, and recent global climate models project a more fire-prone future, especially in high-latitude ecosystems and the western United States (Williams & Abatzoglou 2016; Enright et al. 2015). As patterns of wildfire in forests continue to shift due to climate change, human impacts on forests become even more vital to understand. However, management practices addressing these changes are largely reactive rather than preventative, and the expense of wildfire disasters often falls into the hands of taxpayers. Wildfires in the western US have cost local governments and communities millions of dollars (Colorado Sun 2020), with each subsequent fire season increasing in length and number of severe fires (Williams & Abatzoglou 2016). The 2020 fire season in Colorado was the worst on record, including the Pine Gulch fire (the largest recorded wildfire in Colorado history), which burned 139,007 acres and three additional fires burning 67,563 more acres; as a result, the government spent more than \$77 million to manage these disasters (Colorado Sun 2020).

### *Shifting Fire Regime*

Carbon sequestered by US forests offsets 12-19% of US fossil fuel emissions (Ryan et al. 2010), and thus these forests play a large role in the global carbon cycle and balance (Loudermilk et al. 2013). Climatic conditions are becoming more conducive to wildfires in the Western U.S and stressing forest ecosystems, as earlier snowmelt drives water deficits and increased fire-season fuel aridity (Westerling et al. 2006; Williams & Abatzoglou 2016). Climate-driven changes have implications for the global carbon cycle, namely, the rate of carbon sequestration and carbon storage in forest ecosystems (Loudermilk et al. 2013). Northern-latitude forests act as carbon sinks, uptaking and storing carbon through vegetation growth and accumulating soil organic matter (Loudermilk et al. 2013). Wildfires release stored carbon by

burning both living and nonliving biomass and carbon stocks in soils, further increasing the concentration of CO<sub>2</sub> in the atmosphere, exacerbating the initial drivers (Ryan et al. 2010). Furthermore, climate-enhanced wildfire activity disturbs the ability of forest ecosystems to sequester and store carbon by altering the dynamics of carbon partitioning between vegetation, soil, and the atmosphere (Van Der Heijden et al. 2008).

Soil is the largest terrestrial repository of organic matter (~1500 Gt globally), storing as much carbon as vegetation and the atmosphere combined (Crowther et al. 2019). Within the soil matrix, microbial communities play key roles in carbon and nitrogen cycling and the accumulation of soil organic matter (Van Der Heijden et al. 2008; Noronha et al. 2017). Therefore, given the importance of soil biogeochemical processes in cycling nutrients between the biosphere and atmosphere, management of soil could help combat loss of biodiversity and negative impacts of climate change on fire regimes (Crowther et al. 2019). Global change alters the selective pressures that forest ecosystems are evolutionarily adapted to, and time lags associated with these changes could span into the next century, beyond the timeline of this study (Dove et al. 2020; Loudermilk et al. 2013).

Impacts of fire on soil biogeochemistry and microbial communities vary with severity and time since fire (Dove et al. 2020; Hart et al. 2005). On shorter timescales, wildfire decreases microbial respiration due to the combustion of soil organic matter and denaturing native microbial communities (Knelman et al. 2015; Dove et al. 2020). Volatilization (e.g. converting chemicals to gaseous form with extreme heat) of soil organic matter happens when a severe fire reaches threshold temperatures of at least 202°F (nitrogen threshold = 414°F) on the soil surface (Knoepp et al. 2005). For example, severe fires in California volatilized organic matter, releasing stored carbon to the atmosphere and leading to a 20% decrease in soil carbon (Miesel et al. 2018;

Dove et al. 2020). Nitrogen availability within a few years of fire is generally elevated due to increased rates of organic matter decomposition and increased abundance of nitrogen-fixing plants (Johnson et al. 2005; Dove et al. 2020). Long term effects of high severity fire on soils are poorly understood but are thought to include changes in microbial biomass, enzyme activity, ammonium concentration, and pH (Certini 2005; Knelman et al. 2015). Importantly, the changing climate in the Rocky Mountains of Colorado, associated with increasing temperatures and reduced precipitation, is likely to lessen long-term soil moisture content. While these processes will further impact soil biogeochemical processes, they will also increase the likelihood of more frequent and severe wildfires. Together, these interdependent processes and feedback loops will have long-term impacts on the role of forests in regional and global carbon and nitrogen cycles.

Additionally, climatic shifts like increasing temperatures and decreased precipitation reduces long-term soil moisture content, with subsequent effects on decomposition rates and nitrogen availability (Loudermilk et al. 2013; Littel et al. 2009). Microbial communities also respond to increased temperatures by lowering landscape heterotrophic respiration and decreasing the humification of detritus (e.g., disintegrated organic waste material, like plant litter or rocks), which alters the rate at which nutrients are able to cycle through above and belowground storage mechanisms (Loudermilk et al. 2013). Understanding the effects of global change on shifting soil biogeochemistry and feedbacks with the aboveground biosphere is important for monitoring the productivity of forest sequestration and storage of global carbon stocks (Loudermilk et al. 2013; Dove et al. 2020). The departure of fire regimes from natural frequency and severity has the potential to affect the resistance and resilience of these imperative soil processes and forest revegetation (Dove et al. 2020).

### Lodgepole Pine Ecology

In the western US, specifically in the northern Rocky Mountains of Colorado, Lodgepole pine forests (*Pinus contorta* variation *latifolia*) are adapted to sustain a combination of very infrequent, high-severity crown fires and more frequent low-severity surface fires (OECD 2010). Lodgepole pines typically live for 250-600 years, reaching reproductive maturity early, between 5-10 years (OECD 2010). Given their adaptations to fire, an unaltered fire regime is important for seedling establishment, stand density, age structure, and species composition in Lodgepole pine stands (Lotan 1976). For example, their cones are often serotinous, requiring high temperature events to release their seeds. However, increased frequency of high-severity crown fires can eradicate mature-reproductive trees and viable seeds (OECD 2010). Thus, altered frequency of high severity fires influences the revegetation of Lodgepole pine forests, directly impacting soil characteristics and biogeochemical processes (Knelman et al. 2015). Recognizing the soil characteristics and microbial processes that confine successful revegetation after disturbance can predict how these ecosystems will change within an altered fire regime.

### Interval Squeeze Hypothesis

The interval squeeze hypothesis outlines the compounding effects of climate change and shortened fire-free time intervals on woody species' persistence into the future (Enright et al. 2015). Shifting soil biogeochemistry processes due to climatic conditions and limited forest regeneration can be incorporated into the explanation of threatened woody species persistence. The time period for successful forest regeneration (i.e., the interval) is getting shorter (i.e., squeezed) for three reasons: (1) shorter fire-free intervals increase the risk that woody species will burn before reaching reproductive maturity; (2) drier and warmer conditions drive woody



plants to become reproductive later and produce fewer viable seeds; and (3) heat and drought stress disproportionately impact trees in their youngest stages leading to reduced seedling success (Enright et al. 2015; Stevens-Rumann et al. 2017). In conjunction with altered climatic conditions and squeezed regions of successful forest regeneration, soil biogeochemistry generally shifts to be less fertile, water-limited, and less productive when cycling nutrients (Loudermilk et al. 2013; Littel et al. 2009; Dove et al. 2020). As a result, soil microbial communities may experience compositional and functional shifts that limit their ability to support pre-established tree stands and may contribute to shifting vegetation dynamics from forests to shrubland (Figure 1). The combination of these interval squeeze effects has led to reduced woody species persistence and shifts in tree demographics with increased fire frequency (Enright et al. 2015).

As plants recolonize after fire disturbances, they influence soil microbial communities through root exudation, plant litter inputs, and increased nitrogen demand (Dove et al. 2020) and are the main driver of soil biogeochemical processes in the long term (Hart et al. 2005). Climate induced global shifts of forest to shrublands would likely alter the soil functionality and microbial communities to new stable states. Further, the selective pressures of soil characteristics and microbial communities can transform the conditions of growth to be less suitable for forest recovery and drive stand structure to become prone to severe crown fires (Tiribelli et al. 2018). Thus climate change is threatening forest's futures by influencing the carbon stored within their biomass and the forest floor.

### Forest Management Implications

Western U.S. forests are also threatened due to past policy and forest management techniques. Prior to Euro-American settlement, climate controlled natural fire regimes and Native American tribes used fires to promote valued resources by preserving ecosystems (Littel et al. 2009; Lake et al. 2017). North American tribes used prescribed fires as a tool to maintain habitats that sustained their cultures, economies, and traditions (Lake et al. 2017). Tribal uses of wildfires decreased when Euro-Americans colonized and repeatedly violated trust responsibility with Native American tribes, the effects of colonization on suppressing Native American traditional wildfire knowledge are still perpetuated today (Lake et al. 2017). The U.S. federal government began implementing the U.S. Army to limit the use of fire to manage forests in 1886, when newly founded national parks were patrolled for unauthorized livestock grazing, timber harvesting, and fire suppression (Stephens & Ruth 2005; Lake et al. 2017). An immense amount of dead fuels in forests had built up for almost a century, and wildfires began burning uncontrollably (Williams & Abatzoglou 2016). Army patrols suppressed all wildfires until 1968, when the first prescribed fire was used in Sequoia-kings Canyon National Forest (Stephens & Ruth 2005). Prescribed fires became a national strategy to combat severe wildfires starting in the late 1960s (Stephens & Ruth 2005).

Today, as part of an integrated forest management approach, timber harvesting is followed by slash piling and burning. Harvesting timber produces large amounts of fine fuels and slash debris when using the clear cutting method (Esquilín et al. 2007). Lodgepole pine stands are clear cut to mimic severe fire, as the resulting slash contains a large number of serotinous cones and leads to sufficient seed dispersal for natural regeneration (OECD 2010). To help manage fuel loads, slash pile burning is used to keep harvested timber litter from piling up; fuels

are piled and disposed of by burning, concentrating high severity fire impacts, including destruction of unopened cones and thus seed supply, to discrete patches in the landscape (Esquilín et al. 2007; Lotan 1975).

### Research Questions

The repercussions of clear cutting with and without slash burn pile management on soil biogeochemistry and carbon stocks are unclear. For example, what are the consequences of the intense soil heating (pile burns oftentimes get hotter than most severe fires) on soil characteristics and organic matter pools over the long-term? How does soil heating impact microbial activity, and what factors of soil characteristics play a role in altering microbial productivity? How do resulting changes in soil biogeochemistry and microbial communities potentially impact the global carbon cycle, and the ability of forests to remain as a carbon sink? This study aims to examine the consequences of clear cut and burn pile management and the resulting vegetation shifts on soil biogeochemistry in northern Colorado Lodgepole pine forests.

Given that severe, concentrated fire has lasting implications on organic matter and microbial communities (Knoepp et al. 2005; Hart et al. 2005), it seems likely that both soil composition and microbial activity (as measured by respiration rates) could be affected for decades. Shifts in these essential soil components may impact the vegetation recovery and future elasticity of forest soils amidst a climate crisis. Furthermore, the recolonized vegetation species will have major impacts on soil biogeochemistry. How will a more herbaceous rapid-resprouting understory in burn piles affect the soil biogeochemistry, compared with clear cut plots characterized by enhanced tree recovery (Rhoades & Fornwalt 2015)?

Building off Enright's (2015) interval squeeze hypothesis, the persistence of Lodgepole pine tree stands after clear cut and burn pile treatments will be assessed. Vegetation recovery will

affect the future soil characteristics and alter biogeochemical processes. Understanding the effects of burn pile fires on soil will shed light on the resilience of Lodgepole pine forests after fire disturbances, especially amidst shifting climatic conditions. The conclusions of this research can be applied as a proxy for larger forest-scale disturbances, such as severe wildfires.

## **Methods**

### Study Area

This study was conducted in the Medicine Bow-Routt National Forests managed by the US Forest Service (USFS) in Colorado, USA. The Medicine Bow-Routt Forest covers approximately 1.2 million acres in North-Central Colorado and encompasses seven mountain ranges and parts of six counties (Dersch 2000). The study area was located at a mean elevation of 2900 m and spanned a 500 km<sup>2</sup> portion of the Parks Ranger District (Rhoades & Fornwalt 2015). Mean temperature in winter (January) and summer (July) are -8°C and 13°C respectively, while total annual precipitation averages 65 cm (Rhoades & Fornwalt 2015). Soils are formed from bedrock consisting of sandstone, siltstone, and conglomerate residuum and colluvium, and the primary soil types are loamy-skeletal, sandy-skeletal, and typic cryoboralfs & cryochrepts (Rhoades & Fornwalt 2015). The ecologic study area is encompassed in the Southern Rocky Mountain Steppe Ecoregion (Bailey 1998).

The dominant stand structure in the Medicine Bow-Routt Forest, as described in Rhoades & Fornwalt (2015) is Lodgepole pine (*Pinus contorta*), growing in association with subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and quaking aspen (*Populus tremuloides*). Lodgepole pine grows in pure, even-aged stands on lower elevation southerly aspects, whereas stand structure on higher elevation northerly aspects tend to be relatively

heterogeneous consisting of more firs, spruces, and aspens. Burn scars are dominated by a patchy herbaceous understory composed of graminoids and forbs, while clear cut forest plots were characterized by enhanced growth of adult recolonizing trees. To reduce surface fuel loads and suppress unwanted fires after timber harvests, post-harvest preparation includes piling and burning slash debris in burn piles. Burn piles concentrate a lasting severe fire in a small area when set on fire. Slash piling occurs within a few years of a harvest in the winter to reduce the risk of unintended fire spread. Burn pile scars in harvested forests have no applied management strategies for rehabilitation (Rhoades & Fornwalt 2015).

Burn pile openings within the clear cut regenerating forest were identified on true-color aerial photographs by Rhoades & Fornwalt (2015; Figure 3). Nine clear cut harvest units were randomly selected for soil collection from five decades of treatment ranging from 1960 to 2000. The clear cut harvest sites were matched with an adjacent (20 m apart) burn pile counterpart encompassed within the regenerating forest site. Generally, the sites were selected along a uniform slope contour, avoiding clear indicators of soil disturbance (rutting) unrelated to the study. The regenerating forest sites (i.e., previously clear cut) were located on slopes <30% grade, averaged 15 ha in size, and contained 2.2 burn scars/ha on average. Burn pile scar sites had diameters of 10-15 m (Rhoades & Fornwalt 2015). Soil collection sites ranged from 40.50096°N to 40.38102°N and -106.07336°W to -106.18936°W (Figure 2).

### Soil Collection

Soils (0-10 cm depth) were collected by Amelia Nelson (Ph.D. student at Colorado State University), Dr. Charles Rhoades (USFS), and Tim Fegel (USFS) in August 2020 using a 7.5 cm diameter corer after removal of the O horizon. Soil samples from burn piles and adjacent regenerating forests representing each decade of disturbance were collected (n=98); rocks,

mosses, and lichens were removed, and soils were sieved (2 mm) and further processed at the USFS Lab in Fort Collins. A subset of the soils that were not sieved (n=47) representing each decade of disturbance were sent to Colorado College for incubation experiments and for additional characterization of bulk organic matter in the upper mineral soil.

### Vegetation Characterization

Vegetation data from Rhoades and Fornwalt (2015), collected in 2010 in the same study area describe how vegetative communities differ between treatments (pile burns and regenerating clear cut forests). Briefly, trees and understory vegetation were measured in a 3m radius in paired regenerating forest and burn pile sites. Adult tree diameter at breast height (DBH, 1.4 m above surface) was recorded for trees larger than 2.54 cm DBH, and tree diameters less than 2.54 cm DBH were tallied as seedlings. Tree density (trees/ha), graminoid, forb, and shrub coverage was visually estimated in four 1m<sup>2</sup> quadrants located in each burn scar and regenerating forest pair (Rhoades & Fornwalt 2015).

### Soil Analysis

Unsieved and sieved soils of all decades and treatments were analyzed for their elemental composition. Sieved samples (n=90) were used as the primary analysis of soil characterization and were analyzed by our partners at the USFS (Rhoades & Fegel *unpublished data*). Elemental analysis on sieved soils (2 mm) was completed by the USFS (Rocky Mountain Research Station, Fort Collins, Colorado) on a LECO 1000 CHN Elemental Analyzer (LECO Corporation, St. Joseph, Michigan). Unsieved soil sample analyses were used for the analysis of respiration, bioavailability, and fraction oxidized.

For 47 unsieved, whole soil samples, a ~30 gram portion of each soil sample was removed from storage at 3°C and oven dried at 60°C for ~ 24 hours. Samples were weighed

before and after drying to determine gravimetric soil moisture. The dried samples were ground to a powder using a Certiprep 800 Mixer/Mill and packed in tin capsules for elemental and isotopic analysis. The elemental composition (%C and %N) of each incubated sample (see below) was determined on a CE Elantech elemental analyzer at Colorado College. A known soil standard (C=3.776% and N=0.388%) and duplicate samples (one for every 10 samples) were used to ensure and track quality control.

To determine how bioavailability and respiration rates of soil organic matter change with microbial activity as time since treatment increased, two-week laboratory incubation experiments were conducted on 39 unsieved soils from burn piles and regenerating forests, in triplicate. Soil samples were well mixed within the sampling bag and ~ 30 g was added to pre-combusted (500°C for 5 hrs) glass jars, which were then topped with an airtight lid fitted with a sampling port. After two to four hours of incubation time, the headspace of each jar was sampled and measured for CO<sub>2</sub> concentration (ppmv) on Colorado College's SRI-8610C Gas Chromatograph (FID). Gas standards of 100, 1000, and 10000 ppm of CO<sub>2</sub> were used to calibrate the SRI Gas Chromatograph, and ambient lab air was used to represent the baseline CO<sub>2</sub> conditions in the jars at the start of each incubation period. Soils were kept at room temperature (22°C) throughout the experiment and open to the atmosphere between time-points to prevent anoxia. Before each time point T0 - T4: 2 hrs, 24 hrs, 72 hrs, 168 hrs (one week), and 336 hrs (two weeks) from set up, the soils were weighed and brought back to field moisture conditions by adding MilliQ water based on original mass at start of the experiment.

Data Processing

The CO<sub>2</sub> ppm data collected from the gas chromatograph was converted to soil bioavailability using equation 1.

Equation 1

$$CO_2 \text{ respired (mg/day)} \div \text{Organic C in soil sample (g)} \Rightarrow \text{Bioavailability (mg C - CO}_2\text{/g soil C/day)}$$

Soil respiration rate was calculated using equation 2.

Equation 2

$$CO_2 \text{ respired (mg/day)} \div \text{Soil sample mass (g)} \Rightarrow \text{Respiration Rate (mg C - CO}_2\text{/g soil /day)}$$

Additionally, the cumulative amount of organic carbon oxidized over the two week incubation period was calculated using equation 3.

Equation 3

$$\Sigma CO_2 \text{ respired (mg/2 weeks)} \div (\text{Organic C in soil sample (g)} * 1000) \Rightarrow \text{Fraction carbon oxidized (\%)}$$

Organic carbon in the soil (g) was determined using %C in each soil sample multiplied by the dry soil mass (g). Production of CO<sub>2</sub> was determined by measuring the accumulated CO<sub>2</sub> in the headspace of the jar during the incubation period.

All statistical and graphical analysis was performed in R Studio version 1.1.456. ANOVA tests with Tukey family corrections were performed to compare soil elemental composition, bioavailability rates, respiration rates, and fraction oxidized by disturbance (clear cut versus clear cut and burn) and by time since disturbances. Pearson's correlations and descriptive statistics outlined the general relationships and distributions of soil analysis data. In addition, the 9 pairs of incubated samples (regenerating forest vs burn pile) were matched by location and their soil characteristics and compared using paired t-tests. Significant results were interpreted with 95% confidence, p-values < 0.05.



## **Results**

### *Soil Characterization*

Burn pile unsieved soils contained less carbon ( $3.60 \pm 0.29\%$ ) than regenerating forest soils ( $4.48 \pm 0.38\%$ ,  $p=0.0266$ ). However, nitrogen content was not significantly different between burn pile ( $0.44 \pm 0.14\%$ ) and regenerating forest ( $0.49 \pm 0.16\%$ ) soils ( $p=0.193$ ), and there was also no significant difference between the C:N ratio in the burn pile ( $32.10 \pm 1.63$ ) and regenerating forest soils ( $33.07 \pm 1.16\%$ ,  $p=0.739$ ).

Soil organic matter content remained fairly uniform as time since recovery increased in both burn piles and regenerating forest soils (Figure 4). Mean percent carbon in burn pile soils was lowest at 40 years since burn treatment ( $3.10 \pm 0.52\%$ ) and highest with the most time (60 years) since burn recovery ( $4.2 \pm 0.8\%$ ). Forest soil percent carbon was the largest out of both treatments at 20 years since recovery ( $6.12 \pm 1.02\%$ ) and inconsistently decreased until 60 years after clear cutting ( $3.79 \pm 1.02\%$ ). Overall, there were no significant differences in organic carbon content between all decades since disturbances ( $p=0.127$ ). Nitrogen content in both forest and burn pile soils consistently decreased as time since recovery increased. There were significant differences between organic nitrogen content and decades since clear cut and burn treatment ( $p=0.0003$ ).

### *Soil Respiration and Bioavailability Time Series*

Whole, unsieved soil organic carbon and nitrogen content did not differ between burn pile and regenerating forest samples ( $p=0.739$ ,  $p=0.879$ ). Organic carbon was not different between all years since both treatments occurred ( $p=0.171$ ). However, organic nitrogen content in burn scars was significantly different between 50 years and 30 years since fire ( $p=0.034$ ). There was a difference between soil moisture in the burn pile ( $1.99 \pm 0.24\%$ ) and regenerating

forest soils ( $3.21 \pm 0.24\%$ ,  $p=0.0283$ ). Soil moisture increased with soil organic carbon content in both burn scars ( $R^2=0.25$ ,  $p=0.009$ ) and regenerating forest plots ( $R^2=0.30$ ,  $p=0.052$ , Figure 5). Time since disturbance was not statistically significantly related to soil moisture content ( $p=0.1018$ ).

Organic carbon and nitrogen content were not significantly different between the whole (unsieved) and sieved soil samples ( $p=0.5542$ ,  $p=0.06303$ , respectively), and thus similar relationships with disturbance history hold. Whole soil samples from paired burn piles and regenerating forest plots were incubated over a two week period to assess differences in carbon residence time and microbial activity in the upper soil horizon across this disturbance gradient. The incubation experiments revealed a consistent pattern of respiration and bioavailability rates among all samples over two weeks. Average respiration rates increased through the first week of the time series, with stable respiration rates measured at the end of week 1 and 2 (i.e. T3 and T4, Figure 6). Additionally, bioavailability rates of all samples one and two weeks after the initial set up were also not different from each other. Respiration and bioavailability rates at all time points before one week into incubation (2, 24, 48 hrs) were statistically different from each other across all decades of treatments. Recognizing the differences between respiration (and thus bioavailability) rates before and after the one week time point, the triplicate averages from the week 1 and week 2 time points are used to analyze differences in respiration and bioavailability rates across the chronosequence.

Comparing average respiration rates and bioavailability of regenerating forest soils across the chronosequence revealed no distinct patterns with time since disturbance (Figure 7). Average regenerating forest soil respiration rate was lowest 20 years after clear cutting ( $0.018 \pm 0.008$  mg C- CO<sub>2</sub>/g soil/day) and highest 30 years after clear cutting ( $0.046 \pm 0.014$  mg C- CO<sub>2</sub>/g soil/day).

Overall, regenerating forest soils had no significant difference between average respiration rates with time since disturbance ( $p=0.29$ ). Average bioavailability rates of forest soils were highest 50 years since clear cut ( $0.87 \pm 0.4$  mg C-CO<sub>2</sub>/g soil C/ day) and lowest 60 years since clear cut ( $0.34 \pm 0.21$  mg C-CO<sub>2</sub>/g soil C/ day). Regenerating forest soil bioavailability rates also did not vary significantly with decades since disturbance ( $p=0.653$ , Figure 7).

Average respiration and bioavailability rates of burn pile soils were also analyzed over the chronosequence. Burn pile soils had the lowest respiration rates 30 years since burning ( $0.0127 \pm 0.002$  mg C- CO<sub>2</sub>/g soil/day) and highest 40 years since burning ( $0.0178 \pm 0.002$  mg C- CO<sub>2</sub>/g soil/day). Average respiration rates in burn piles increased from 20-40 years since fire then stabilized around  $\sim 0.0175$  mg C- CO<sub>2</sub>/g soil/day from 40-60 years since fire. Bioavailability of burn piles soils followed a similar increasing trend through 20-40 years since fire and stabilized around  $\sim 0.5$  mg C- CO<sub>2</sub>/g soil C/day from 40-60 years since fire (Figure 7). Ultimately, there was no significant difference in burn pile soil bioavailability or respiration rates as time since fire increased ( $p=0.50$  ,  $p=0.65$ ).

Regenerating forest soils had a higher rate of respiration ( $0.028 \pm 0.005$  mg C- CO<sub>2</sub>/g soil/day) than burn pile soils ( $0.017 \pm 0.005$  mg C- CO<sub>2</sub>/g soil/day) ( $p=0.00367$ ). There was no significant difference between bioavailability rates of forest soils ( $0.64 \pm 0.11$  mg C-CO<sub>2</sub>/g soil C/ day) and burn pile soils ( $0.46 \pm 0.04$  mg C-CO<sub>2</sub>/g soil C/ day) ( $p=0.653$ ). Total carbon oxidized over the experiment in the burn pile and regenerating forest soils were not statistically different ( $p=0.072$ ) and time since disturbance did not affect the total amount oxidized ( $p=0.112$ ).

## **Discussion**

The openings created by slash burn piles have multi-decadal impacts on the soil characteristics and vegetation dynamics in Lodgepole pine forests (Rhoades & Fornwalt 2015). While clear cutting itself may impact the recovery of the ecosystem, this study documented the mechanisms in which slash burn piles perpetuate a longer landscape legacy than clear cutting alone. Additionally, soil and vegetative response to slash pile burning served as a proxy for larger forest-scale processes and shed light on the trajectory of Lodgepole pine forests in a changing climate.

### *Soil Response to Disturbance*

The extreme heating associated with burn pile fires penetrates the soil, destroying seed reserves (248°F), plant root tissue (158°F), soil microbes (320°F), organic matter (202°F), and plant nutrients (Certini 2005; Knelman et al. 2015; Esquilín 2007), likely leading to the observed persistent differences in the soil biogeochemistry between clear cut Lodgepole pine forests and enclosed burn pile scars (e.g. soil C and C:N, Figure 4). Slash pile soils experienced temperatures as high as 347°F-572°F under the pile in a study documenting soil geochemical response of pile burning in a clear cut Lodgepole pine forest (Esquilín 2007). Considering the nature of fire in burn pile management, the majority of the organic carbon and nitrogen in the burn scars likely reached its threshold temperature and volatilized (Knoepp et al. 2005, Figure 4) along with mortality of plant roots and microbial communities (Esquilín 2007). Results indicate that soil moisture was significantly lower in burn pile soils and, unsurprisingly, positively related to soil carbon content within the regenerating forest and burn scar plots (Figure 5), given the adsorptive nature of SOM (Knoepp et al. 2005). The root systems of old lodgepole pine stands in clear cut plots likely remained intact and helped preserve the underlying soil characteristics

below the top soil horizons (Dove et al. 2020; Esquilín 2007), corresponding with greater moisture and organic matter content in these soils.

Pile burning decreases microbial community activity, as indicated by significantly lower respiration rates in burn scars (Figure 7). Burning the piles of forest litter destroyed not only the underlying root systems and microbes near the surface but likely negatively affected the microbial communities in deeper layers of the soil that processed organic matter (Certini et al. 2005; Hart 2005). Mortality of plant root tissues and microbes in the burn piles with oxidation of organic matter initiated the lasting differences in burn scars and surrounding clear cut lodgepole pine forests by disturbing pools of organic matter and biogeochemical methods of processing and cycling. Respiration rates in the burn scars remained low and consistent as the time since fire increased in burn scars, whereas in clear cut plots microbial activity increased nonlinearly in the chronosequence (Figure 7). The variability in microbial respiration rates of clear cut plots in the chronosequence can be attributed to the heterogeneity in soil organic matter and moisture (Figure 8). While respiration rates were highly correlated with soil carbon ( $p=0.0002$ ); multivariate regression revealed that moisture was the main determiner of microbial respiration and explained 60% of the variance in respiration rates ( $p<0.0001$ ).

The bifurcated states of soil recovery in a mosaic of burn scars and clear cut forests further the long-term consequences of burn scars and exacerbate the threat of shifting microbial communities to be better adapted to drier conditions and shorter-fire intervals (Esquilín 2007). As climatic conditions become drier, this research indicates that microbial activity will decrease with moisture content in both burn scars and regenerating forests. The shifting microbial activity associated with drier conditions and increased wildfires affect which species are able to recolonize after fire events, in turn this vegetation will exert dominance over the soil

biogeochemical processes creating a disturbance legacy (Dove et al. 2020; Hart et al. 2005). Thus the mortality of microbial communities, in conjunction with altered soil characteristics, have long-term effects on soil carbon pools and processes, and support the importance of implementing post burn pile management techniques to minimize the impacts of drier conditions on ecosystem productivity.

### Vegetation Succession

Temporal vegetation dynamics play a large role in the uptake and storage of carbon and nitrogen in forest plots (Hart 2005; Dove et al. 2020). According to data reported in Rhoades & Fornwalt (2015) vegetative recovery following disturbance(s) differed between burn pile and regenerating forests; adult tree recovery was greater ( $p=0.0119$ ) in forest soils ( $2979 \pm 825$  trees/ha) than burn pile soils ( $293.5 \pm 88.6$  trees/ha). Tree seedling density was also significantly greater ( $p=0.0185$ ) in forest soils ( $4005 \pm 1188$  trees/ha) than burn piles ( $494.2 \pm 82.6$  trees/ha). Herbaceous plants like graminoids and forbs dominated burn scars ( $19.17 \pm 2.98$  graminoid percent coverage,  $13.85 \pm 2.86$  forbs percent coverage) in comparison to regenerating forest plots ( $9.38 \pm 2.59$  graminoid percent coverage,  $10.00 \pm 2.06$  forbs percent coverage,  $p=0.026$ ,  $p=0.025$ ). Not surprisingly, regenerating forests had more adult tree recovery and woody shrubs, while plots from burn scars illustrate a recovery trajectory of a mosaic of vascular plants, graminoids, and forbs. Recovery of adult tree populations increased rapidly as time since clear cut increased in regenerating forest plots, whereas burn scars generally had less adult tree recovery and tree seedlings dominated woody succession along with shrubs (Rhoades & Fornwalt 2015).

Lodgepole pine is an adaptive specialist species, meaning that populations differ genetically over fairly short physical distances due to their highly flexible needs (Klinka et al.

2000). Although Lodgepole pine forest stands are resilient and adaptive, some characteristics of soil composition limit the success of tree revegetation. The major determinants of Lodgepole pine tree growth are soil moisture, presence of ectomycorrhizal fungi (EMF), and nitrogen availability (OECD 2010). While burn scars contained more available inorganic nitrogen, rates of net nitrogen immobilization (e.g., microbes consuming extractable inorganic nitrogen) in burn scars were greater (Rhoades & Fornwalt 2015). Although not statistically significant, the organic C:N ratio of burn scar SOM over the chronosequence (Figure 4) demonstrates the effects of net immobilization, as the soil becomes more depleted in organic nitrogen only after net mineralization becomes positive value (Rhoades and Fornwalt 2015). Additionally, increased inorganic nitrogen availability has the potential to reduce the diversity of terrestrial vegetation by favoring common fast-growing herbaceous species adapted to high nutrient availability rather than tree species preferring nitrogen-limited soils (Soons et al. 2017; Chapin & Eviner 2014; OECD 2010). The lack of tree seedling establishment and a shift in herbaceous species within the burn piles perpetuated the differences in soil organic matter composition compared to the surrounding regenerating forest.

Regenerating forest plots demand more inorganic nitrogen for lignin production, slowly cycling nitrogen back to the soil through litterfall and subsequently greater recovery of Lodgepole pine characterized by increased water budget and mineralization of organic nitrogen (OECD 2010; Chapin & Eviner 2014; Rhoades & Fornwalt 2015). Nitrogen is often bonded directly to the carbon skeleton of organic matter, so increased organic matter and moisture in regenerating forest plots (Figure 5) induced greater mineralization of organic matter (Chapin & Eviner 2014), i.e. increased rates of respiration (Figure 8). These soil biogeochemical characteristics suggest that regenerating forest soils were better suited for successful recovery of

trees. Furthermore, net mineralization and more woody recovery in regenerating forest plots suggests the return of the natural stable state of soil in Lodgepole pine forests, which are usually nitrogen-limited (Certini et al. 2005; Rhoades & Fornwalt 2015; Figure 4).

The recovery of adult, reproductive trees is imperative for the Lodgepole pine ecosystem to regenerate and remain intact (Enright et al. 2015; Tiribelli et al. 2018). The fire-free period in forests must increase to allow reproductive maturity among woody species, ensuring a successful self-replacement of tree stand structure before the next wildfire event (Enright et al. 2015; Tiribelli et al. 2018; Figure 1). A general lack of Lodgepole seedling establishment within the burn piles over the entire sixty year chronosequence as compared to surrounding clear cut areas (Rhoades & Fornwalt 2015), similar to what is expected in a warming drier climate, suggests that accompanying shifts in soil biogeochemistry can be used to understand the implications of the interval squeeze hypothesis on soils. The results of this study demonstrate how severe burn pile fires impact soil organic matter pools (Figure 4) and resulting microbial activity (Figures 5 & 8), shifts that reinforce the bifurcation of stable states from a self-replacing Lodgepole pine forest stand to a vascular resprouter dominant shrubland.

Although soil provides essential conditions and nutrients that determine revegetation after fire disturbances, studies suggest that the recolonized vegetation drives the majority long-term effects on soil biogeochemical processes (Hart 2005; Dove et al. 2020). Alterations to microbial communities in burn scars further influence patterns of revegetation and formation of shrublands (Dove et al. 2020). This study illustrates that changes in climate and disturbance regime affect both revegetation dynamics and soil carbon processing, in many cases reinforcing shifts that threaten Lodgepole pine forests. Using slash pile burning furthers this stable state shift, as this study documents the numerous ways in which burning alters soil composition, microbial activity,



and vegetation succession. Burn piles can act as a model system for what might happen on larger scales as forests become drier and burn more frequently/severely. Managing the effects of pile burning on vegetation recovery and therefore soil biogeochemical processes is an urgent recommendation, as climate continues to shorten fire intervals in Lodgepole pine forests and stresses the ecosystem to adapt to changing conditions. Building an ecosystem through timber harvesting management that is already adapting to severe fire events through shifts in soil and vegetation is of great concern as climate trends perpetuate these shifts without human involvement.

### Conclusions

The effects of pile burning on soil biogeochemical processes and microbial activity reinforced the severe fire disturbance, shifting vegetation recovery from mature tree stands to a patchy herbaceous understory. In return, the feedback between established vegetation and soil biogeochemistry persisted for decades. Lodgepole pine forests in the Northern Rocky Mountains proved to be vulnerable to severe fire events. The relationships established in this study between severe fire, shifting soil biogeochemical processes, and vegetation dynamics will compound as climatic conditions stress forested ecosystems without management involvement. The mosaic of fire-adapted burn pile soils and vegetation surrounded by recovering tree stands threatens the resilience of the forest ecosystem. Shifting the feedback mechanisms between soil, vegetation, and the microbiome may change the ecosystem to function as a carbon source, further shifting climatic conditions.

Moving forward, this study could be expanded upon by lengthening the temporal study period to understand if a clear cut forest eventually matures to a developed Lodgepole pine stand

and biogeochemical processes are resilient as well. Understanding the lasting effects of clear cut and burn pile management with comparison to an undisturbed forest would quantitatively characterize the implications of clear cutting alone on Lodgepole pine forests. Implementing soil management after slash burn pile fires is recommended, as this study demonstrated that shifting soil characteristics within a forest ecosystem have a multidecadal legacy on the landscape and may contribute to worsening climatic conditions for successful forest recovery.

## References

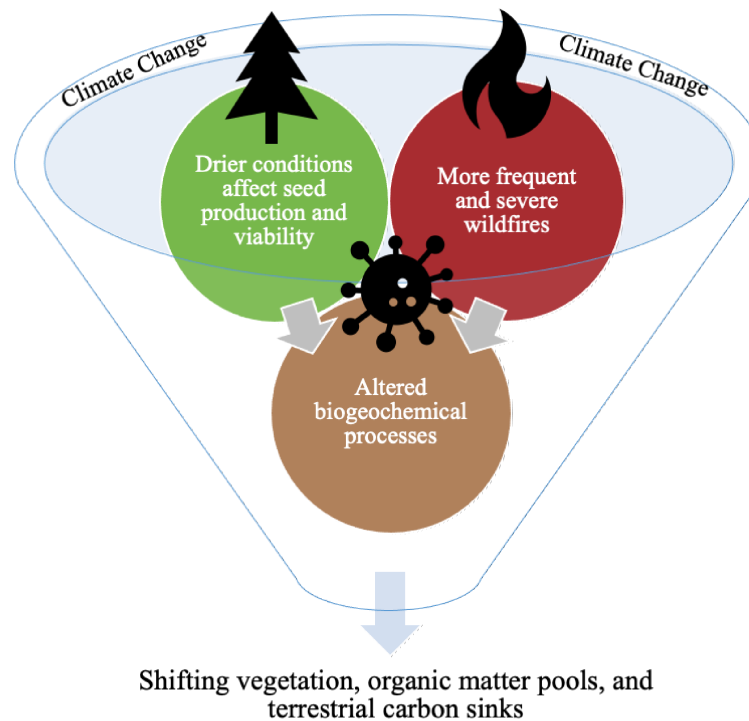
- Abatzoglou, John T., and A. Park Williams. "Impact of Anthropogenic Climate Change on Wildfire across Western US Forests." *PNAS*, National Academy of Sciences, 18 Oct. 2016, [www.pnas.org/content/113/42/11770.short](http://www.pnas.org/content/113/42/11770.short).
- Ahlgren, C. E., and I. F. Ahlgren. "Ecological Effects of Forest Fires." *The Botanical Review*, Springer-Verlag, 1960, [link.springer.com/article/10.1007/BF02940573](http://link.springer.com/article/10.1007/BF02940573).
- Bailey, R. G. "Delineation of Ecosystem Regions." *Environmental Management*, Springer-Verlag, 1983, [link.springer.com/article/10.1007/BF01866919](http://link.springer.com/article/10.1007/BF01866919).
- Certini, Giacomo. "Effects of Fire on Properties of Forest Soils: a Review." *Oecologia*, Springer-Verlag, 2 Feb. 2005, [link.springer.com/article/10.1007/s00442-004-1788-8](http://link.springer.com/article/10.1007/s00442-004-1788-8).
- Chapin, F.S., and V.T. Eviner. "Biogeochemical Interactions Governing Terrestrial Net Primary Production." *Science Direct*, Treatise on Geochemistry, 2014, [www.sciencedirect.com/coloradocollege.idm.oclc.org/science/article/pii/B9780080959757008068#s0105](http://www.sciencedirect.com/coloradocollege.idm.oclc.org/science/article/pii/B9780080959757008068#s0105).
- "Consensus Documents on the Biology of Trees: Lodepole Pine." *OECD*, 2010, [www.oecd-ilibrary.org/science-and-technology/consensus-documents-on-the-biology-of-trees\\_g218b5c70-en](http://www.oecd-ilibrary.org/science-and-technology/consensus-documents-on-the-biology-of-trees_g218b5c70-en).
- Crowther, T. W., et al. "The Global Soil Community and Its Influence on Biogeochemistry." *Science*, American Association for the Advancement of Science, 23 Aug. 2019, [science.sciencemag.org/content/365/6455/eaav0550/tab-figures-data](http://science.sciencemag.org/content/365/6455/eaav0550/tab-figures-data).
- Dai, K'O, et al. "Organic Matter Chemistry and Dynamics in Clear-Cut and Unmanaged Hardwood Forest Ecosystems." *Biogeochemistry*, Kluwer Academic Publishers, 2001, [link.springer.com/article/10.1023/A:1010697518227](http://link.springer.com/article/10.1023/A:1010697518227).
- Dersch, J. S. "Mineral Resource Potential and Geology of the Routt National Forest and the Middle Park Ranger District of the Arapaho National Forest, Colorado." *Professional Paper*, 1 Jan. 2000, [pubs.er.usgs.gov/publication/pp1610](http://pubs.er.usgs.gov/publication/pp1610).
- Dove, Nicholas C., et al. "High-Severity Wildfire Leads to Multi-Decadal Impacts on Soil Biogeochemistry in Mixed-Conifer Forests." *The Ecological Society of America*, John Wiley & Sons, Ltd, 4 Feb. 2020, [esajournals.onlinelibrary.wiley.com/doi/full/10.1002/eap.2072?casa\\_token=N3enXH5rFf4AAAAA%3AhSUb5cBqafimb8LFOkAKI0Y3-KALWPeToXBKNhDNec9\\_KeE\\_pu3DoWWODglPfOgFQJV7E-fr113zWJok](http://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/eap.2072?casa_token=N3enXH5rFf4AAAAA%3AhSUb5cBqafimb8LFOkAKI0Y3-KALWPeToXBKNhDNec9_KeE_pu3DoWWODglPfOgFQJV7E-fr113zWJok).
- Enright, Neal J, et al. "Interval Squeeze: Altered Fire Regimes and Demographic Responses Interact to Threaten Woody Species Persistence as Climate Changes." *The Ecological Society of America*, John Wiley & Sons, Ltd, 1 June 2015, [esajournals.onlinelibrary.wiley.com/doi/10.1890/140231](http://esajournals.onlinelibrary.wiley.com/doi/10.1890/140231).
- Esquilín, Aida E. Jiménez, et al. "Microbial Community Structure and Activity in a Colorado Rocky Mountain Forest Soil Scarred by Slash Pile Burning." *Soil Biology and Biochemistry*, Pergamon, 10 Jan. 2007, [www.sciencedirect.com/science/article/abs/pii/S0038071706005281](http://www.sciencedirect.com/science/article/abs/pii/S0038071706005281).

- “Four Large Wildfires Burning in Colorado Have Cost \$77 Million to Fight -- so Far.” *The Colorado Sun*, 1 Sept. 2020, [coloradosun.com/2020/09/01/wildfire-costs-colorado-2020-pine-gulch-fire/](https://coloradosun.com/2020/09/01/wildfire-costs-colorado-2020-pine-gulch-fire/).
- Hart, Stephen C., et al. “Post-Fire Vegetative Dynamics as Drivers of Microbial Community Structure and Function in Forest Soils.” *Forest Ecology and Management*, Elsevier, 7 Sept. 2005, [www.sciencedirect.com/science/article/abs/pii/S0378112705004792](https://www.sciencedirect.com/science/article/abs/pii/S0378112705004792).
- Johnson, D.W., et al. “The Effects of Wildfire, Salvage Logging, and Post-Fire N-Fixation on the Nutrient Budgets of a Sierran Forest.” *Forest Ecology and Management*, Elsevier, 19 Sept. 2005, [www.sciencedirect.com/science/article/abs/pii/S0378112705004780](https://www.sciencedirect.com/science/article/abs/pii/S0378112705004780).
- Klinka, K., et al. “Classification of Natural Forest Communities of Coastal British Columbia, Canada.” *Plant Ecology*, Kluwer Academic Publishers, 1 Jan. 1996, [link.springer.com/article/10.1007/BF00044648](https://link.springer.com/article/10.1007/BF00044648).
- Klinka, Karel, et al. “The Distribution and Synopsis of Ecological and Silvical Characteristics of Tree Species of British Columbia's Forests.” *Open Collections*, Forest Sciences Department, University of British Columbia, 2000, [open.library.ubc.ca/cIRcle/collections/facultyresearchandpublications/52383/items/1.0107280](https://open.library.ubc.ca/cIRcle/collections/facultyresearchandpublications/52383/items/1.0107280).
- Knelman, Joseph E, et al. “Rapid Shifts in Soil Nutrients and Decomposition Enzyme Activity in Early Succession Following Forest Fire.” *MDPI*, Multidisciplinary Digital Publishing Institute, 15 Sept. 2017, [www.mdpi.com/1999-4907/8/9/347/htm](https://www.mdpi.com/1999-4907/8/9/347/htm).
- Knelman, Joseph E., et al. “Fire Severity Shapes Plant Colonization Effects on Bacterial Community Structure, Microbial Biomass, and Soil Enzyme Activity in Secondary Succession of a Burned Forest.” *Soil Biology and Biochemistry*, Pergamon, 15 Aug. 2015, [www.sciencedirect.com/science/article/abs/pii/S0038071715002734](https://www.sciencedirect.com/science/article/abs/pii/S0038071715002734).
- Knoepp, Jennifer, et al. *Chapter 3: Soil Chemistry | Publications | SRS*. 2005, [www.srs.fs.usda.gov/pubs/45941](https://www.srs.fs.usda.gov/pubs/45941).
- Lake, Frank K., et al. “Returning Fire to the Land: Celebrating Traditional Knowledge and Fire.” *OUP Academic*, Oxford University Press, 20 Apr. 2017, [academic.oup.com/jof/article/115/5/343/4599880?login=true](https://academic.oup.com/jof/article/115/5/343/4599880?login=true).
- Littell, Jeremy S., et al. “Climate and Wildfire Area Burned in Western U.S. Ecoprovinces, 1916–2003.” *Ecological Applications*, Wiley, 1 June 2009, [www.scilit.net/article/0646691178b400da0ca4bf8d6addfd76](https://www.scilit.net/article/0646691178b400da0ca4bf8d6addfd76).
- Lotan, James E. “Cone Serotiny - Fire Relationships in Lodgepole Pine.” *DigitalCommons@USU*, 1976, [digitalcommons.usu.edu/barkbeetles/8/](https://digitalcommons.usu.edu/barkbeetles/8/).
- Loudermilk, E. Louise, et al. “Carbon Dynamics in the Future Forest: the Importance of Long-Term Successional Legacy and Climate–Fire Interactions.” *Wiley Online Library*, John Wiley & Sons, Ltd, 2 July 2013, [onlinelibrary.wiley.com/doi/full/10.1111/gcb.12310?casa\\_token=r6qAnteKXbEAAA%3ARoZtUc8CuauBSRc1xXm-popjkJI9DNmVP92m\\_Uk5nmcZKK4kXGvLQo\\_WcaND3OkBnP3E9\\_Krjlf1YA](https://onlinelibrary.wiley.com/doi/full/10.1111/gcb.12310?casa_token=r6qAnteKXbEAAA%3ARoZtUc8CuauBSRc1xXm-popjkJI9DNmVP92m_Uk5nmcZKK4kXGvLQo_WcaND3OkBnP3E9_Krjlf1YA)
- McKinley, Duncan C., et al. “A Synthesis of Current Knowledge on Forests and Carbon Storage in the United States.” *The Ecological Society of America*, John Wiley &

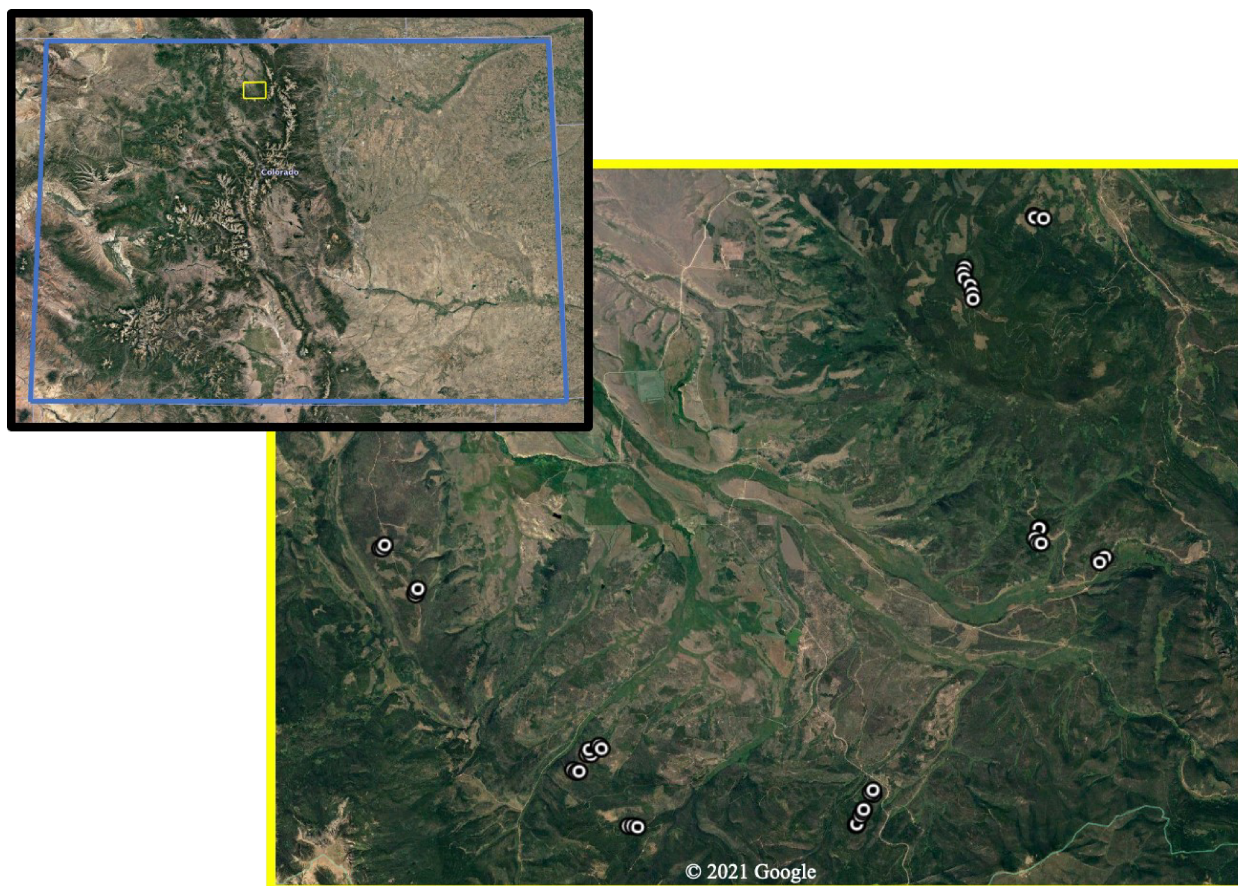
- Sons, Ltd, 1 Sept. 2011, [esajournals.onlinelibrary.wiley.com/doi/full/10.1890/10-0697.1?casa\\_token=1yv5FZ0Kcl4AAAAA%3A1eM2VTz8wJ7i36YiGvX2Ju3CWhhgLNLWPZoCue8VL9pBZZIJRauhiugucSHDV\\_\\_wwy5qbgS2XxEoiVE](https://doi.org/10.1890/10-0697.1?casa_token=1yv5FZ0Kcl4AAAAA%3A1eM2VTz8wJ7i36YiGvX2Ju3CWhhgLNLWPZoCue8VL9pBZZIJRauhiugucSHDV__wwy5qbgS2XxEoiVE).
- Noronha, Melline Fontes, et al. "Taxonomic and Functional Patterns across Soil Microbial Communities of Global Biomes." *Science of The Total Environment*, Elsevier, 3 Aug. 2017, [www.sciencedirect.com/science/article/abs/pii/S0048969717318624](https://www.sciencedirect.com/science/article/abs/pii/S0048969717318624).
- Rhoades, Charles C., and Paula J. Fornwalt. "Pile Burning Creates a Fifty-Year Legacy of Openings in Regenerating Lodgepole Pine Forests in Colorado." *Forest Ecology and Management*. 336: 203-209., 2015, [www.fs.usda.gov/treearch/pubs/47805](http://www.fs.usda.gov/treearch/pubs/47805).
- Rhoades, Charles C., et al. "Are Soil Changes Responsible for Persistent Slash Pile Burn Scars in Lodgepole Pine Forests?" *Forest Ecology and Management*, Elsevier, 15 Mar. 2021, [www.sciencedirect.com/science/article/pii/S0378112721001791?dgcid=author](https://www.sciencedirect.com/science/article/pii/S0378112721001791?dgcid=author).
- Ryan, Michael G., et al. "Factors Controlling Eucalyptus Productivity: How Water Availability and Stand Structure Alter Production and Carbon Allocation." *Forest Ecology and Management*, Elsevier, 1 Feb. 2010, [www.sciencedirect.com/science/article/abs/pii/S0378112710000198](https://www.sciencedirect.com/science/article/abs/pii/S0378112710000198).
- Soons, Merel B., et al. "Nitrogen Effects on Plant Species Richness in Herbaceous Communities Are More Widespread and Stronger than Those of Phosphorus." *Biological Conservation*, Elsevier, 2017, [www.sciencedirect.com/science/article/pii/S0006320716309831](https://www.sciencedirect.com/science/article/pii/S0006320716309831).
- Stephens, Scott L., and Lawrence W. Ruth. "FEDERAL FOREST-FIRE POLICY IN THE UNITED STATES." *The Ecological Society of America*, John Wiley & Sons, Ltd, 1 Apr. 2005, [esajournals.onlinelibrary.wiley.com/doi/full/10.1890/04-0545?casa\\_token=YOaMzCUnDwwAAAAA%3AA\\_yxzMPYNI0KO-3za0uzvRC\\_EhBwsm0PGD8-H7ZZjxfK\\_0TxIxKfFBjH9t7UPea9L0LysQq-SMNuJ6ao](https://doi.org/10.1890/04-0545?casa_token=YOaMzCUnDwwAAAAA%3AA_yxzMPYNI0KO-3za0uzvRC_EhBwsm0PGD8-H7ZZjxfK_0TxIxKfFBjH9t7UPea9L0LysQq-SMNuJ6ao).
- Stevens-Rumann, Camille S., et al. "Evidence for Declining Forest Resilience to Wildfires under Climate Change." *Wiley Online Library*, John Wiley & Sons, Ltd, 12 Dec. 2017, [onlinelibrary.wiley.com/doi/full/10.1111/ele.12889](https://onlinelibrary.wiley.com/doi/full/10.1111/ele.12889).
- Tiribelli, Florencia, et al. "Changes in Vegetation Structure and Fuel Characteristics along Post-Fire Succession Promote Alternative Stable States and Positive Fire–Vegetation Feedbacks." *Wiley Online Library*, John Wiley & Sons, Ltd, 14 Mar. 2018, [onlinelibrary.wiley.com/doi/full/10.1111/jvs.12620?casa\\_token=mntLlok8r0IAA AAA%3AuLsi-b-Aq8LHB3iKr6TaFhMTsydGkwrJIXJvwRoInDEF0pdOixGLtZ5GnZbyltdfaeAyDjR5wKxho3Y](https://onlinelibrary.wiley.com/doi/full/10.1111/jvs.12620?casa_token=mntLlok8r0IAA AAA%3AuLsi-b-Aq8LHB3iKr6TaFhMTsydGkwrJIXJvwRoInDEF0pdOixGLtZ5GnZbyltdfaeAyDjR5wKxho3Y).
- Turner, Monica G., et al. "Feast Not Famine: Nitrogen Pools Recover Rapidly in 25-Yr-Old Postfire Lodgepole Pine." *The Ecological Society of America*, John Wiley & Sons, Ltd, 25 Feb. 2019, [esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecy.2626?casa\\_token=UtSymf-Wks8AAAAA%3ANtb4-uTRxtKssbntkBlEl5XLjOw5xOewZTPqTrE-6spMm8MpMW4UTb6cpLZPiJ5CHd58pScJMRYpma](https://doi.org/10.1002/ecy.2626?casa_token=UtSymf-Wks8AAAAA%3ANtb4-uTRxtKssbntkBlEl5XLjOw5xOewZTPqTrE-6spMm8MpMW4UTb6cpLZPiJ5CHd58pScJMRYpma).

- Turner, Monica G., et al. "Inorganic Nitrogen Availability after Severe Stand-Replacing Fire in the Greater Yellowstone Ecosystem." *PNAS*, National Academy of Sciences, 20 Mar. 2007, [www.pnas.org/content/104/12/4782](http://www.pnas.org/content/104/12/4782).
- Van Der Heijden, Marcel G. A., et al. "The Unseen Majority: Soil Microbes as Drivers of Plant Diversity and Productivity in Terrestrial Ecosystems." *Wiley Online Library*, John Wiley & Sons, Ltd, 29 Nov. 2007, [onlinelibrary.wiley.com/doi/full/10.1111/j.1461-0248.2007.01139.x](http://onlinelibrary.wiley.com/doi/full/10.1111/j.1461-0248.2007.01139.x).
- Westerling, Anthony L, et al. "Increasing Western US Forest Wildfire Activity: Sensitivity to Changes in the Timing of Spring." *Philosophical Transactions of the Royal Society B: Biological Sciences*, 5 June 2016, [royalsocietypublishing.org/doi/full/10.1098/rstb.2015.0178](http://royalsocietypublishing.org/doi/full/10.1098/rstb.2015.0178).

## Figures

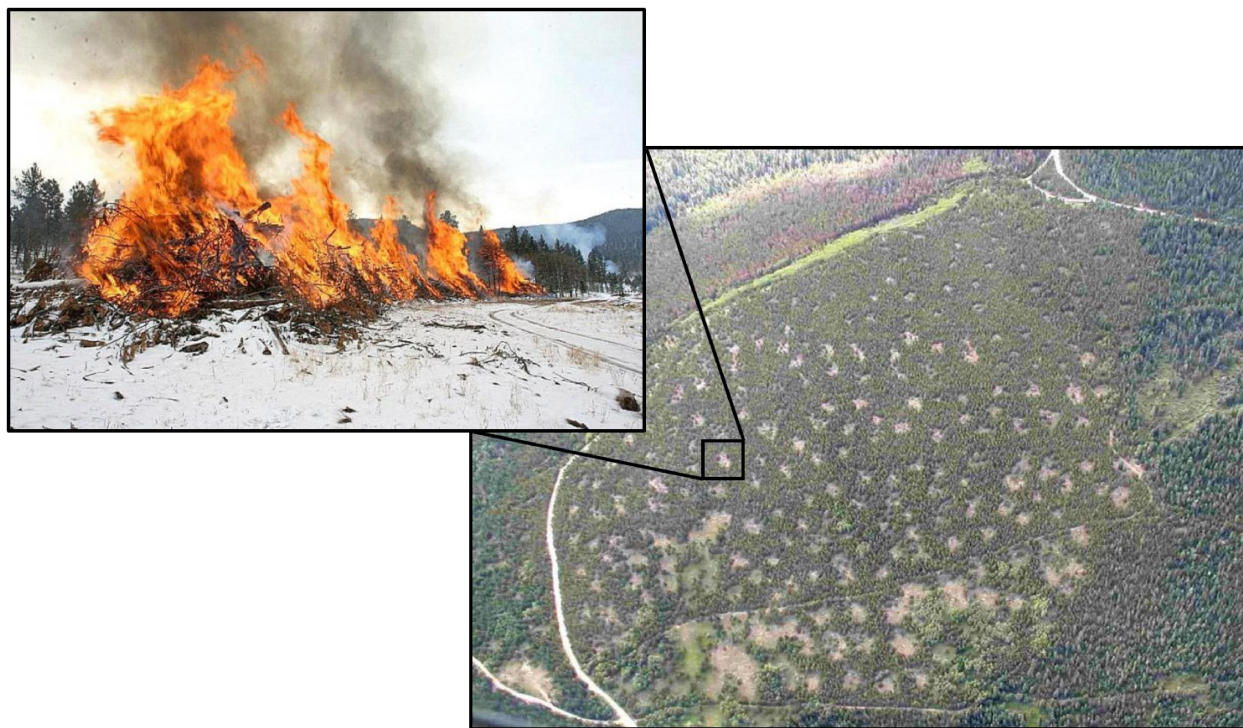


**Figure 1.** Conceptual figure outlining the components of the Interval Squeeze Theory (Enright et al, 2015). Climate change shortens fire-free intervals and imposes drier conditions on forest ecosystems (Red & Green). Risk of stand-replacing fires increases as climatic conditions shift and trees are less likely to produce viable seeds (Green). Shorter fire-free intervals in combination with less tree recovery induces altered soil biogeochemical processes that reflect the shift in environmental conditions and recolonized vegetation (Brown). Changes in climatic conditions, disturbance regimes, revegetation, and soil processes provoke adaptation of dominant vegetation, organic matter pools, and soil microbial communities to reflect new conditions. Ultimately, the shift from a forest to shrubland alters the ability of the ecosystem to remain a terrestrial carbon sink.

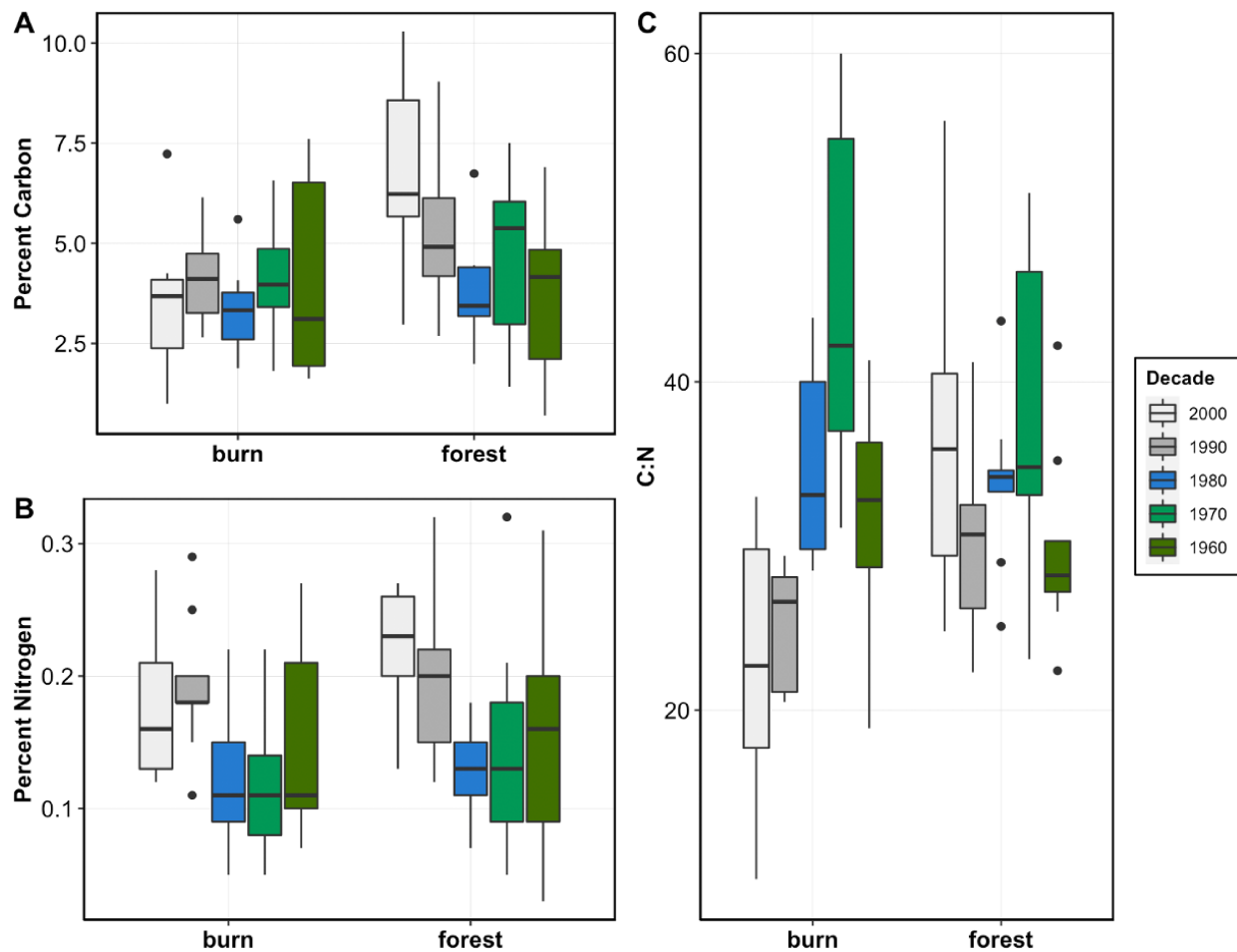


**Figure 2.** Map of sampling locations in the Medicine Bow-Routt National Forest, Colorado, USA are represented by white circles (right). Overview map showing the location of the Medicine Bow-Routt National Forest within Colorado is highlighted in yellow (left). Soil collection sites ranged from  $40.50096^{\circ}\text{N}$  to  $40.38102^{\circ}\text{N}$  and  $-106.07336^{\circ}\text{W}$  to  $-106.18936^{\circ}\text{W}$ . Site locations from Rhoades & Fornwalt (2015).

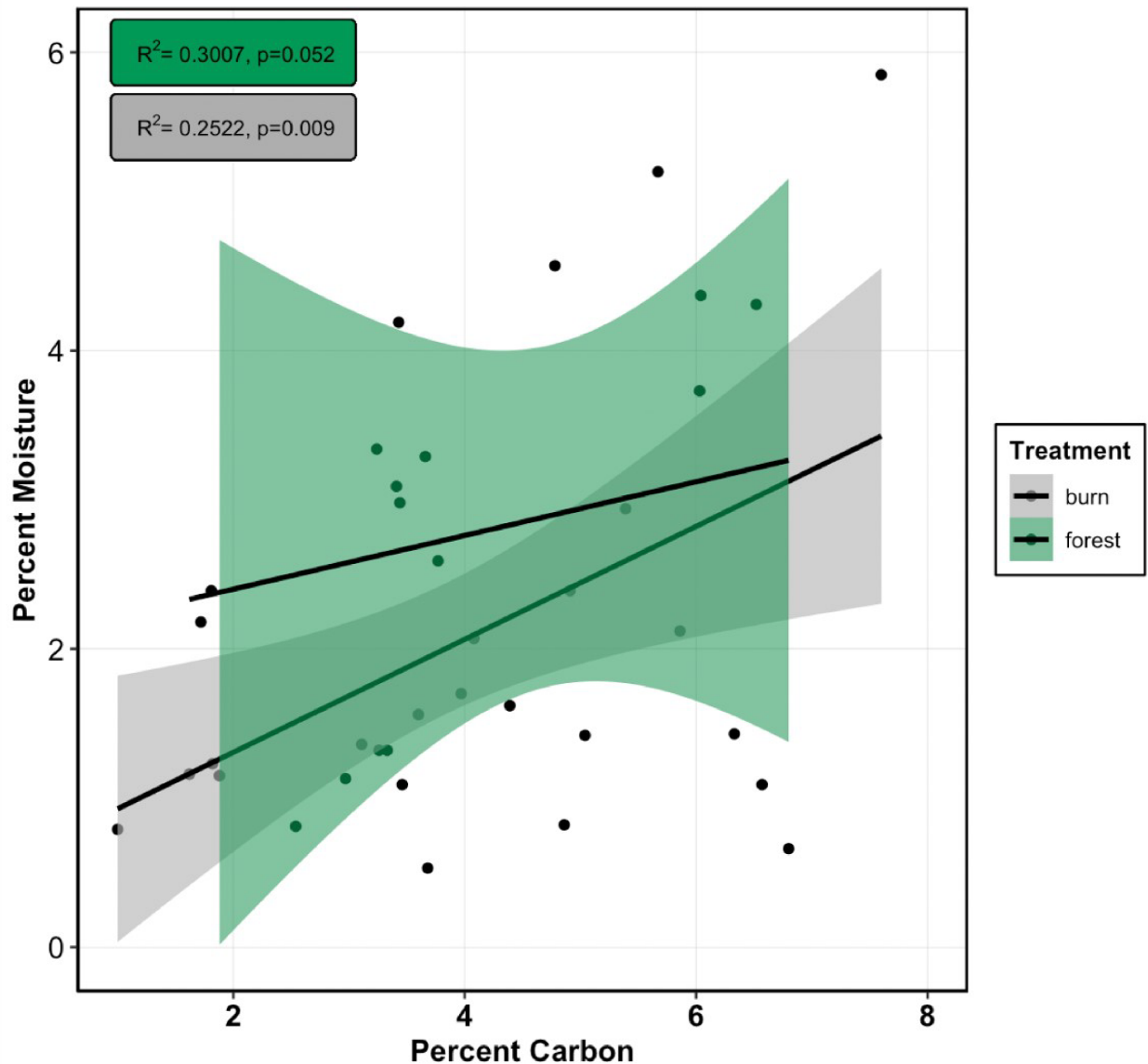




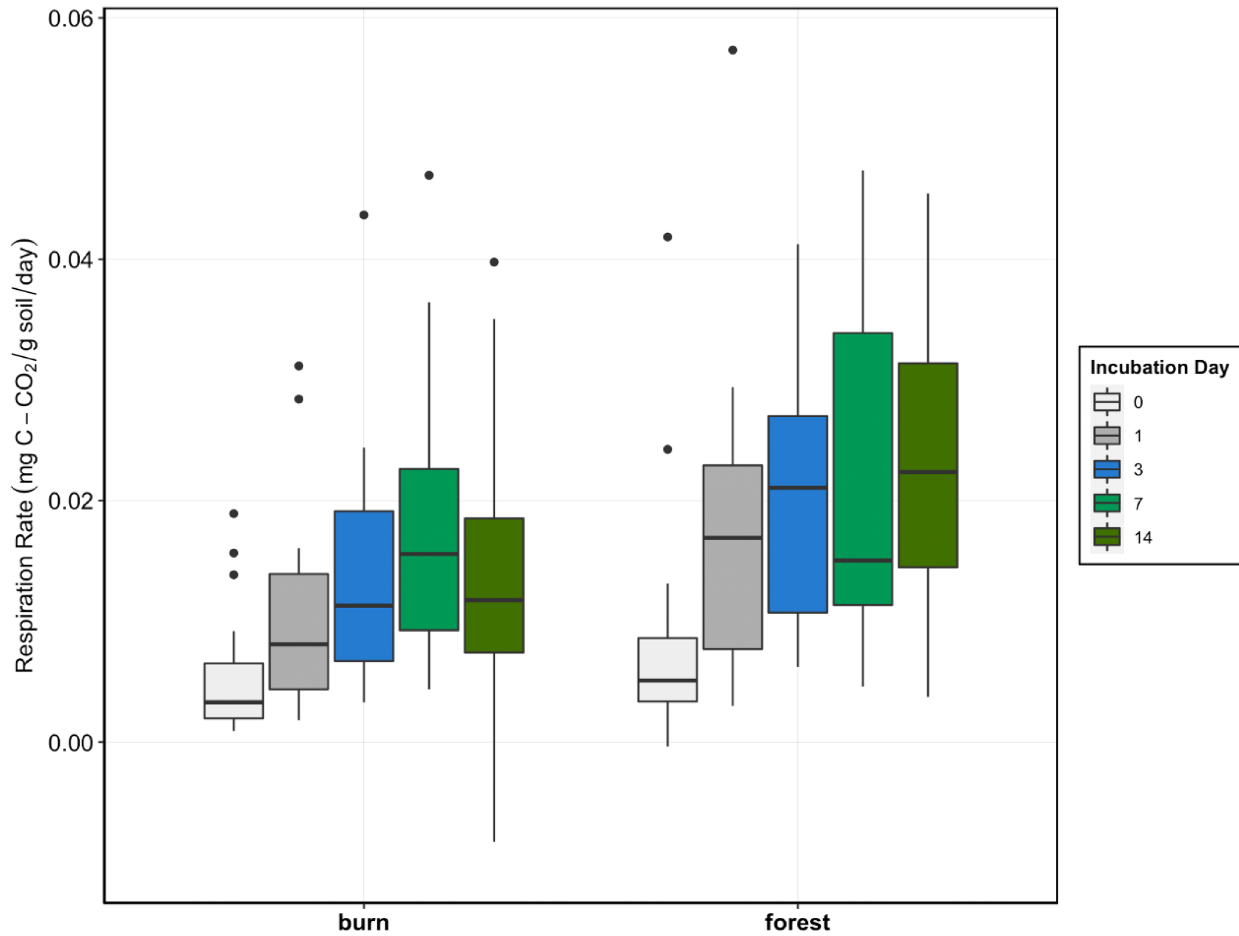
**Figure 3.** Aerial photograph of burn pile openings in a regenerating clear cut forest (right; photo by Dr. Chuck Rhoades). The burning of slash piles is a forestry practice to reduce fuel loads and is the most common method of removing clear cut debris (Rhoades & Fornwalt, 2015). Slash burn piles concentrate a lasting severe fire in a small area (left; photo by L. Asherin). The long-term legacy of burn piles in a regenerating forest are visually noted, as scarred areas create grass and forb-filled openings with minimal tree recovery (right; Rhoades & Fornwalt, 2015).



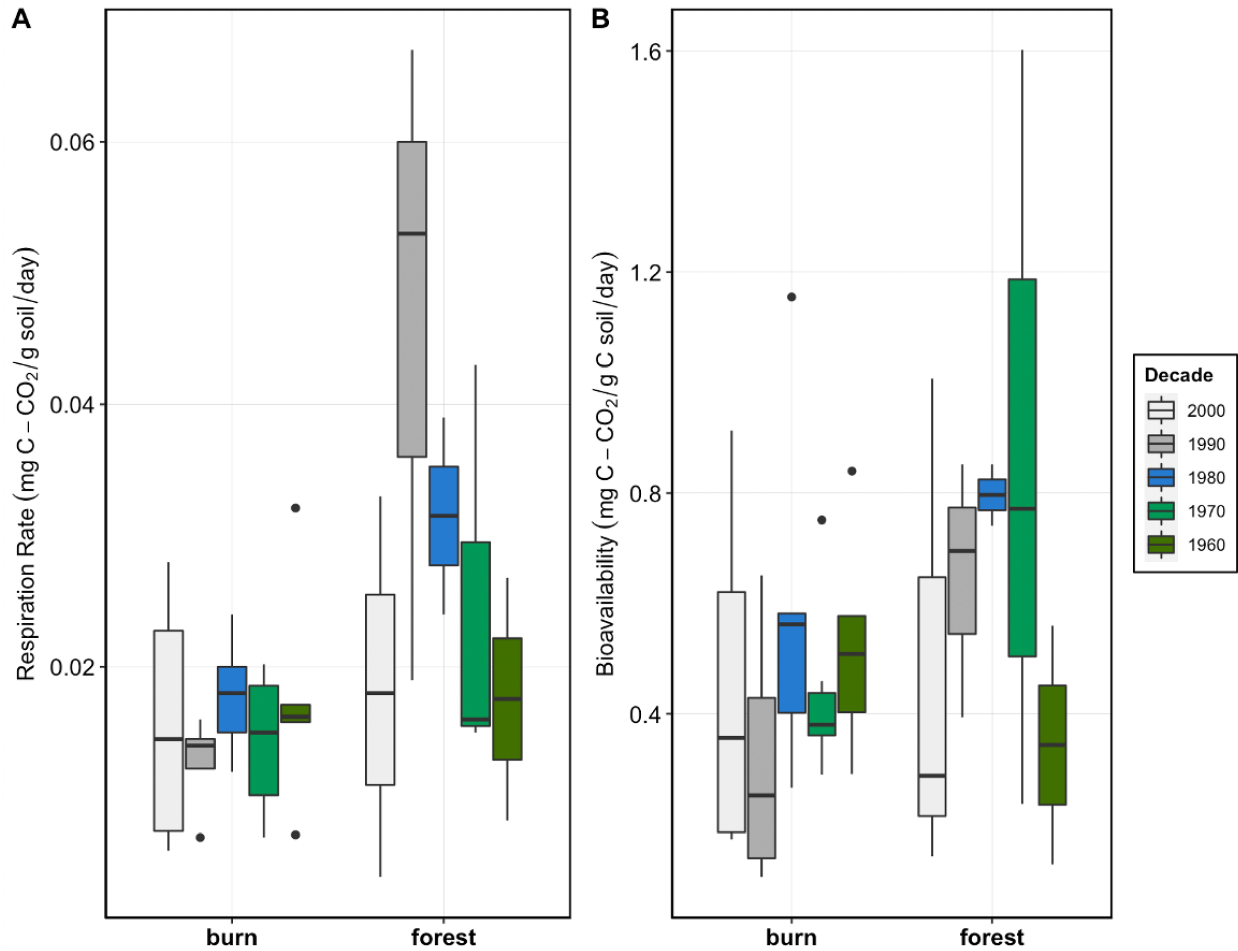
**Figure 4.** Mineral soil organic carbon (A) and organic nitrogen (B) in burn scars and adjacent regenerating forest plots as time since recovery increased over the 60 year chronosequence. Calculated C:N ratio of burn scars and regenerating forest soils were also analyzed in the chronosequence (C). Soils ( $n=90$ , sieved, 0-10 cm depth) were collected by Amelia Nelson (PhD student at Colorado State University), Dr. Charles Rhoades (USFS), and Tim Fegel (USFS) in August 2020 and were characterized by treatment (clear cut and slash burn pile/clear cut) and decade of applied treatment.



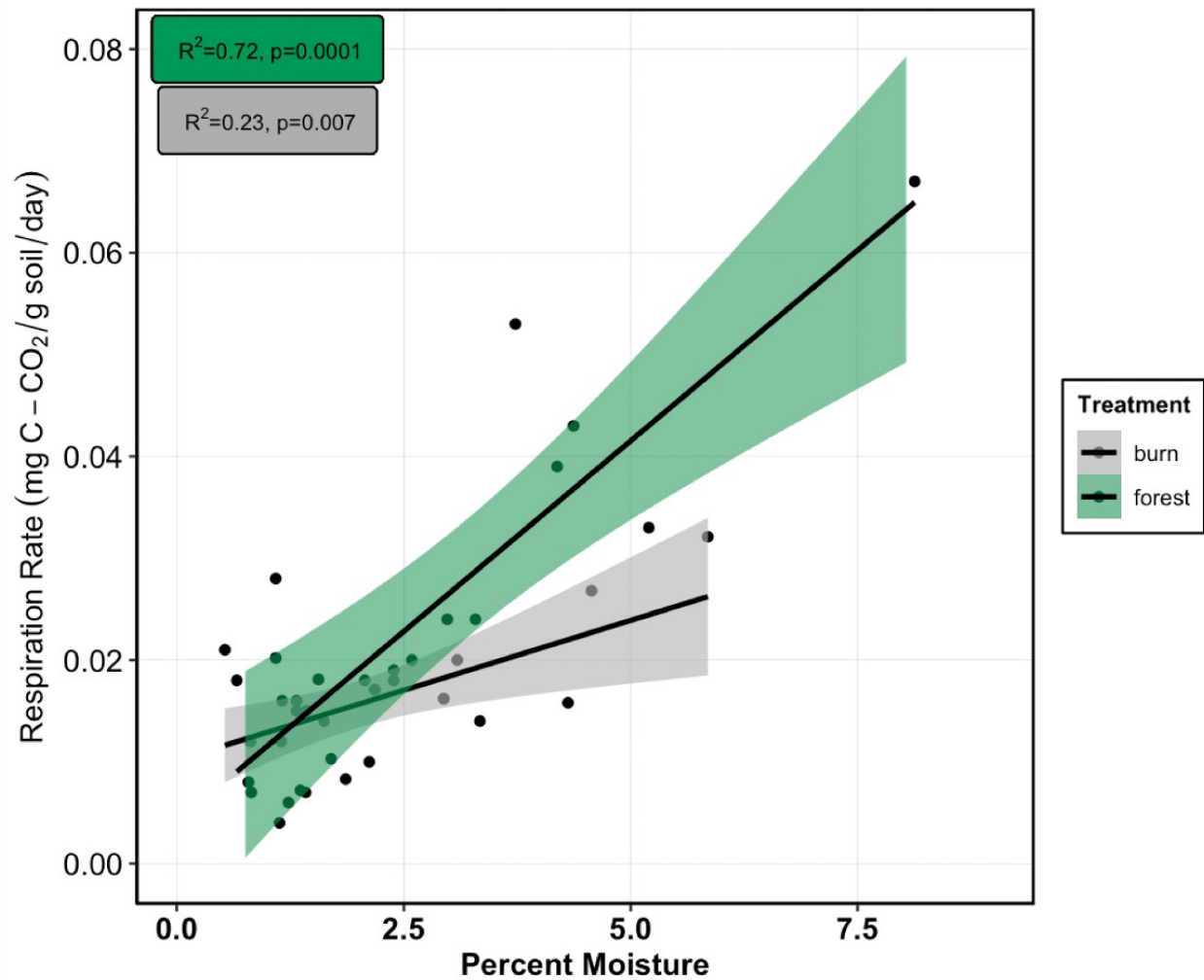
**Figure 5.** Percent organic carbon against percent moisture for burn scars (grey) and regenerating forest plots (green). In both treatments, percent moisture is correlated with percent carbon represented by linear regression with 95% confidence intervals. Burn pile soils contained less carbon ( $3.60 \pm 0.29\%$ ) than the regenerating forest soils ( $4.48 \pm 0.38\%$ ,  $p=0.0266$ ). Soil moisture was elevated in regenerating forest soils ( $3.21 \pm 0.24\%$ ,  $p=0.0283$ ) compared to the burn scars ( $1.99 \pm 0.24\%$ ,  $p=0.0283$ ).



**Figure 6.** Average respiration rate (mg-C-CO<sub>2</sub>/g soil/day) of burn scars and regenerating forest soils across the 14 day incubation time series, each day of incubation is represented by different colors. Respiration rate increased through the first week of the time series and stabilized in the last weeks. Respiration rates increased and were statistically different before one week into the incubation time series, the one and two week incubation period stabilized and were not statistically different. Bioavailability (mg-C-CO<sub>2</sub>/g soil C/day) of both treatments demonstrated the same trend as time increased in the incubation series.



**Figure 7.** Respiration (mg-C-CO<sub>2</sub>/g soil/day) and bioavailability rates (mg-C-CO<sub>2</sub>/g soil C/day) for burn scars and regenerating forest soils as time since recovery increased in the 60 year chronosequence, each decade of treatment is represented by a different color. Regenerating forest soils had elevated rates of microbial respiration ( $0.028 \pm 0.005$  mg C- CO<sub>2</sub>/g soil/day) compared to burn pile soils ( $0.017 \pm 0.005$  mg C- CO<sub>2</sub>/g soil/day ;  $p=0.00367$ ). There was no significant difference between bioavailability rates of forest soils ( $0.64 \pm 0.11$  mg C-CO<sub>2</sub>/g soil C/ day) and burn pile soils ( $0.46 \pm 0.04$  mg C-CO<sub>2</sub>/g soil C/ day ;  $p=0.653$ ). The differences of microbial respiration and bioavailability rates between treatments were not statistically significant across the chronosequence, although each treatment demonstrated different patterns of microbial activity recovery.



**Figure 8.** Percent moisture against microbial respiration rate (mg-C-CO<sub>2</sub>/g soil/day) for burn scars (grey) and regenerating forest plots (green). In both treatments microbial respiration rate is highly correlated with percent moisture, represented by linear regression with 95% confidence intervals.