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# Clonal Plants' Traits and Responses Following Fire Disturbance in Ponderosa pine Ecosystems in the Colorado Front Range

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UNIVERSITY OF NORTHERN COLORADO

Greeley, Colorado

The Graduate School

# CLONAL PLANTS' TRAITS AND RESPONSES FOLLOWING FIRE DISTURBANCE IN PONDEROSA PINE ECOSYTEMS IN THE COLORADO FRONT RANGE

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of
Master of Science

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College of Natural and Health Sciences
Department of Biological Sciences

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This Thesis by: Raymond Erskine
Entitled: *Clonal Plants' Traits and Responses Following Fire Disturbance in Ponderosa Pine Ecosystems in the Colorado Front Range*

has been approved as meeting the requirement for the Degree of Master of Science in College of Natural and Health Sciences in the Department of Biological Sciences

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# ABSTRACT

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Mountain ecosystems are currently experiencing increasing impacts of disturbances (e.g., wildfire) due to global changes in climate and land use, leading to significant changes in vegetation composition and landscape dynamics. Clonal plants, characterized by their vegetative reproduction strategies, offer a range of ecologically important traits to cope with disturbances. However, clonality is often excluded in studies of post-fire vegetation dynamics in mountain ecosystems, and our knowledge of the ability of clonal plants to respond to differing disturbance regimes is limited. Therefore, I examined the response of understory vegetation following fire disturbance in burned and unburned ponderosa pine stands of the Arapahoe-Roosevelt National Forest in the Colorado Front Range. I collected data from 40 total burned (n=20) and unburned plots (n=20) (10m x 10m) including relative percent cover of all plant species and five environmental variables. There was a greater overall relative percent cover and diversity of clonal plants in burned plots compared to unburned plots. While there were statistically distinct differences in species composition between burned versus unburned plots, these differences may not be ecologically meaningful – with side-steps multiple significances. A fourth corner analysis (FCA) showed relationships between elevation and slope and type of clonal growth organs (CGOs), suggesting that elevation, slope and fire history interact significantly in shaping vegetation community structure. Combined responses of lateral spread and ramet length of

*Arctostaphylos uva-ursi* (L.) differed significantly in areas impacted by wildfire to those burned, while that of *Antennaria parviflora* (Nutt.) showed no differences, suggesting a species-specific response of clonal traits following fire. My findings indicate that following fire disturbance, clonal plants dominate the understory of burned ponderosa pine stands in the Arapahoe-Roosevelt National Forest in the Colorado Front Range. I suggest managers and modelers account for plant clonal traits to have a more holistic picture of forest response following fire disturbance.

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# CHAPTER I

# INTRODUCTION

Mountain ecosystems are currently experiencing a wide range of natural and anthropogenic disturbances due to global changes in climate and land use, among which wildfire plays a significant part (Hansen et al., 2001; IPCC, 2023; Korb et al., 2019). Wildfires play a critical role in shaping forest ecosystems, often leading to significant changes in ecological processes, landscape dynamics, and the structuring of vegetation communities (Johnston et al., 2016; Stevens-Rumann & Morgan, 2019). Wildfires are generally thought of as unfavorable, however, some fires with a mix of low and high intensities can increase the diversity of understory vegetation by reducing fire-intolerant species and changing growing conditions (Keyser et al., 2008; Nuttle et al., 2013; Stephens et al., 2014). The mortality of trees can increase immediately after a fire, making resources available and decreasing competition for more resilient understory vegetation, which may include clonal plants (Tubbesing et al., 2020).

Clonal plants, a group of perennial plants, vegetatively reproduce multiple young individuals called ramets (often called daughter ramets) that can become physically and functionally independent from the parent individual (Herben & Klimešová, 2020; Klimešová et al., 2021; S. B. Franklin et al., 2020). The young individuals (i.e., daughter ramets) are initially dependent on the parent but subsequently form their own root and shoot systems and create an interconnected system of genetically identical individuals (Klimeš et al., 1997; Klimešová & Klimeš, 2008). Clonal plants are highly modular organisms with localized organization (Eriksson

& Jerling, 1990; J. Harper & White, 1974). This distinguishing feature is evident in their capacity for rapid colonization, stress tolerance, and the ability to distribute and share resources efficiently (Eriksson & Jerling, 1990; Mogie & Hutchings, 1990), traits that provide advantages over non-clonal plants in disturbed and heterogenous environments (S. B. Franklin et al., 2020).

Mountain ponderosa pine forests are dynamic environments susceptible to periodic disturbances such as fire (Shaw et al., 2022). Clonal traits including clonal growth organs (e.g., rhizomes, bulbils, and stolons), lateral spread, multiplication rate, and persistence of connection provide various functions to facilitate post disturbance recovery of clonal plants (Klimešová et al., 2019). For example, following disturbance, there are significant changes in soil nutrient pools. Rhizomes and stolons as aboveground structures can explore nutrient-rich patches and colonize bare ground by growing vegetatively and spreading horizontally (Klimeš et al., 1997; Wolfer, 2008). Such lateral spread is a major trait clonal plants utilize to compete for resources in post-disturbed conditions (Pausas et al., 2018). A study by Herben et al. (2012) found that lateral spread can have significant negative impacts on seed production, suggesting a trade-off between vegetative and clonal growth, which ultimately is advantageous for clonal plants that can vary their reproduction method based on environmental conditions.

Clonal plants exhibit four primary responses to disturbance which enable them to flourish under heterogeneous conditions: **(1)** Sharing of resources among functionally independent and integrated ramets when disturbance results in diversity of resource availability, **(2)** Foraging in search for available resources, **(3)** Longevity if they survive disturbance (at least part of them, e.g., rhizome) resulting in persistence, and **(4)** Short distance dispersal of integrated ramets resulting in dominance. While some of these responses are also exhibited by non-clonal plants, clonal plants have a more direct and immediate means of expressing these responses in heterogenous and disturbed environments, providing advantages for clonal plants over non-clonal plants (Klimešová et al., 2017; Lu & Franklin, 2022; Svensson et al., 2013).

As wildfires play significant roles in shaping vegetation patterns in ecosystems (Lloret & Zedler, 2009; Sousa, 1984), understanding plant community responses following these events requires exploration of various adaptive strategies utilized by plants including plant clonality. Furthermore, our understanding regarding the trajectory of vegetation recovery and the factors that shape it will allow us to predict short and long-term understory vegetation resilience in disturbed mountain ecosystems (Seidl & Turner, 2022; Viana-Soto et al., 2020) providing knowledge on strategies for effective forest management and conservation efforts (S. A. Hart & Chen, 2006).

While several past studies have documented the responses of understory vegetation to both prescribed burning and wildfires in ponderosa pine forests (e.g., Armour et al., 1984; Griffis et al., 2001; Kerns et al., 2011), there remains a paucity of studies explicitly focusing on clonality, and how clonal plants influence post-fire recovery dynamics in mountain ecosystems. In this study, my goal was to address this knowledge gap by investigating the post-fire responses and traits of clonal plants in burned and unburned plots of ponderosa pine stands. The objectives of this study were to: **(1)** assess the relative percent cover and diversity of clonal plants in burned and unburned plots of ponderosa pine stands; **(2)** investigate the differences in plant species composition in burned and unburned plots of ponderosa pine stands, focusing on the contributions of clonal and non-clonal plants to these changes, and **(3)** investigate the response of clonal traits (lateral spread and ramet length) of *A. uva-ursi* and *A. parviflora*, comparing burned and unburned plots.

Percent cover and diversity provide insights into understanding post-fire vegetation dynamics (Capitanio & Carcaillet, 2008). In ecology, percent cover tells the proportion of an area covered by the vertical projection of plants onto a surface. It helps to quantify the abundance or density of vegetation in a particular area (Damgaard, 2014). Diversity on the other hand describes the variety of species present in a community and the distribution of their abundances (Magurran & Magurran, 1988). Common diversity indices used in ecology, such as the Shannon-Wiener index or Simpson's index, quantify the evenness and richness of a community. These indices consider both the number of species (richness) and the relative abundance of each species (evenness) (Kunakh et al., 2023; Stirling & Wilsey, 2001). Our knowledge of species diversity is critical as it provides a comprehensive knowledge and understanding of community resistance and resilience (Mori et al., 2013). High species diversity can indicate a resilient community which can adapt and recover from disturbances such as wildfires. Therefore, having a variety of species with different ecological roles and niches in a community ultimately enhances the community in terms of recovery in post disturbance conditions (Lavorel, 1999).

I hypothesized that clonal plants would exhibit greater relative percent cover and diversity in burned plots compared to unburned plots. This is attributed to their ability to adapt in disturbed and heterogenous conditions. Furthermore, the ability of clonal plants to reproduce vegetatively allows them to rapidly recolonize disturbed areas, contributing to greater relative cover and diversity. Thus, I expected a significant difference in community composition in burned and unburned plots due to shifts in species relative cover and diversity, with an increased representation of clonal plants in the burned plots. The contribution of clonal plants to changes in community composition should be more pronounced in burned plots because clonal plants possess unique mechanisms for vegetative spread and rapid post disturbance recovery. Lateral and ramet length are clonal traits that can shed light on how *A. uva ursi* and *A. parviflora* respond to disturbances (Klimešová et al., 2019). Lateral spread, often indicative of horizontal expansion and resource acquisition, and ramet length, a measure of individual vertical growth, serve as indicators of clonal plants fitness and growth strategies (Klimešová & Klimeš, 2008). Finally, I hypothesized that the clonal traits, lateral spread and ramet length of *A. uva-ursi* and *A. parviflora* (Nutt.), would differ significantly between burned and unburned plots. These differences in clonal traits may reflect adaptive responses to the altered post-fire environment, suggesting that the plants are actively adjusting these traits in response to fire disturbance.

# CHAPTER II

# REVIEW OF LITERATURE

## Plant Clonal Ecology

Plant clonal ecology is a subfield of ecology which has emerged as a major area of study in plant research, though it has received relatively little attention over the past several years (J. E. Larson & Funk, 2016; Salguero-Gómez, 2018). This inattention is due to our limited knowledge of clonal plants' responses to disturbances, clonal plant architecture and morphology, and the challenge of studying belowground organs (e.g., rhizomes, stolons, tubers, and bulbs) which provide functions such as carbohydrate storage, bud bank formation, and expansion (Klimešová & Klimeš, 2008; S. Franklin et al., 2021).

Clonal plants are a group of perennial plants that vegetatively reproduce multiple young individuals called ramets (often called daughter ramets) that can become physically and physiologically independent from the parent individual. The multiple daughter ramets initially depend on their parent plants but eventually grow their own roots and shoots to form an interconnected system of the same genetic individuals, known as genet (Herben & Klimešová, 2020; Klimešová et al., 2021; S. B. Franklin et al., 2020). In addition, clonal plants are highly modular organisms. This high degree of modularity exhibited by clonal plants provides them with a competitive advantage over non-clonal plants in disturbed and heterogenous environments, where the ability to efficiently utilize and share resources becomes significant (Eriksson & Jerling, 1990; J. Harper & White, 1974; Stuefer, 1996).

Clonality is a widespread phenomenon in nature among plant species (e.g., grasses, shrubs, and many woody plants), though it is not universal (Aarssen, 2008; Schenk, 1999; Suzuki & Stuefer, 1999). For example, a study by Herben and Klimešová (2020) indicates that clonality does not occur in a few large groups of plant families including Caryophyllaceae and Apiaceae. Existing data suggest that plant clonality dates to the earliest evolution of vascular and non-vascular plants including Bryophytes and Charales (Mogie & Hutchings, 1990; Van Groenendael et al., 1996) but has received little research attention over the years (J. E. Larson & Funk, 2016; Salguero-Gómez, 2018). It was John L. Harper and other colleagues in the 1970s who kindled interest in plant clonality (J. L. Harper, 1977). John L. Harper (1977) invented the term 'ramet' asserting that a clonal plant gives rise to new individuals (also called daughter ramets) with the same genes as the parent. When the ramet is separated from the parent individual, it can carry out all life activities and functions independently of the parent but is a clone (J. L. Harper, 1977; P. J. Clarke et al., 2013). Since the 1990s, a subset of plant researchers and botanists have focused interest on clonal plant research (e.g., Callaghan et al., 1992; De Kroon & Van Groenendael, 1990; Herben et al., 1994; Oborny & Podani, 1996).

Plant clonality is exhibited in several modes via vegetative reproduction. Clonal plants can produce adventitious stems, both aboveground and belowground (e.g., rhizomes, stolons). Furthermore, plants can grow clonally by forming specialized organs such as fragments, bulbils, and tubers (Grace, 1993; Klimeš et al., 1997; Mogie & Hutchings, 1990). This type of reproduction allows clonal plants to colonize new habitats and spread rapidly (Fahrig et al., 1994; Oborny et al., 2000) without sexual reproduction, so the number of individuals is less important than in non-clonal populations. Past data indicate that plant clonality provides numerous benefits to plants in diverse ways, for example, increasing production in several economically important crops such as banana, sweet potato, and manioc (Denham et al., 2020; McKey et al., 2010). Additionally, clonal plants, particularly those with widespread rhizomes or root systems, play a significant role in mitigating soil erosion (Guerrero-Campo et al., 2008) making our knowledge and understanding of plant clonal ecology very crucial (Maguire & Menges, 2011; S. Franklin et al., 2021).

## Fire Disturbance in Ponderosa Pine Forests

Ponderosa pine (*Pinus ponderosa Douglas ex C. Lawson)* forests are a type of coniferous forest widely distributed in the western part of North America, particularly in the Rocky Mountains and Sierra Nevada range (Benson, 1987; Korb et al., 2019; R. S. Anderson, 1989). According to McKinney (2019), there are two distinct varieties of ponderosa pine in Colorado: Rocky Mountains ponderosa pine (*Pinus ponderosa var. scopulorum*) and Southwestern ponderosa pine (*Pinus ponderosa var. brachyptera*). However, these varieties are not always recognized as distinct in existing studies (McKinney, 2019), and we also do not recognize them as distinct in this thesis. Fires are important ecological processes that shape and maintain the stability of ecosystem health and services in ponderosa pine communities (Johnston et al., 2016; Newland & DeLuca, 2000). Fires, both natural and controlled, form an integral part of ponderosa pine forest dynamics across the United States (Korb et al., 2019; McKinney, 2019; Savage et al., 2013). Several past studies indicated that ponderosa pine forests experienced multiple centuries of frequent low- to moderate-intensity fires (e.g., Gartner at al., 2012; Goldblum & Veblen, 1992; P. M. Brown & Shepperd, 2001). Nonetheless, there are variations in fire regimes in ponderosa pine forests which are characterized by fires with an average return of 5 to 25 years (Sherriff, 2004; Veblen et al., 2000). These variations in fire regimes create spatially varied or heterogeneous environments (Bataineh et al., 2006; Keyser et al., 2008). Many documented fires were surface fires that burned through understory vegetation but still had significant impacts on the structure and composition of ponderosa pine forests (A. J. Larson et al., 2013; Johnston et al., 2016).

Fires in ponderosa pine forests affect ecological processes and vegetation dynamics in both the short term and long term. In the short term, fires can cause an initial change in understory vegetation species cover, diversity, and composition (Kerns et al., 2011; S. A. Hart & Chen, 2006). Furthermore, fires in the short term can increase tree mortality and render burned landscapes susceptible to other disturbances such as flooding, plant invasions, and soil erosion (Crawford et al., 2001; Naveh, 1994). Fire also opens the forest canopy, allowing the penetration of sunlight to the forest floor, and creating favorable conditions for the colonization of additional, often shade-intolerant, plant species which may include clonal plants (Nepstad et al., 2001).

In the long-term, fire contributes to the overall health and diversity of ponderosa pine forests (Busse & Gerrard, 2020). Kane et al. (2017) found that fire can regulate tree density by thinning smaller trees and reducing competition for resources. Fire also promotes the growth of fire-adapted understory plant species, such as grasses and forbs (Coppoletta et al., 2016; White & Long, 2019). In addition, fire plays a key role in nutrient cycling, as it releases stored nutrients stimulating new growth (S. C. Hart et al., 2005).

Following fire disturbance, ponderosa pine forests go through several post-fire successional stages which vary in duration, species regeneration, composition, and diversity, depending on several factors including the fire regime (i.e., intensity, frequency, and timing) and climatic conditions (Moore et al., 2006; White & Long, 2019). For instance, after fire, there is bare soil and ash; clonal plants can colonize the burned areas and quickly establish themselves vegetatively via underground structures such as rhizomes and bulbs to form patchy understory vegetation (Bradley, 1992; Burrows & Burrows, 1990). Even though the impacts of fire disturbance in ponderosa pine forests have been extensively studied, exploring clonal plant traits and their responses following fire disturbance may provide a more mechanistic explanation of the broader ecological implications of such events.

## Clonal Plant Traits and Responses Following Fire Disturbance

Several studies indicate that clonal plants often dominate the understory of mountain forests, and their responses to fire are driven by the interactions between species, climatic conditions, and resource availability (e.g., Crausbay & Martin, 2016; Sousa, 1984). These interactions have played a crucial role in the evolution of various clonal plants traits and responses to disturbances such as fire, flood, wind, and drought (Table 1) (Klimešová et al., 2017).

Regarding clonal plant traits and response following fire disturbances, numerous studies have reported on clonal plant ability to resprout from bud banks, that is accessory buds or buds on the stems or roots (e.g., Kaufmann, 1990; Klimešová & Klimeš, 2008; P. J. Clarke et al., 2013). These bud banks provide a reservoir of meristematic tissue that can sprout and produce new growth after a fire. Del Tridici (2001) defines resprouting as the production of new vegetative growth following an injury or disturbance. Additionally, clonal plants' ability to resprout following fire disturbance may occur via clonal growth organs (e.g., rhizomes, stolons, bulbils, and tubers), lateral spread, and a bud bank (Klimešová et al., 2021; S. Franklin et al., 2021). These traits and responses enable clonal plants as part of understory vegetation in mountain forests to better colonize burned areas and resprout or regenerate from belowground organs that have survived fires (P. J. Clarke et al., 2013).

Clonal plants have various traits and growth strategies that enhance their fitness. These strategies include clonal integration and foraging for resources (Liu et al., 2016; Svensson et al., 2013). Clonal integration among physiologically dependent and interconnected daughter ramets is an important way clonal plants respond to disturbances (Lu & Franklin, 2022; S. B. Franklin et al., 2020). Clonal integration involves the translocation of resources in a more specialized cooperative system during disturbed conditions (De Kroon et al., 2005; Svensson et al., 2013). This gives clonal plants the ability to exhibit different ways of responding to disturbances and environmental gradients. Several past studies have also reviewed the benefits of clonal integration during disturbances (e.g., B. C. Dong et al., 2017; Liu et al., 2016; Svensson et al., 2013). Data indicate that clonal integration allows for sharing of available resources between interconnected ramets during disturbances ultimately helping them compete better for those resources (B. C. Dong et al., 2017; Liu et al. 2016; Svensson et al., 2013). Having understood the several ways clonal plants respond to disturbances, it is critical to investigate the specific impacts of fire disturbance on these resilient plants.

**Table 1**

*List of Clonal and Belowground Traits and the Respective Disturbance Response(s).*

| Clonal trait | Disturbance | Response | Reference |
|---|---|---|---|
| Clonal growth organs (e.g., rhizome, and stolon) | Fire, herbivory/grazing, wind | Regeneration from surviving rhizomes after fire, tolerance to herbivory/grazing | Brewer & Platt, 1994; Liu et al., 2014; Gao et al., 2014; Dong et al., 2017 |
| Bud bank | Fire, herbivory/grazing, drought | Recruitment from the bud bank post-fire, herbivory/grazing avoidance, drought tolerance | Franklin et al., 2010; Clarke et al. 2013; Vanderweide & Hartnett 2015; Ma et al. 2019 |
| Clonal integration | Fire, windstorm, flood, mowing | Resource sharing between interconnected ramets | Kui et al. 2013; Yu et al. 2018; Franklin et al. 2020; Franklin et al. 2021; Liu et al. 2016; Xiao et al. 2010 |
| Clonal resource foraging | Fire, grazing | Enhanced resource acquisition and nutrient uptake strategies | Matlack 1997; Gao et al. 2014; Liu et al; 2016 |
| Clonal spread | Cutting, flood | Vegetative propagation and expansion | Mony et al. 2011 |

## Impacts of Fire Disturbance on Clonal Plants

Past studies have examined a variety of disturbances (e.g., fire, flood, and wind) and how they have impacted ecological communities (e.g., Bellingham & Sparrow, 2000; Ottaviani et al., 2017; Swanson et al., 2010; Westoby, 1998). I focus here on fire, which can have significant impacts on clonal plants depending on fire intensity, frequency, and the life history characteristics of clonal species in that area (Bond & Keeley, 2005; Oliver & Larson, 1996).

High intensity fires can damage and remove underground and aboveground structures of clonal plants which can disrupt their ability to resprout. For example, Hartnett (1987) found that fire significantly impacted clonal growth, demography, and dynamics of *Pityopsis graminifolia* (Michx.) Nutt. (a perennial clonal forb), thereby decreasing ramet biomass and height. However, other authors reported a positive correlation between fire and clonal plant response. For example, Smith and Nelson (2011) studied the impacts of fire on bamboo-dominated forest in the south-west Amazon. The authors found that fire significantly accelerated the spread and dominance of bamboo species in the south-west Amazon. A similar study by Gagnon and Platt (2008) suggested that fire increased the rate of clonal growth. The authors investigated the responses of *Arundinaria gigantea* (woody clonal bamboo) to fire and wind which revealed an increase in ramet density.

Fires can influence and generate a patchy mosaic of burned and unburned areas, as well as altered competitive interactions between clonal and non-clonal plants, resulting in a wide spectrum of microhabitats (Doherty & Doherty, 2000; Lane et al., 2003). Because distinct genotypes within a population may be more resilient and better respond to changes in community structure and dynamics, this patchiness can increase genetic diversity in clonal populations (Pluess & Stöcklin, 2004). This increase in genetic diversity may enable clonal plants to acquire additional resources to grow new individuals from various regions of their rhizomes or stolons, facilitating colonization and dominance of disturbed areas (Pausas et al., 2018).

## Research Aims and Hypotheses

The current study of this thesis has the following research aims and research hypotheses.

A1 To assess the relative percent cover and diversity of clonal plants in burned and unburned plots of ponderosa pine stands.

H1 Clonal plants will exhibit higher percent cover and diversity in burned plots compared to unburned plots.

A2 To investigate the differences in plant species composition in burned and unburned plots of ponderosa pine stands, focusing on the contributions of clonal and non-clonal plants to these changes.

H2 Species composition in burned plots will significantly differ from those in unburned plots with increased representation of clonal plants.

A3 To investigate the response of clonal traits (lateral spread and ramet length) of *A. uva-ursi* and *A. parviflora*, comparing burned and unburned plots.

H3 Clonal traits (lateral spread and ramet length) of *Arctostaphylos uva-ursi* and *Antennaria parviflora* will show significant responses between burned and unburned plots.

# CHAPTER III

# METHODOLOGY

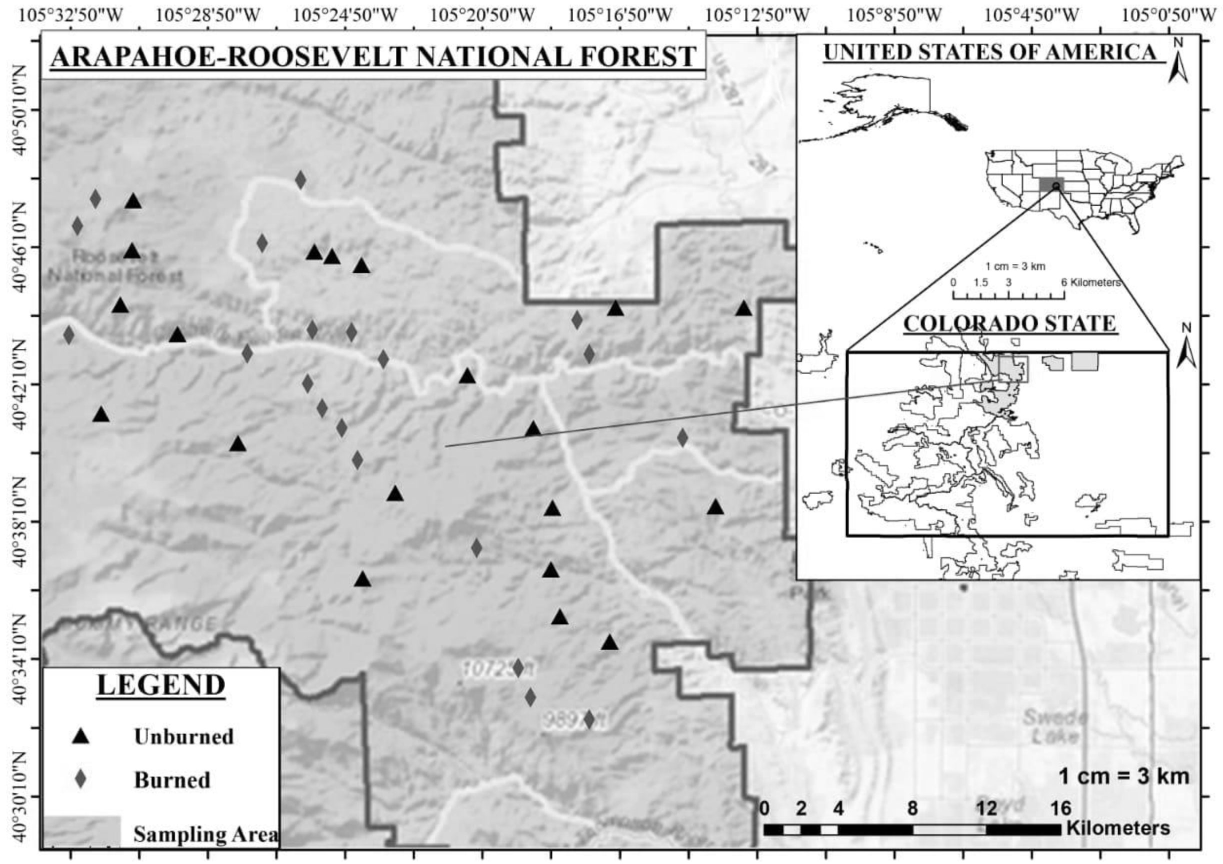
## Study Area

The study was conducted in ponderosa pine (*Pinus ponderosa Douglas ex C. Lawson*) forests of the Arapahoe-Roosevelt National Forest in the Colorado Front Range during the summer of 2023, inside the perimeters of the Cameron Peak Fire, which occurred in 2020 (Figure 1). The Arapahoe-Roosevelt National Forest is a diverse ecosystem that encompasses about 1 516 930 acres of the western United States, dominated by coniferous forest. Ponderosa pine *(Pinus ponderosa)* was dominant in our study sites at low elevations (1800m – 2500m), with several types of understory species including graminoids, forbs, and shrubs (Fryer, 2018). Other conifer species found in our study sites included lodgepole pine (*Pinus contorta)*, Douglas-fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilis*), Rocky Mountain Juniper (*Juniperus scopulorum*) and quaking aspen (*Populus tremuloides*). However, these species were seen chiefly at mid-high elevations (2000m – 2800m) where the forest transitions to a mixed-conifer type. All plots were located throughout the montane zone of the Colorado Front Range and identified through a systematic sampling approach, with elevations ranging from about 1800m to 2500m, with an average annual precipitation of 38.3 cm, most occurring from May through September. Temperatures averaged a high of 32ºC in June to a low of 2ºC in January (data from 1991 to 2020; Western Regional Climate Center, 2007).

The Cameron Peak Fire was one of the largest wildfires in the history of Colorado; it ignited on August 13, 2020, in the Arapahoe-Roosevelt National Forest, near Cameron Pass and Chambers Lake in Larimer County, Colorado (McGrath et al., 2023). According to McGrath et al. (2023), this mountain fire burned an area larger than 840 square kilometers, from around 1600m to about 3400m in elevation. The fire had several impacts on local mountain ecosystems (e.g., increase in overstory and understory mortality, biofuel accumulation, and wildlife habitat loss), and resulted in evacuations and the loss of several structures (Goodwin et al., 2021; Swayze et al., 2021).

**Figure 1**

*Map of the 40 Plots Sampled from Understory Vegetation Distributed within Burned (n=20) and Unburned (n=20) Ponderosa Pine Stands in the Colorado Front Range.*



## Field and Understory Vegetation Measurements

This study was designed to characterize post-fire understory vegetation dynamics, assessing the relative percent cover and diversity of clonal plants in burned and unburned plots within ponderosa pine stands, as well as the differences in composition of clonal and non-clonal plants in burned and unburned plots. Sampling area was delineated and informed based upon the combination of historical fire data in the Colorado Front Range and on-site inspection. Prior to on-field visit, I reviewed historical data on the Cameron Peak wildfire to provide guidance on sampling locations and understand the spatial extent and severity of the fire (data from ArcGIS Story Maps, 2023; https://storymaps.arcgis.com/stories). I then systematically drove through ponderosa pine stands within the potential sampling area to inspect potential burned and unburned plots. Based upon on-field inspection, the 20 burned plots were sampled by assessing ponderosa pine stands that had experienced complete canopy fire consumption during the wildfire event. Similarly, the 20 unburned plots used as controls were sampled plots that had not experienced fire damage. While sampling techniques relied on visual assessment during field visits, the locations of plots were recorded using GPS devices to ensure accurate locations of plots (Appendix B). Plot sampling was conducted in a systematic manner to minimize bias and ensure representation across the study area. Each of the 40 total burned and unburned plots was 10m x 10m, with plots at least 50m apart. In every sampled plot, I took the following environmental data from the plot center: elevation, slope, aspect, longitude, and latitude.

Past studies assert that using plant cover data effectively characterizes plant communities, describes plant-environment interactions, and monitors plant ecosystems through time (Bannari et al., 1995; E. W. Anderson, 1986). Visual estimates of relative percent cover were done using the ocular method of estimating percent cover for all plant species in each plot, both clonal and non-clonal (Godínez-Alvarez et al., 2009; Helm & Mead, 2004). I estimated percent cover of each individual plant species separately within each plot. This involved pooling plant species abundances before calculating relative percent cover. The choice of percent cover over an ordinal cover scale is supported by a recent study by Dengler and Dembicz (2023). In their study, authors found that direct percent cover estimation produces lower mean absolute and relative errors compared to the use of ordinal scales, particularly for cover values above 1% after doing simulations with 121 plant species (Dengler & Dembicz, 2023). Based on the findings, the authors asserted that there is little justification for employing ordinal cover scales in analyses involving numerical data, as percent cover estimation proves to be more accurate and efficient (Dengler & Dembicz, 2023). If a plant could not be identified, I followed the Assessment Inventory and Monitoring methods (Toevs et al., 2011) and initially named that plant as an unknown species. The plant was collected, with detailed descriptions and photos, brought to the University of Northern Colorado herbarium to be keyed and identified, and once identified, reclassified to species in the data set. Clo-Pla 3 (Klimeš & Klimešová, 1999; Klimeš & Klimešová, 2008) and Try plant trait databases (Kattge et al., 2020) were used to label species as clonal or non-clonal based on their dominant clonal growth organ (CGO) (Table 2). In addition, the USDA Plants database was used to provide other ecological traits including life form (forb, shrub or graminoid) and photosynthetic pathway (C3, C4, or CAM).

## Clonal Traits Measurements

For 10 plots each of burned and unburned areas, *A. uva-ursi* and *A. parviflora* were chosen for analysis of clonal traits' response. These plots were chosen primarily based on composition and dispersion throughout the study area. The objective was to investigate whether lateral spread and ramet length differed between burned and unburned plots. *A. uva-ursi* and *A.*

*parviflora* were chosen because they were found in most of plots. For each clonal plant, measurements on lateral spread and ramet length were taken following protocols and standards outlined by Klimešová et al. (2019). These traits are indicative of clonal reproduction and can provide insights into clonal plant recovery in post disturbed conditions (Pausas et al., 2018). Clonal plants are polycyclic and exhibit sympodial branching and so to measure lateral spread (LS), the plants were excavated and the distance between offspring and rooting units was measured (Klimešová et al., 2019). Ramet length (RL) was the linear measurement of an individual shoot from the base to the tip. To account for potential variations within each clonal plant, measurements were taken on multiple individuals, and an average was calculated.

## Data Analyses

I was primarily interested in assessing the relative percent cover and diversity of clonal plants in burned and unburned plots of ponderosa pine stands. I calculated relative percent cover from field estimates of percent cover, in that all species in each plot summed to 100%. All analyses were based on relative percent cover. Diversity variables (i.e., richness, evenness, Shannon, and Simpson) were calculated using a full species matrix for 40 total plots with 27 clonal taxa/species in PC – ORD. Since my percent cover and diversity data did not meet assumptions of normality and homoscedasticity of variances, unpaired non-parametric Mann-Whitney U tests were conducted to assess whether each of our response variables: relative percent cover, richness, evenness, Shannon, and Simpson differed between burned versus unburned plots for clonal plants. For clonal plant trait measurements, one MANOVA (multivariate analysis of variance) was used to detect the effects of burned versus unburned plots on lateral spread and ramet length for each clonal plant *A. uva-ursi* and *A. parviflora* in a combined model. This method was chosen to assess the overall effect of burned versus unburned plots on multiple traits simultaneously. While lateral spread and ramet length may respond differently, analyzing them together allowed for a comprehensive assessment of trait responses. All analyses were conducted using R Statistical Software (version 4.3.1; R Core Team, 2021).

PC-ORD 7.10 (McCune & Mefford, 2018) was used to perform multivariate analyses to explore differences in species composition in burned and unburned plots, and how clonal and non-clonal plants contribute to these changes. More specifically, four distinct types of multivariate analyses were used to explore these differences in species composition: non-metric multidimensional scaling (NMS), multi-response permutation procedures (MRPP), indicator species analysis (ISA), and the fourth corner analysis (FCA).

NMS ordinates points (burned and unburned plots in our case) in a reduced-dimensional space, preserving the pairwise dissimilarity among them. This helps to visualize patterns and relationships in ecological communities (Hakkenberg et al., 2018). NMS was used because the data did not follow linear, parametric assumptions for normality and homogeneity of variances, and this is common with ecological community data (McCune & Grace, 2002; K. R. Clarke, 1993). Autopilot with the “Slow and Thorough” setting using **“**Sørensen distance” measure was used to run 50 iterations to create a configuration for the ordination including 104 clonal and non-clonal taxa/species in the primary species matrix and 40 total burned and unburned plots. The second matrix had five environmental variables collected at each plot from the center (elevation, slope, aspect, latitude, and longitude). MRPP and ISA were performed to complement and help interpret the NMS ordination.

MRPP is a non-parametric statistical test which determines whether there are significant differences between groups based on multivariate response variables (Pillar, 2013). In this case, I used MRPP to assess the dissimilarity in species composition between burned and unburned plots using the "Sørensen distance" measure. Based on the weighting technique, the analysis can generate the chance-corrected within-group agreement (*A*) and probability (*p*) of smaller or equal delta (McCune & Mefford, 1999).

ISA was used to determine which plants were significantly associated with burned and unburned plots. From there, I was able to identify whether those plants were clonal or non-clonal. Additionally, ISA generates indicator values with significance for each plant species (McCune & Grace, 2002).

The fourth corner analysis (FCA) explores species trait-environment relationships. It is called the "fourth corner" because it combines three corners of species ecological traits, environment variables, and species cover data, and then leaves the fourth corner to be analyzed to examine the relationship between species, environmental variables, and plant ecological traits (A. M. Brown et al., 2014; Dray et al., 2014). Specifically in this study, the FCA was used to determine whether environmental variables had any relationship with species ecological traits and with differences in species composition observed in the NMS ordination.

# CHAPTER IV

# RESULTS

## Relative Percent Cover and Diversity of Clonal Plants

One hundred and four (104) understory species (27 clonal and 77 non-clonal) were identified in all 40 total burned and unburned plots during the summer of 2023: 53 forbs, 22 graminoids, 21 woody shrubs, 7 tree species and 1fern species (see Appendix A). Invasive species were found to be relatively rare in all plots. Clonal plants (see Table 2; with dominant clonal growth organs) and non-clonal plants were found mostly as forbs, with a few shrubs and graminoids. Both burned and unburned plots had an overstory dominated by *Pinus ponderosa* but included *Pinus flexilis* and *Pseudotsuga menziesii* to a lesser extent. *Achillea millefolium, Campanula rotundifolia,* and *Antennaria parviflora* showed the greatest cover among forb species. *Arctostaphylos uva-ursi, Artemisia ludoviciana, Artemisia frigida*, *Cercocarpus montanus*, and *Purshia tridentata* were the shrub species with the most cover. In terms of graminoids, *Carex rossii, Bromus tectorum,* and *Poa bulbosa* were the species with the greatest cover in our plots.

**Table 2**

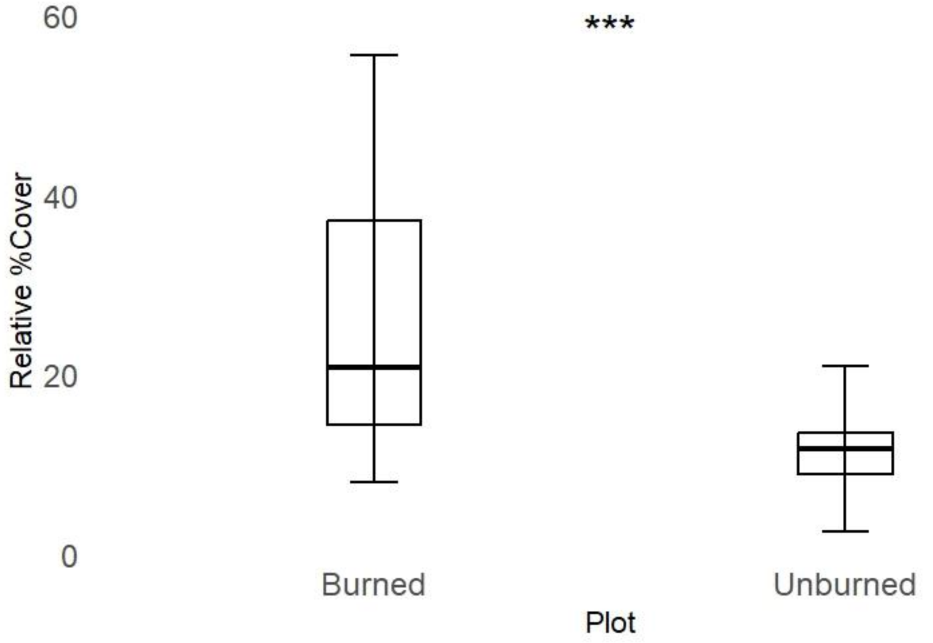
*Clonal Species with Dominant Clonal Growth Organs (CGOs) in Sampled Plots of Ponderosa Pine Stands in the Colorado Front Range (from Clo-Pla 3 & Try Databases).*

| Species | Clonal Growth Organ |
|---|---|
| *Achillea millefolium* | epigeogenous stem (rhizome) |
| *Antennaria parviflora* | epigeogenous stem (rhizome) |
| *Arctostaphylos uva-ursi* | epigeogenous stem (rhizome) |
| *Bromus inermis* | hypogeogenous stem (rhizome) |
| *Campanula rotundifolia* | epigeogenous stem (rhizome) |
| *Cerastium arvense* | root-splitter |
| *Carex rossii* | epigeogenous stem (rhizome) |
| *Cirsium arvense* | roots with adventitious buds |
| *Chenopodium album* | horizontal above-ground stem |
| *Cymopterus lemoniid* | epigeogenous stem (rhizome) |
| *Cystopteris fragilis* | epigeogenous rhizome |
| *Draba graminea* | root-splitter |
| *Koeleria macrantha* | root-splitter |
| *Oxytropis campestris* | bulb |
| *Phleum pratens* | epigeogenous stem (rhizome) |
| *Ribes aureum* | roots with adventitious buds |
| *Rubus idaeus* | epigeogenous stem (rhizome) |
| *Poa bulbosa* | epigeogenous stem (rhizome) |
| *Poa pratensis* | hypogeogenous stem (rhizome) |
| *Pulsatilla patens* | epigeogenous stem (rhizome) |
| *Purshia tridentata* | epigeogenous stem (rhizome) |
| *Salix spp.* | horizontal above-ground stem |
| *Symphoricarpos orbicalatus* | epigeogenous stem (rhizome) |
| *Taraxacum officinale* | root-splitter |
| *Thalictrum alpinum* | epigeogenous stem (rhizome) |
| *Tragopogon dubius* | epigeogenous stem (rhizome) |
| *Vicia sativa* | epigeogenous stem (rhizome) |

The relative percent cover of clonal plants was expected to differ significantly between burned and unburned plots. The Mann Whitney U test indicates a significant difference in the percent cover of clonal plants between burned and unburned plots ($U = 332$; $p < 0.001$) with the percent cover of clonal plants being significantly higher in burned plots compared to unburned plots (Figure 3).

**Figure 2**

*Relative Percent Cover of Clonal Plants from Burned versus Unburned Ponderosa Pine Stands in the Colorado Front Range.*



An average of 12 species (i.e., diversity) in burned plots and 6 species in unburned plots were found for all taxa. Similarly, richness of clonal plants showed a significant difference between burned and unburned plots ($U = 397$; $p < 0.001$). Richness was significantly greater for clonal plants in burned plots compared to unburned plots (Figure 4). However, evenness of clonal plants did not significantly differ between burned and unburned plots ($U = 203.5$; $p = 0.935$). (Figure 5).

**Figure 3**
*Richness of Clonal Plants from Burned versus Unburned Ponderosa Pine Stands in the Colorado Front Range.*

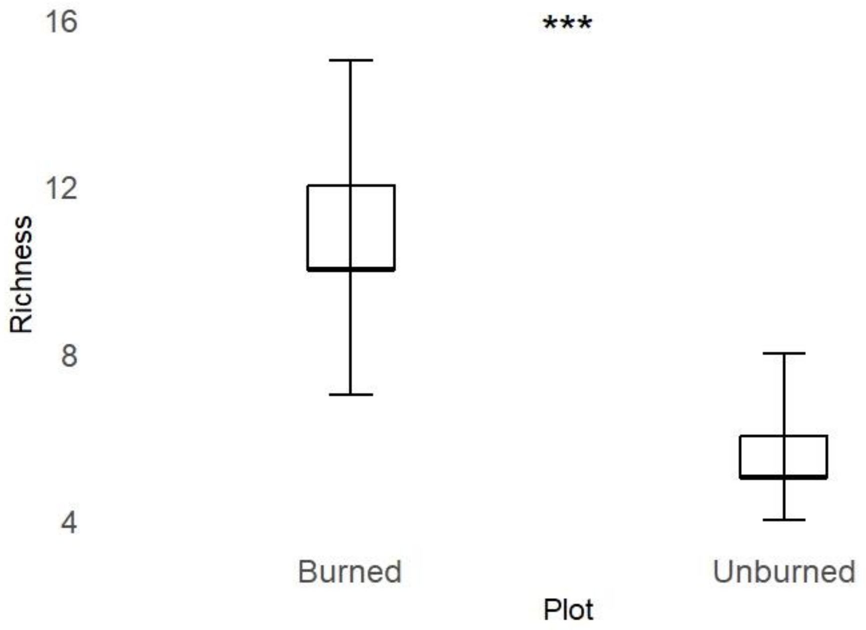
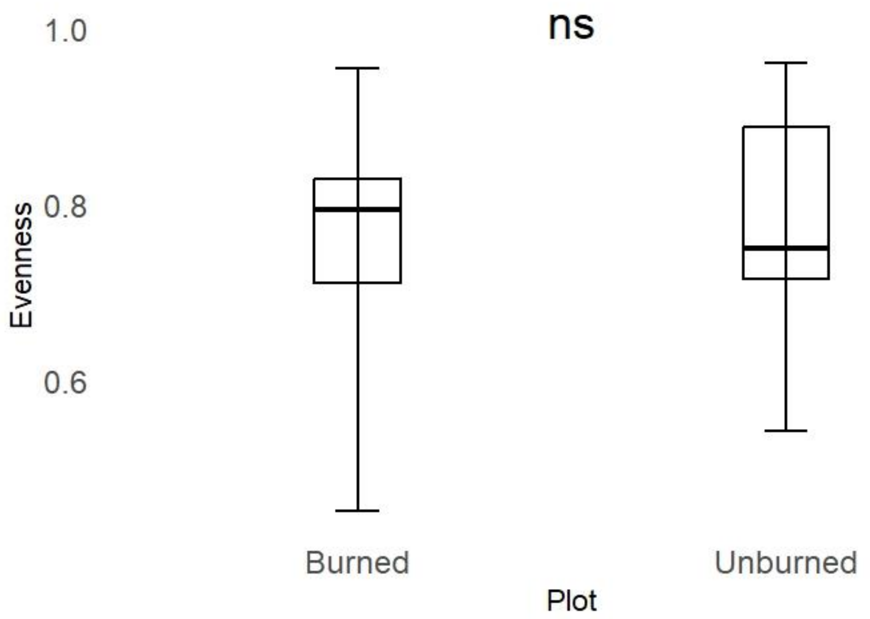


**Figure 4**
*Evenness of Clonal Plants from Burned versus Unburned Ponderosa Pine Stands in the Colorado Front Range.*



Shannon and Simpson's diversity indices showed significant differences between the burned and unburned plots (*U* = 360; *p* < 0.001; *U* = 316; *p* = 0.002; respectively) with both being significantly greater in burned plots than unburned plots (Figures 5 and 6).

**Figure 5**

*Shannon's Diversity of Clonal Plants from Burned versus Unburned Ponderosa Pine Stands in the Colorado Front Range.*

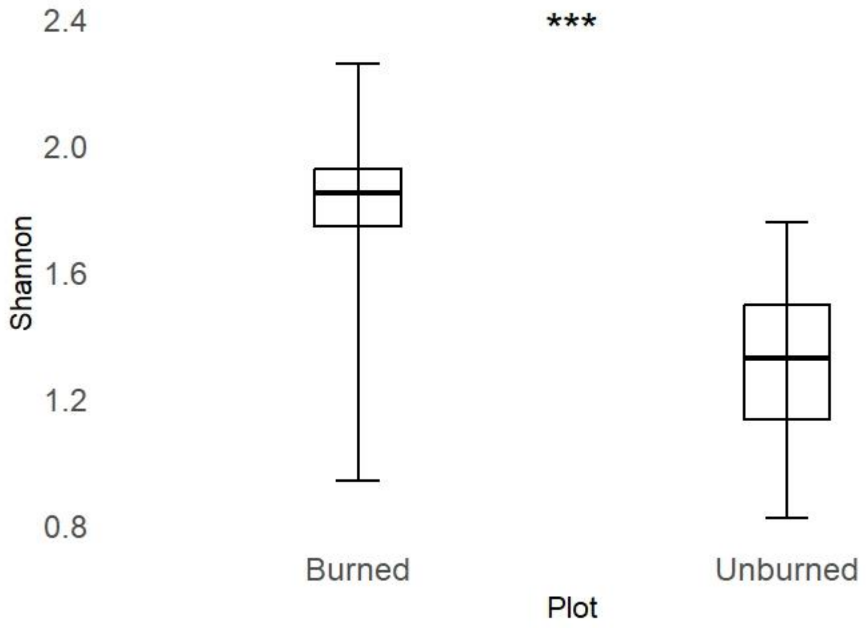
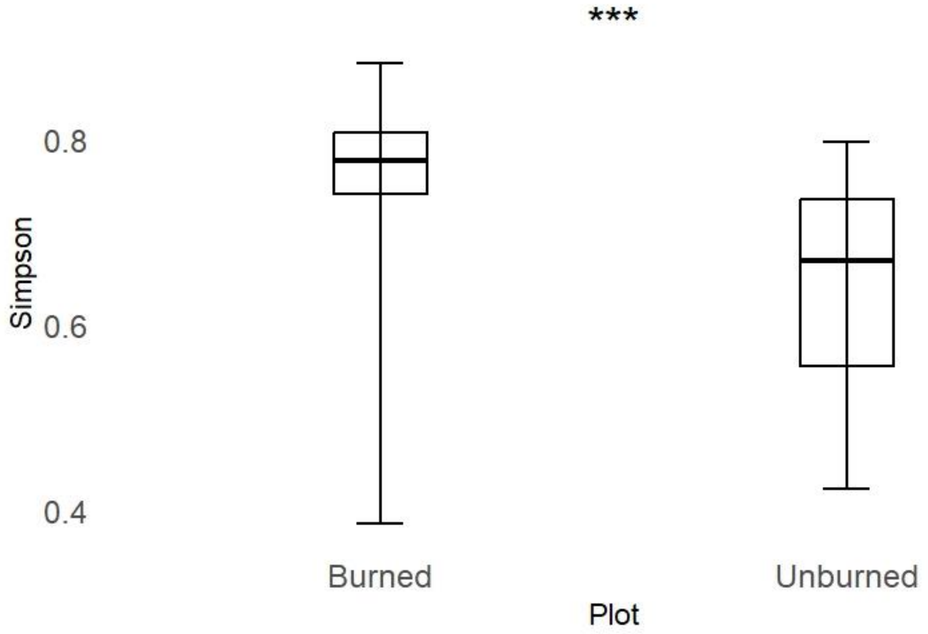


**Figure 6**

*Simpson's Diversity of Clonal Plants from Burned versus Unburned Ponderosa Pine Stands in the Colorado Front Range*



## Community Structure

I examined species community composition comparing differences in burned and unburned plots. Non-metric multidimensional scaling (NMS) ordination, multi-response permutation procedure (MRPP), indicator species analysis (ISA), and the fourth corner analysis (FCA) were used to explore differences in species composition. The NMS ordination recommended an optimal three-dimensional solution (*p* = 0.004) explaining 64.3% variation in the understory species composition. It achieved an acceptable final stress level of 18.11 and a final solution instability of < 0.0001 with 102 iterations.

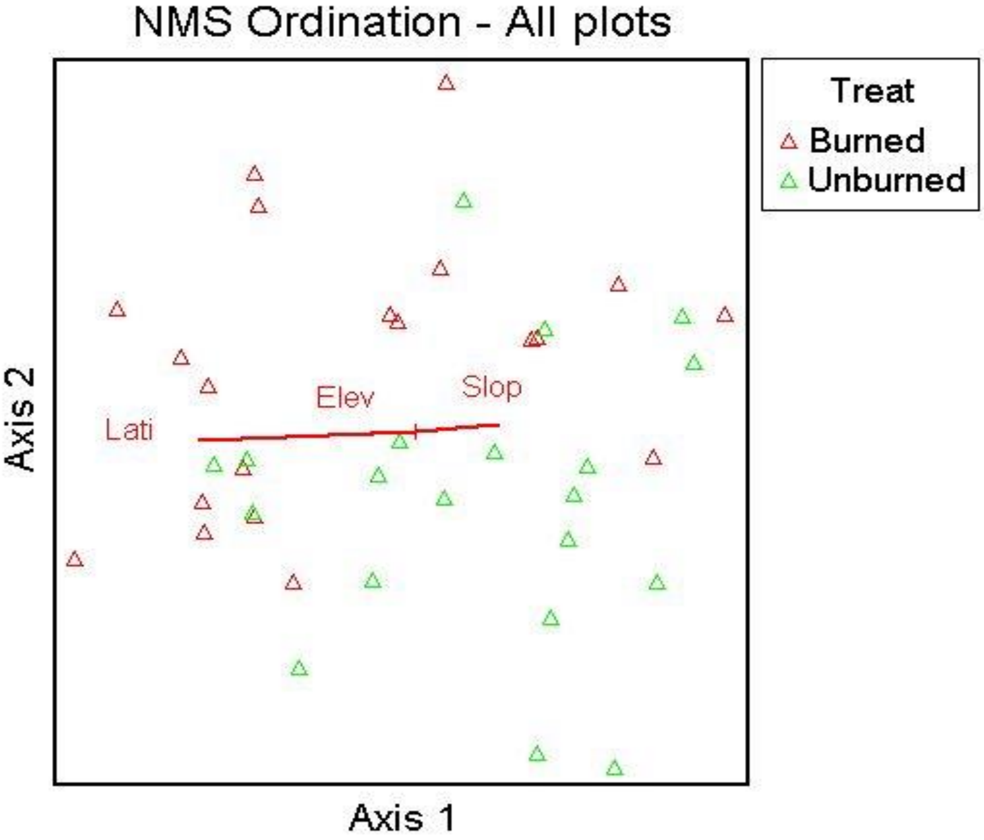
Axis 1 explained 25.2% of the variance, indicating that it captures a substantial portion of the overall variation in species composition. The positive end of axis 1 was observed to have corresponded with higher *Carex rossii* (*r* = 0.588)*, Pascopyron spp.* (*r* = 0.481), *Helianthus pumilus* (*r* = 0.476), and to a lesser extent *Poa bulbosa* (*r* = 0.438) and *Mertensia ciliata* (*r* = 0.427). Conversely, the negative end of axis 1 correlated with *Cirsium arvense* (*r* = -0.504) and to a lesser extent *Geranium spp.* (*r* = -0.490) and *Achillea millefolium* (*r* = -0.435). The only environmental variable that was positively correlated with axis 1 was slope (*r* = 0.471) whereas elevation and latitude were negatively correlated (*r* = -0.763; *r* = -0.485; respectively). Plots formed distinct burned and unburned groups in ordination space (Figure 7).

The second axis contributed an additional 23.4% of the variance. Species that correlated strongly with the positive end of axis 2 were *Taraxacum officinale* (*r* = 0.494), *Potentilla fissa* (*r* =0.454) and *Carex rossii* (*r* = 0.451). Moreover, there were weak positive correlations between axis 2 with *Viburnum edule* (*r* = 0.389), *Campanula rotundifolia* (*r* = 0.380), and *Achillea millefolium* (*r* = 0.315). Negative correlations of species on the second axis included *Erigeron eximius* (*r* = -0.393), *Sedum lanceolatum* (*r* = -0.383), *Poa bulbosa* (*r* = -0.382) and to a lesser extent *Draba graminea* (*r* = -0.379). All environmental variables had weak correlations with axis 2. However, the unburned plots tended to cluster at the negative end of axis 2, while burned plots clustered toward the positive end of this axis.

The third axis accounted for 13.4 % of the explained variance. The positive end of axis 3 had strong correlations with *Castilleja puberula* (*r* = 0.421) and *Viburnum edule* (*r* = 0.382). The negative end was strongly correlated with *Artemisia ludoviciana* (*r* = -0.573), *Purshia tridentata* (*r* = -0.549), *Heterotheca villosa* (*r* = -0.439), *Helianthus pumilus* (*r* = -0.406), *Bromus inermis* (*r* = -0.405), and *Cercocarpus montanus* (*r* = -0.403). Slope was strongly negatively correlated (*r* = -0.490) while elevation, aspect, longitude, and longitude all had very weak correlations with axis 3.

**Figure 7**

*NMS Ordination of the Understory Species Composition for all 40 Burned and Unburned Plots of Ponderosa Pine Stands in the Colorado Front Range. A Three-Dimensional Solution was Recommended, but only Two Dimensions are Shown Here. Burned Plots are Marked by Red Triangles whereas Unburned Plots are Marked by Light Green Triangles with Five Environmental Variables (Elevation, Slope, Aspect, Latitude and Longitude).*



MRPP analysis was performed to assess the differences in species composition between groups (burned vs. unburned plots). MRPP ($T$ = -9.970, $A$ = 0.021, $p$ < = 0.001) analysis revealed statistically significant differences in vegetation composition between burned versus unburned plots. However, these differences may not be ecologically meaningful. ISA identified species that were driving differences between burned and unburned plots. Sixteen significant indicator species were found for both burned and unburned plots out of the 104 clonal and non-clonal taxa/species in the species matrix ($p \leq 0.05$). Fifteen species (63% clonal; 37% non-clonal) were significant indicators of burned plots and only one species (100% clonal) was a significant indicator of unburned plots (Table 3).

**Table 3**

*Results of Indicator Species Analysis (ISA) for Species Across Study Plots from Ponderosa Pine Stands in the Colorado Front Range.*

| *Species* | *Plant type* | *Plot Indicated* | *Observed Indicator Value* | *P-value* |
|---|---|---|---|---|
| *Achillea millefolium* | Clonal | Burned | 80.0 | 0.0002 |
| *Campanula rotundifolia* | Clonal | Burned | 67.0 | 0.0004 |
| *Purshia tridentata* | Clonal | Burned | 55.0 | <0.001 |
| *Oxytropis campestris* | Clonal | Burned | 45.0 | 0.002 |
| *Taraxacum officinale* | Clonal | Burned | 37.3 | 0.041 |
| *Circium arvense* | Clonal | Burned | 35.0 | 0.009 |
| *Poa pratensis* | Clonal | Burned | 35.0 | 0.007 |
| *Rubus idaeus* | Clonal | Burned | 25.0 | 0.023 |
| *Thalictrum alpinum* | Clonal | Burned | 25.0 | 0.045 |
| *Mertensia ciliata* | Non-clonal | Burned | 25.0 | 0.043 |
| *Potentilla fissa* | Non-clonal | Burned | 66.8 | 0.001 |
| *Artermisia ludoviciana* | Non-clonal | Burned | 48.6 | 0.046 |
| *Festuca saximontana* | Non-clonal | Burned | 40.0 | 0.002 |
| *Bromus madritensis* | Non-clonal | Burned | 30.0 | 0.020 |
| *Verbascum thapsus* | Non-clonal | Burned | 45.0 | 0.001 |
| *Cystostopteris fragilis* | Clonal | Unburned | 25.0 | 0.048 |

Fourth corner analysis (FCA) was used to examine the relationship between environmental variables with clonality (clonal or non-clonal), life form (forb, shrub or graminoid), type of CGO, and photosynthetic type (C3, C4 or CAM). Elevation and slope did not significantly relate to life form. Similarly, latitude and longitude had no significant relationships with life form. None of the environmental variables showed statistically significant relationships with clonality (all $p > 0.05$) suggesting a weak relationship between environmental variables and clonality. However, the type of CGOs was significantly associated with elevation ($p = 0.002$) and slope ($p = 0.028$). Specifically, elevation showed relationships with the CGOs horizontal aboveground stems, epigeogenous rhizomes, and root splitters ($r = -0.165$, $p = 0.025$; $r = -0.167$, $p = 0.019$; $r = 0.189$, $p = 0.032$; respectively). Slope also had significant relationships with epigeogenous rhizomes ($p = 0.023$). Aspect, latitude, and longitude generally displayed insignificant relationships with type of CGOs (all $p > 0.05$). There were no significant relationships among environmental variables and photosynthetic type (all $p > 0.05$). Elevation and slope exhibited relationships with the type of CGOs, which suggest that elevation, slope and fire history interact significantly in shaping vegetation community structure, consistent with the NMS ordination results (Table 4).

**Table 4**

*Results of Fourth Corner Analysis (FCA) Examining the Relationship of Environmental Variables with Species Ecological Traits from Ponderosa Pine Stands in the Colorado Front Range.*

| *Environmental variable* | *Species ecological trait* | *F Value* | *P Value* |
|---|---|---|---|
| Elevation | clonality | 0.745 | 0.837 |
| | life form | 7.734 | 0.632 |
| | CGOs | 35.401 | 0.002 |
| | photosynthetic type | 5.812 | 0.319 |
| Slope | clonality | 0.71 | 0.822 |
| | life form | 5.174 | 0.698 |
| | CGOs | 23.21 | 0.028 |
| | photosynthetic type | 2.633 | 0.433 |
| Aspect | clonality | 4.994 | 0.380 |
| | life form | 4.499 | 0.436 |
| | CGOs | 5.384 | 0.601 |
| | photosynthetic type | 2.182 | 0.437 |
| Latitude | clonality | 1.544 | 0.753 |
| | life form | 9.643 | 0.372 |
| | CGOs | 11.218 | 0.272 |
| | photosynthetic type | 3.712 | 0.465 |
| Longitude | clonality | 4.676 | 0.395 |
| | life form | 8.676 | 0.127 |
| | CGOs | 4.281 | 0.724 |
| | photosynthetic type | 3.647 | 0.330 |

## Clonal Traits Response in Burned and Unburned Plots

MANOVA results suggested that the combined responses of lateral spread (LS) and ramet length (RL) of *A. urva-ursi* responded significantly to recent fires, with both traits greater in burned plots compared to unburned (Pillai Trace $F = 0.5624$, $p < 0.001$; Figure 8). In burned plots the lateral spread and ramet length for *A. urva-ursi* varied in their degree of plasticity following fire. However, in unburned plots lateral spread and ramet length for *A. urva-ursi* showed relatively lower variability compared to burned plots. *A. parviflora*, in contrast, did not show a significant difference between burned and unburned plots for the combined responses lateral spread or ramet length (Pillai Trace $F = 0.1042$, $p = 0.393$; Figure 9). In unburned plots lateral spread and ramet length of *A. parviflora* showed relatively lower variability compared to burned plots.

**Figure 8**

*Response of Lateral Spread and Ramet Size of Arctostaphylos urva-ursi from Burned versus Unburned Ponderosa Pine Stands in the Colorado Front Range.*

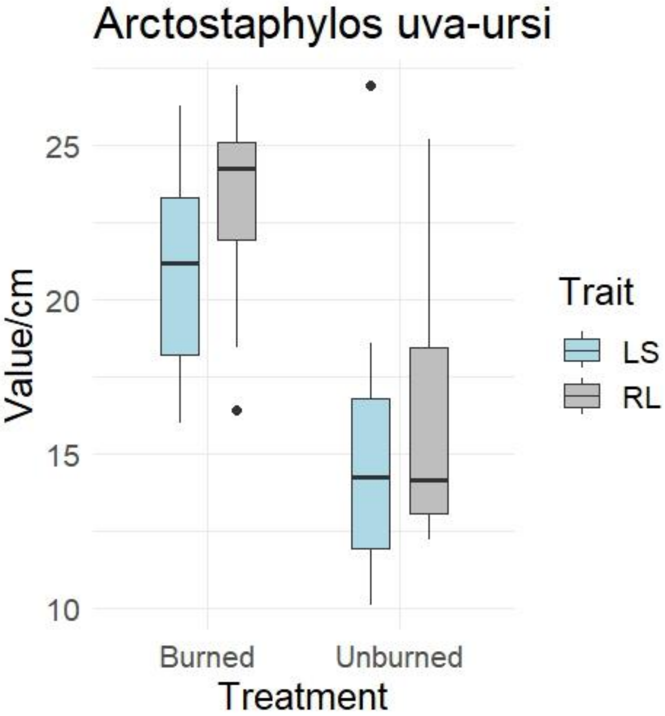
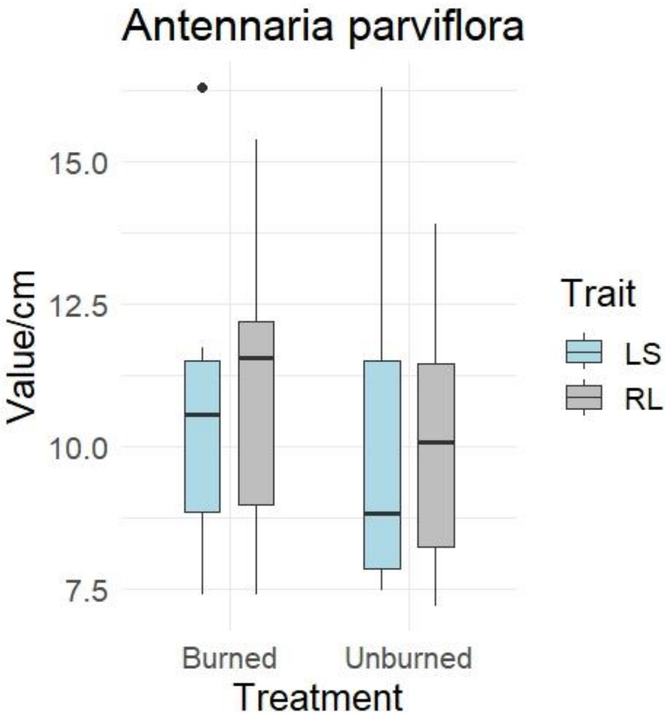


**Figure 9**

*Response of Lateral Spread and Ramet Size of Antennaria parviflora for Burned versus Unburned Ponderosa Pine Stands in the Front Range of Colorado.*



# CHAPTER V

# DISCUSSION

## Relative Percent Cover and Diversity of Clonal Plants

In this study, I was primarily interested in examining the response of understory clonal plants following fire disturbance in burned and unburned plots of ponderosa pine stands of the Colorado Front Range. I hypothesized that clonal plants would have greater relative percent cover and diversity in burned plots compared to unburned plots. I also predicted that the different responses of clonal and non-clonal plants would result in significant changes in overall species composition between burned and unburned plots. In addition, I hypothesized that clonal traits of *A. uva ursi* and *A. parviflora* would differ in their responses between burned and unburned plots. Overall, the findings partially supported my hypotheses. First, I observed greater relative percent cover and diversity of clonal plants in burned plots, consistent with my hypotheses. However, while there were statistically significant changes in species composition, these changes may not be ecologically meaningful. In addition, clonal traits' responses of *A. uva-ursi* and *A. parviflora* did not differ ecologically between burned and unburned plots, although there were variations in the extent of these differences.

Several studies have highlighted the significant ecological role of plant clonality in facilitating ecosystem recovery and promoting community restoration in post-fire systems (e.g., Fahrig et al., 1994; Oborny et al., 2000; S. Franklin et al., 2021; Van Mantgem et al., 2020). Here, I found a greater overall percent cover of clonal plants in burned plots compared to unburned plots. I attribute the shift in percent cover post-fire to the resilience, colonization, and the inherent abilities of clonal plants for vegetative reproduction and resprouting from belowground organs that possess a strong bud bank, such as rhizomes, stolons, and bulbils (Klimešová & Klimeš, 2008; Klimešová & Martínková, 2022). This advantage becomes apparent as clonal plants outcompete non-clonal plants in disturbed environments (Stuefer, 1996; Svensson et al., 2013). In addition, post-fire environments may be characterized by increased environmental heterogeneity particularly at broader spatial scales beyond the specific plots we measured. The effects of fire can influence the landscape, creating variations in soil properties, microclimates, and vegetation composition at a larger scale (Schoennagel et al., 2008). While this study focused on the plot level, the potential for increased heterogeneity extends to the landscape level in post-fire conditions (Fernández-García et al., 2018), and clonal plants benefit from such conditions (Herben & Klimešová, 2020; Klimešová et al., 2021) due to their ability to quickly regrow and exploit post-fire available resources and openings (Klimešová et al., 2018; Svensson et al., 2013). Furthermore, the increased percent cover of clonal plants in burned plots may be due to physiological integration of interconnected ramets, allocation and storage of resources, lateral spread, multiplication rate and persistence of connection which are significant clonal traits that have been found to help clonal plants recover and dominate in post-disturbed ecosystems (Herben et al., 2018; Liu et al., 2016).

My data suggest that clonal plants increase in overall species richness following fire, and this is likely due to their vegetative reproduction and persistence. This is seen in the greater number of species recorded for clonal plants especially in burned plots compared to unburned plots; similar findings come from other studies of increased clonal plant richness in post-disturbed ecosystems (e.g., McMahon et al., 2017; Pausas et al., 2018). However, clonal plant evenness was not significantly different between burned and unburned plots though a little higher in burned plots. The similarity in evenness between burned and unburned plots implies that the impact of fire on clonal plant distribution is not significantly altering the relative abundance of different clonal species. Evenness is often associated with the ability of an ecosystem to withstand disturbances, and the dominance of specific genotypes within populations (Battisti et al., 2016). This means that similar evenness of clonal plants in both burned and unburned plots may influence the stability and resilience of the entire plant community as it may impact the community's ability to recover after fire disturbance (Sasaki & Lauenroth, 2011). Lastly, the greater Shannon and Simpson indices further support the idea of greater diversity of clonal plants post-fire. This is potentially due to recolonization of clonal plants in a mosaic of heterogenous habitats following fire disturbance.

## Community Structure

### Axis 1: Elevational Gradient

Ordination axis 1 primarily represents elevational gradient in vegetation community structure. I can attribute these patterns to topography particularly in the unburned ponderosa pine plots in the study system. On the positive end of axis 1, which associated with plots from higher elevations, the species that were associated included *Carex rossii, Pascopyron spp., Helianthus pumilus, Poa bulbosa,* and *Mertensia ciliata*. These species likely thrive in cooler conditions typical of higher elevations in the unburned ponderosa communities. The negative end of axis 1 was correlated with *Cirsium arvense*, *Geranium spp.,* and *Achillea millefolium*. The negative end of axis 1 may suggest conditions which are warmer at lower elevations. This could be influenced by other topographical features such as the dense canopy cover of ponderosa pine trees in the unburned plots. While elevation emerges as the main driver of species along axis 1, particularly in unburned plots, there might be an interaction between elevation and fire history in shaping vegetation community structure.

### Axis 2 – Post-Fire Disturbance and Species-Specific Response Gradient

Axis 2 corresponds to a post-fire disturbance and species-specific response gradient. The driving differences in post-fire disturbance can be seen along Axis 2 between burned and unburned plots (Figure 7). The positive end represents plots that are more likely burned and occupied by species that respond better to fire; whereas plots at the negative end are occupied by species which prefer unburned or less frequently burned areas, where vegetation has had more time to establish. On the positive end, *Taraxacum officinale*, *Potentilla fissa*, and *Carex rossii* were strongly correlated with this axis. Burned plots mostly clustered at the positive end of this gradient. *Taraxacum officinale* and *Carex rossii* exhibit some form of clonality, though they can make use of their seeds which enable them to thrive in certain post-fire microhabitats. For example, *Taraxacum officinale* though a clonal plant*,* can respond and thrive in fire disturbed habitats by means of its wind-dispersed seeds (Toth, 1991). *Potentilla fissa*, a perennial herb, and *Carex rossii*, a sedge species, both highly shade tolerant, may also benefit from the heterogeneous conditions in post-fire microhabitats, allowing them to establish. On the negative end of axis 2, species like *Erigeron eximius*, *Sedum lanceolatum*, *Poa bulbosa*, and *Draba graminea* may also have preferred certain microhabitats. Further, unburned plots mostly clustered at the negative end of this axis. I believe that fire regimes in the Colorado Front Range may have had an impact on the landscape of my study area.

### Axis 3 – Species Frequency Gradient

Axis 3 likely corresponds to variation in species frequency related to post-fire vegetation structure. The positive end was associated with only two species *Castilleja puberula* and

*Viburnum edule* that are not indicative of post-fire environments in the literature. However, at the negative end of the gradient, I found that plots were associated with frequent species commonly found in post-fire environments. These species included *Artemisia ludoviciana*, *Purshia tridentata*, *Heterotheca villosa*, *Bromus inermis* and *Cercocarpus montanus.* Also, the negative correlation with slope for axis 3, suggests that slope plays a significant role in shaping the distribution of species along axis 3. Steeper slopes may experience different fire behavior and severity compared to areas with gentler slopes, which may influence the frequency of species leading to variation in post-fire community structure (Bassett et al., 2015).

### Multi-Response Permutation Procedures (MRPP)
### and Indicator Species Analysis (ISA)

The data suggest that there are species compositional differences observed between burned and unburned plots. However, the magnitude of this difference was very small suggesting that community structure in burned and unburned plots may not be ecologically meaningful. The ISA showed 16 significant indicator species between the burned and unburned plots. I found only three species with indicator value greater than 60 which suggests that overall, in this study species did not have high indicator values partly due to low group fidelity because of the several species occurring in large proportions of the total sampled plots. Several clonal plants including *Achillea millefolium, Campanula rotundifolia, Circium arvense, Oxytropis campestris*, *Purshia tridentata, Taraxacum officinale,* and *Poa pratensis* emerged as significant indicators in burned plots, which was not surprising as I expected clonal plants to have a more direct and immediate means of responding in burned plots compared to unburned plots. This further confirms that clonal plants do well in post disturbed environments and might contribute to post-fire ecosystem resilience (Falk et al., 2019; Lloret & Zedler, 2009).

## Fourth Corner Analysis (FCA)

I found no relationships between clonality (clonal or non-clonal), life form (forb, shrub or graminoid), photosynthetic type (C3, C4, or CAM) and environmental variables (elevation, slope, aspect, longitude, and latitude). My initial hypothesis posited no relationships with the reason being that clonality, life form, and photosynthetic type are ecological traits that might be relatively stable and inherent within plant species regardless of environmental variations (Liu et al., 2016). While clonality, life form, and photosynthetic type may show relatively stable and inherent abilities within plant species, their responses can vary. For instance, clonal plants might exhibit diverse strategies in response to disturbance, with some species showing resilience and others undergoing shifts in clonal growth patterns. Elevation and slope were significantly related with type of CGOs specifically with horizontal aboveground stems, epigeogenous rhizomes and root splitters. This suggests clonal plants invest in these GCOs at higher elevations or steeper slopes. This allocation could be an adaptive response that may enhance the ability of clonal plants to spread efficiently and access resources, especially in post disturbed conditions (Šťastná et al., 2012). Additionally, the significant relationships of elevation and slope with horizontal aboveground stems, epigeogenous rhizomes, and root splitters suggest that individual clonal species may have multiple CGOs which could indicate a nuanced response to environmental conditions, with certain CGOs being preferentially utilized over others in specific conditions (Andrea, 2005). Elevation was highly correlated with NMS axis 1 which was the strongest of all the environmental variables and seeing that it also had significant relationships with the type of CGOs in the FCA further suggests that elevation and fire history interact significantly in shaping vegetation community structure in these ponderosa pine dominated ecosystems of the Colorado Front Range.

## Clonal Traits Response in Burned and Unburned Plots

The different responses of the two clonal plant species *A. uva ursi* and *A. parviflora* in burned plots suggest that clonal plants have various ways of responding, and it is crucial to think about how each species uniquely responds following disturbances (Bell et al., 2023; S. B. Franklin et al., 2020). More specifically, *A. uva-ursi* showed increased lateral spread and ramet length in burned plots which might help the plant recover after a fire and grow more. While there are almost no studies explicitly investigating *A. uva-ursi* and *A. parviflora* clonal traits response following fire, a study by Hutchings and de Kroon (1994) reveals how lateral spread and other clonal traits vary in response to different environmental conditions though authors emphasized that genetic factors could constrain or facilitates the lateral spread and other clonal traits reponse in heterogenous environments. The varying plasticity of these traits in post disturbed conditions is crucial in competing or foraging for resources (Dietz & Steinlein, 2001; Hutchings & de Kroon, 1994; M. Dong & de Kroon, 1994). These varying responses have practical implications for managing ecosystems, especially those prone to wildfires. The fact that clonal plants have unique trait responses emphasizes the need for customized management plans that consider the specific needs of each plant species following fire disturbances.

## Conclusions

The findings of this study suggest that elevation, slope and fire history interact to have significant impacts on the understory vegetation of ponderosa pine stands in the Arapahoe-Roosevelt National Forest in the Colorado Front Range. Three years after the fire, clonal plants are recovering with greater relative percent cover and diversity in burned plots due to their ability to spread vegetatively, revealing their resilience, adaptability, and colonization in the face of ecological disturbances. While statistically significant changes in species composition between burned and unburned plots were observed, it is important to recognize that these differences did not have a clear ecological or floristic significance. My results should inform foresters, managers, and modelers about the performance of clonal plants, and more importantly how clonal plant traits are utilized in response to changes in fire regimes. As clonal plants become increasingly important especially due to their traits and roles in rapid propagation, and regeneration following disturbances, further studies should investigate the mechanisms underlying their success in post-disturbance recovery.  Long-term monitoring studies of post-fire ecosystems would help us to better understand the sustainability of clonal plants and their traits over time.

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# APPENDIX A

# SPECIES LIST INDICATED BY PLOT TYPE (BURNED, UNBURNED OR BOTH) AND PLANT TYPE (CLONAL OR NON-CLONAL) IN STUDY AREA

**Table A1: Continued**

| Species | Plot Type | Plant Type |
|---|---|---|
| *Achillea millefolium* | Both | Clonal |
| *Antennaria parviflora* | Both | Clonal |
| *Arctostaphylos uva-ursi* | Both | Clonal |
| *Artemisia frigida* | Both | Non-clonal |
| *Artemisia ludoviciana* | Both | Non-clonal |
| *Artemisia tridentata* | Both | Non-clonal |
| *Bromus tectorum* | Both | Non-clonal |
| *Campanula rotundifolia* | Both | Clonal |
| *Carex rossii* | Both | Clonal |
| *Carex scopulorum* | Both | Non-clonal |
| *Castilleja puberula* | Both | Non-clonal |
| *Cerastium arvense* | Both | Clonal |
| *Cercocarpus montana* | Both | Non-clonal |
| *Chenopodium album* | Both | Clonal |
| *Chrysothamnus spp.* | Both | Non-clonal |
| *Cirsium arvense* | Both | Clonal |
| *Cymopterus lemonii* | Both | Clonal |
| *Erigeron annuus* | Both | Non-clonal |
| *Erigonum umbellatum* | Both | Non-clonal |
| *Erysimum capitatum* | Both | Non-clonal |
| *Euyonomus spp.* | Both | Non-clonal |
| *Geranium spp.* | Both | Non-clonal |
| *Helianthus pumilus* | Both | Non-clonal |
| *Hesperostipa comata* | Both | Non-clonal |
| *Heterotheca villosa* | Both | Non-clonal |
| *Heuchera bracteata* | Both | Non-clonal |
| *Heuchera parviflora* | Both | Non-clonal |
| *Juniperus communis* | Both | Non-clonal |
| *Koeleria macrantha* | Both | Clonal |
| *Lupinus angustifolius* | Both | Non-clonal |
| *Lupinus argenteus* | Both | Non-clonal |
| *Oxytropis campestris* | Both | Clonal |
| *Packera multilobata* | Both | Non-clonal |
| *Pascopyron spp.* | Both | Non-clonal |
| *Penstemon strictus* | Both | Non-clonal |
| *Phleum pratense* | Both | Clonal |
| *Poa bulbosa* | Both | Clonal |
| *Pulsatilla patens* | Both | Clonal |
| *Purshia tridentata* | Both | Clonal |
| *Ribes aureum* | Both | Clonal |

**Table A2: Continued**

| Species | Plot Type | Plant Type |
|---|---|---|
| *Rubus idaeus* | Both | Clonal |
| *Taraxacum officinale* | Both | Clonal |
| *Tragopogon dubius* | Both | Clonal |
| *Verbascum thapsus* | Both | Non-clonal |
| *Pinus flexilis* | Both | Non-clonal |
| *Pinus ponderosa* | Both | Non-clonal |
| *Pseudotsuga menziesii* | Both | Non-clonal |
| *Sedum lanceolatum* | Both | Non-clonal |
| *Solidago multiradiata* | Both | Non-clonal |
| *Solidago simplex* | Both | Non-clonal |
| *Trifolium pratense* | Both | Non-clonal |
| *Luzula parviflora* | Burned | Non-clonal |
| *Symphoricarpos albus* | Burned | Non-clonal |
| *Tradescantia occidentalis* | Burned | Non-clonal |
| *Tradescantia spp.* | Burned | Non-clonal |
| *Allium montanum* | Burned | Non-clonal |
| *Festuca arizonica* | Burned | Non-clonal |
| *Bouteloua gracilis* | Burned | Non-clonal |
| *Bromus inermis* | Burned | Clonal |
| *Bromus madritensis* | Burned | Non-clonal |
| *Centaurea montana* | Burned | Non-clonal |
| *Chamaenerion angustifolium* | Burned | Non-clonal |
| *Ericameria nuaseosa* | Burned | Non-clonal |
| *Euphorbia brachycera* | Burned | Non-clonal |
| *Festuca octoflora* | Burned | Non-clonal |
| *Festuca saximontana* | Burned | Non-clonal |
| *Gaillardia aristata* | Burned | Non-clonal |
| *Poa pratensis* | Burned | Clonal |
| *Populus tremuloides* | Burned | Clonal |
| *Salix spp.* | Burned | Clonal |
| *Symphoricarpos orbicalatus* | Burned | Clonal |
| *Thalictrum alpinum* | Burned | Clonal |
| *Viscia sativa* | Burned | Clonal |
| *Physaria acutifolia* | Burned | Non-clonal |
| *Polemonium spp.* | Burned | Non-clonal |
| *Penstemon whippleanus* | Burned | Non-clonal |
| *Rosa spp.* | Burned | Non-clonal |
| *Rosa woodsi* | Burned | Non-clonal |

**Table A3: Continued**

| Species | Plot Type | Plant Type |
|---|---|---|
| *Sporobolus cryptandrus* | Burned | Non-clonal |
| *Trisetum spicatum* | Burned | Non-clonal |
| *Galium triflorum* | Unburned | Non-clonal |
| *Arnica cordifolia* | Unburned | Non-clonal |
| *Bromus ciliatus* | Unburned | Non-clonal |
| *Bromus marginatus* | Unburned | Non-clonal |
| *Cactus opuntia* | Unburned | Non-clonal |
| *Calamagrostis rubescens* | Unburned | Non-clonal |
| *Carex geyeri* | Unburned | Non-clonal |
| *Cystopteris fragilis* | Unburned | Clonal |
| *Draba graminea* | Unburned | Clonal |
| *Echinocereus spp.* | Unburned | Non-clonal |
| *Elymus smithii* | Unburned | Non-clonal |
| *Galium boreale* | Unburned | Non-clonal |
| *Heracleum maximum* | Unburned | Non-clonal |
| *Juniperus scopulorum* | Unburned | Non-clonal |
| *Mertensia ciliata* | Unburned | Non-clonal |
| *Oxalis albicans* | Unburned | Non-clonal |
| *Pinus contorta* | Unburned | Non-clonal |
| *Poa nervosa* | Unburned | Non-clonal |
| *Ranunculus adoneus* | Unburned | Non-clonal |
| *Senecio intergerrimus* | Unburned | Non-clonal |
| *Thalictrum fendleri* | Unburned | Non-clonal |
| *Thermopsis montana* | Unburned | Non-clonal |
| *Viburnum edule* | Unburned | Non-clonal |
| *Yucca glauca* | Unburned | Non-clonal |

# APPENDIX B

## ELEVATION, SLOPE, ASPECT AND GLOBAL POSITIONING SYSTEM (GPS) COORDINATES OF PLOT LOCATIONS IN STUDY AREA

**Table B1: Continued**

| Plot number | Plot type | Elevation | Slope | Aspect | Latitude | Longitude |
|---|---|---|---|---|---|---|
| 1 | Burned | 1927 | 30 | 50 | 40.7927 | -105.54 |
| 2 | Burned | 1918 | 30 | 49 | 40.7797 | -105.54 |
| 3 | Burned | 1910 | 33 | 49.5 | 40.7713 | -105.45 |
| 4 | Burned | 1901 | 34 | 52 | 40.7339 | -105.30 |
| 5 | Burned | 1908 | 36 | 40 | 40.7267 | -105.55 |
| 6* | Burned | 2458 | 32 | 190 | 40.7178 | -105.46 |
| 7* | Burned | 2416 | 35 | 180 | 40.6660 | -105.41 |
| 8* | Burned | 2428 | 30 | 230 | 40.7530 | -105.39 |
| 9* | Burned | 2425 | 15 | 290 | 40.5650 | -105.33 |
| 10* | Burned | 2416 | 25 | 270 | 40.6769 | -105.25 |
| 11 | Burned | 2420 | 25 | 50 | 40.7173 | -105.29 |
| 12 | Burned | 2434 | 20 | 170 | 40.7280 | -105.41 |
| 13 | Burned | 2409 | 35 | 242 | 40.6233 | -105.35 |
| 14 | Burned | 2391 | 25 | 190 | 40.5401 | -105.29 |
| 15* | Burned | 2487 | 10 | 110 | 40.5508 | -105.32 |
| 16* | Burned | 2490 | 25 | 110 | 40.6816 | -105.42 |
| 17 | Burned | 2484 | 20 | 50 | 40.7030 | -105.43 |
| 18* | Burned | 2488 | 17 | 60 | 40.7149 | -105.39 |
| 19* | Burned | 2472 | 8 | 110 | 40.6912 | -105.43 |
| 20* | Burned | 2477 | 28 | 286 | 40.7292 | -105.43 |
| 21* | Unburned | 2103 | 30 | 326 | 40.7922 | -105.52 |
| 22* | Unburned | 2187 | 29 | 290 | 40.7679 | -105.52 |
| 23 | Unburned | 2230 | 31 | 310 | 40.7672 | -105.43 |
| 24 | Unburned | 2313 | 33 | 299 | 40.7651 | -105.42 |
| 25* | Unburned | 2352 | 36 | 302 | 40.7608 | -105.41 |
| 26 | Unburned | 2012 | 10 | 76 | 40.7415 | -105.52 |
| 27 | Unburned | 1995 | 25 | 25 | 40.7272 | -105.50 |
| 28 | Unburned | 1986 | 30 | 90 | 40.6501 | -105.39 |
| 29 | Unburned | 1953 | 34 | 84 | 40.7401 | -105.28 |
| 30 | Unburned | 1881 | 35 | 10 | 40.7073 | -105.36 |
| 31* | Unburned | 2486 | 15 | 28 | 40.5780 | -105.29 |
| 32 | Unburned | 2475 | 4 | 72 | 40.5902 | -105.31 |
| 33* | Unburned | 2473 | 10 | 254 | 40.6087 | -105.40 |
| 34* | Unburned | 2471 | 12 | 340 | 40.6887 | -105.53 |
| 35* | Unburned | 2477 | 10 | 104 | 40.6744 | -105.47 |
| 36 | Unburned | 2473 | 5 | 210 | 40.7401 | -105.22 |
| 37 | Unburned | 2471 | 4 | 300 | 40.6437 | -105.23 |
| 38* | Unburned | 2466 | 2 | 280 | 40.6816 | -105.32 |
| 39* | Unburned | 2464 | 2 | 128 | 40.6430 | -105.31 |
| 40* | Unburned | 2461 | 8 | 170 | 40.6130 | -105.31 |

*Plots chosen for clonal traits responses