

**EVALUATING THE IMPACT OF MULTIPLE STRESSORS ON VEGETATION
SUCCESSION AFTER WILDFIRE**

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ABSTRACT

Succession has been studied since the early days of ecology, yet it is uncertain how the properties of succession are affected by stressors such as climate change, human activity, and increasingly severe disturbance events. In this study, I examined post-fire vegetation succession in Waterton Lakes National Park (WLNP), located in the southern Canadian Rocky Mountains, to ask how climate change, human disturbance and distance to seed sources affect the rate and trajectory of succession. I compared succession in burned sites with unburned sites to determine how the properties and drivers of succession after fire differed. To characterize the shifts in community types affected by fire and determine the persistence of those shifts, I described 12 community types and compared tree seedling densities between burned and unburned sites of those community types. I did not find strong evidence that climate change, human disturbance or increased distance to seed sources affected the rate or trajectory of vegetation succession post-fire. The trajectory of succession in burned plant communities tended to be consistent with a return to their pre-fire state, while in unburned communities the trajectory generally diverged from pre-fire composition. Burned areas shifted away from forested community types, and towards two new shrub dominated community types which were not present in WLNP prior to the fire. Most burned forested community types had regeneration of their dominant tree species, indicating a likely return of the pre-fire community type over time. My study shows that post-fire plant community succession in WLNP is largely resilient to modern stressors.

CONTRIBUTIONS OF AUTHORS

Chapter 2 represents original and unsubmitted work by Genoa Alger (primary author) that is co-authored by Dr. Jenny McCune. Genoa Alger contributed to: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing – original draft, and writing – review & editing. Dr. Jenny McCune contributed to: conceptualization, methodology, project administration, resources, supervision, and writing – review & editing.

USE OF GENERATIVE AI

I acknowledge the use of generative AI to edit and error check R code used for data analysis in Chapter 2.

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LIST OF ABBREVIATIONS

AIC	Aikaike's Information Criterion
AIC _c	Small sample size corrected Aikaike's Information Criterion
DF	Degrees of Freedom
GPS	Global Positioning System
LiDAR	Light Detection and Ranging
MS	Mean Squares
PERMANOVA	Permutational Analysis of Variance
PERMDISP	Permutational Analysis of Dispersion
SS	Sum of Squares
WLNP	Waterton Lakes National Park

CHAPTER 1: INTRODUCTION

1.1 The study of succession

In ecology, the term “succession” refers to how ecological communities change over time in response to a disturbance. A disturbance is “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (Pickett & White, 1985). Succession has long been a topic of study in ecology, yet much remains to be understood. Early concepts of succession saw it as an orderly process, with plant communities sequentially replacing one another until eventually a predetermined climax community is reached (Clements, 1936; Cooper, 1923; Cowles, 1899). This climax community is then maintained in equilibrium by the local climate until the next disturbance occurs (Clements, 1936). However, like most ecological processes, it is difficult to fit succession into one tidy theory. It has since been shown that random processes such as the order of species arrival can affect long-term plant community composition, resulting in multiple possible successional pathways (Buma et al., 2019; del Moral et al., 2009; Norden et al., 2015). Additionally, species and communities are not always fully replaced in later successional stages; many species are present through multiple stages of succession with only their relative abundance changing (Gendreau-Berthiaume et al., 2015; Lyon & Stickney, 1976). Finally, the idea that a community will always reach a particular climax state has not held true. It has been shown that multiple communities can form under the same conditions, and in some cases communities are in a continuous non-equilibrium state (Fill et al., 2015; McCune & Allen, 1985).

Numerous models have been developed to explain how succession proceeds and what drives it, each with their own strengths and weaknesses (Poorter et al., 2023). The work of Pickett *et al.* (1987) and later Meiners *et al.* (2015), organizes the successional drivers proposed in previous models into a hierarchical framework. Causes of succession are initially divided into three broad categories: 1) site conditions and history, 2) species availability, and 3) species performance. Specific drivers can then be classified within each category (Meiners et al., 2015; Pickett et al., 1987). For example, the frequency and intensity of prior disturbances and climatic conditions at a site would be classified as site conditions and history. Proximity of seed sources and regeneration strategies are aspects of species availability. Finally, competitive ability and life history are part of species performance. This framework is useful for understanding and categorizing the numerous potential successional drivers. Additionally, a framework like this allows for easier comparison across studies.

Studies of succession have been plagued by many challenges. When studying natural disturbances, sites that are subjected to the disturbance and sites that are not subjected to the disturbance are not randomly located and therefore true controls are lacking (Wiens & Parker, 1995). Many studies lack controls entirely, and measure sites affected by the disturbance only (e.g. Lyon & Stickney 1976; Rodman *et al.* 2020; Stevens *et al.* 2019). Because succession occurs over long time spans, space for time substitutions are often used to measure how plant communities farther along in succession differ from those disturbed more recently. These studies rely on the assumption that the communities studied are separated by age and nothing else (Johnson & Miyanishi, 2008). Many classic studies of succession now used in ecology textbooks (e.g. Cooper 1923; Cowles 1899) were conducted this way, which sometimes resulted in misleading conclusions (Johnson & Miyanishi, 2008). For example, Cowles (1899) inferred that

plant communities establish on sand dunes in a particular order, based on the communities that were present on differently aged dunes. However, subsequent study demonstrated that the spatial distribution of plant communities had more to do with disturbance frequency and environmental characteristics of sites than dune age (Johnson & Miyanishi, 2008).

Over the past century and a quarter, succession has been measured in many different ways. Traditionally plant communities have been the focus of successional research (Poorter *et al.*, 2023), however more recently the concepts of succession have been expanded to other organisms (e.g. Fierer *et al.* 2010; Kalucka & Jagodzinski 2016; McKindsey & Bourget 2001). Goals of successional studies range from describing compositional changes, to quantifying the rate of succession, to determining trajectory by counting tree seedling densities (e.g. Johnstone & Chapin 2006; Lyon & Stickney 1976; del Moral & Chang 2015). Successional trajectory in particular is a growing topic of study due to concerns that humans are altering successional pathways, potentially resulting in altered communities. A web of science search for “successional trajectory” or “successional trajectories” currently returns 794 results. In general terms, “successional trajectory” as used in the literature refers to the pathway or direction of succession followed by a community, usually in terms of species composition or community structure. However, what is measured is highly variable between studies. Many studies measure some aspect or aspects of a plant community over time (e.g. species diversity; see Buma *et al.* 2019; Lorentzen Kolstad *et al.* 2018; Thorn *et al.* 2020). This is only possible with either very long-term data, or very rapid succession. Additionally, this method presents challenges when attempting to determine the influence of different drivers on trajectory. Until recently, the multivariate statistical techniques needed to quantify successional trajectory in terms of community composition were not available (De Cáceres *et al.*, 2019). Instead, observations for

each visit in a time series could be compared to one another (e.g. comparing the species composition of sites that burned at low, medium and high severity at visit 1, visit 2, visit 3 and so on). Or alternatively, the changing composition of sites could be plotted on an ordination and the different pathways of sites assessed visually. As an alternative to assessing community composition, another common strategy for forested areas is to infer trajectory from tree seedling regeneration (e.g. Johnstone *et al.* 2010; Johnstone & Chapin 2006; Urza & Sibold 2017). The first method records the pathway; the second method infers the future outcome based on a moment in time. With so many different strategies for measuring succession it can be confusing to determine what is being measured and challenging to compare between studies. As stated by Meiners *et al.* (2015), “because successional dynamics are measured in multiple ways... there is as yet no common currency for placing a comprehensive model of successional dynamics into a biogeographic context”.

Advancement in our understanding of ecological succession would be facilitated if researchers used a standardized terminology to describe the properties of succession. Multiple ways of measuring those properties may be useful (e.g. see del Moral & Chang 2015 for multiple measures of rate), however the definition of what is measured should be consistent. This can be compared to the study of physics, from which many of the terms used to describe properties of succession originate. In physics, different properties can be measured, for example speed or acceleration. These properties could be measured using different units, however it would be misleading to measure multiple properties and classify them all as speed. Informed by how the terms “trajectory” and “rate” have been used in previous studies, I have defined these terms as follows. In this study, I refer to “trajectory” as the direction of change relative to the pre-disturbance vegetation community, and “rate” as the speed of change.

1.2 Succession in the context of modern stressors

The possible formation of altered ecosystems following disturbance is a concern for many ecologists and land managers. Most ecosystems are resilient to disturbance, however when multiple disturbances or stressors combine, succession could take unexpected pathways (Paine et al., 1998). For example, increased fuel loading due to damage from severe cyclones can result in forested coastal ecosystems transitioning to grassland after wildfire, especially when those ecosystems are not fire adapted (Ibanez et al., 2022). In another example, extreme drought can increase tree susceptibility to insect attack, shifting forest composition away from the insects' host species (Abella, 2018; Das et al., 2025). According to Turner & Seidl (2023), resilience is most likely to be impacted when the frequency or intensity of disturbances are outside the range of historic variability (e.g. severe cyclones, extreme drought, short-interval wildfire) or novel to an area (e.g. exotic insects, wildfire in non-fire adapted ecosystems). When this occurs, classical successional theory is ineffective at predicting outcomes (Paine et al., 1998).

Wildfire is part of the natural disturbance regime in many regions. However, wildfire size, severity, and frequency are increasing in ecosystems around the world (Collins et al., 2022, 2025; Dennison et al., 2014; Hanes et al., 2019). Research in Canada has linked increase in area burned to climate change (Gillett et al., 2004; Kirchmeier-Young et al., 2019), and wildfire risk modelling predicts that the area burned by fire in Canada will continue to increase over the 21st century (Flannigan et al., 2005). Fire adapted ecosystems are expected to be resilient to wildfire (Turner et al., 1997; Veblen et al., 1991). However, there are recent examples of additional stressors impacting plant community recovery after fire. Hotter and drier conditions have caused tree seedling regeneration failures in many areas of the western United States (Stevens-Rumann et al., 2018). Exotic invasive species can also alter successional pathways. In one example, a

single high severity fire in combination with annual grass invasion was sufficient to shift the community away from a woody community to one dominated by invasive grasses (Klinger & Brooks, 2017). Because of the increasing prevalence of wildfire, it is important to understand how post-fire succession is influenced by additional stressors.

Successional pathways after fire vary on a regional and even community scale. Therefore, it is valuable to study plant community resilience to wildfire in a variety of geographic locations and stress contexts. Tracking responses to wildfire on a community level allows for tailored management strategies that will be the best use of available resources (e.g. Coop 2023). This is particularly important because in some cases plant communities may be highly resilient to wildfire, even in the presence of additional stressors (e.g. Anderson & Bailey 2026; Donovan *et al.* 2020; Niziolek *et al.* 2024). In communities experiencing good regrowth, post-fire management interventions are unnecessary (Turner *et al.*, 2003). Emotions and past experience strongly influence both public and professional perceptions of burned landscapes (Kooistra *et al.*, 2018; Rapp & Nelson, 2025), so post-fire studies are key to understanding when management actions are warranted. If intervention is deemed beneficial, an understanding of which factors limit recovery (e.g. lack of seed, climate) is needed so that actions can be implemented strategically (Larson *et al.*, 2022).

1.3 Research Objectives

In this study, I investigate successional patterns after wildfire in a small national park in the southern Canadian Rocky Mountains. I compare early succession after wildfire to changes in plant communities occurring in unburned areas of the same park with the goal of addressing both practical and theoretical questions relating to post-fire succession. My objectives are:

1. Quantify successional trajectory and rate over seven to eight years post-fire.
2. Determine whether climate change, human disturbance and distance to seed sources impact trajectory or rate of succession.
3. Determine which distinct plant community types increase in frequency and which decline in response to wildfire.
4. Investigate the capacity of plant community types in decline to return to their pre-fire state.

CHAPTER 2: EVALUATING THE IMPACT OF MULTIPLE STRESSORS ON VEGETATION SUCCESSION AFTER WILDFIRE

2.1 Abstract

Wildfire is a typical disturbance in many temperate ecosystems, however due to climate change wildfires are becoming increasingly large and severe. When wildfire occurs in combination with stressors such as climate change or human disturbance, plant community succession could be altered. In 2017, a wildfire burned a third of Waterton Lakes National Park (WLNP), in the southern Canadian Rockies. In 2024/25 I remeasured burned and unburned vegetation plots in WLNP, which were previously measured in 1994/95 and 2019/20. I calculated the rate and trajectory of succession based on shifts in community composition between the three visits. I then modeled how successional trajectory and rate in all plots and burned plots only vary with temperature (i.e. aspect, degree of climate warming), human disturbance (i.e. trails), distance from the burn edge, and other environmental predictors. To determine which community types increase postfire, I classified plant communities using a cluster analysis and examined patterns of transitions between community types. In WLNP, warming temperature, human disturbance and distance to seed sources did not result in divergent succession. Instead, increasing frost free days tended to be correlated with a greater chance of returning to a pre-fire state, but only in sites with deep soils. Overall, trajectories were more likely to be convergent in burned areas and divergent in unburned areas. Successional rate was difficult to predict, and there were no strong correlates of rate in the burn. Two new plant community types appeared post-fire, both shrub dominated, while community types dominated by long-lived species such as trees and bunchgrasses declined. By measuring multiple aspects of

succession, I show that despite shifts in plant community structure and composition, successional processes in WLNP are largely resilient to modern stressors.

2.2 Introduction

Wildfires are becoming increasingly large and severe in many ecosystems around the globe (Collins et al., 2022, 2025; Dennison et al., 2014). Although these ecosystems are often adapted to fire as a disturbance, shifts to novel states may be triggered when disturbances are combined or disturbance characteristics change (Paine et al., 1998; Turner et al., 1993). For example, when wildfire occurs at high severity or burns exceptionally large continuous areas plant communities may not recover as expected (Harvey et al., 2016; Johnstone et al., 2010). Additionally, plant communities are experiencing novel stressors, such as intensifying human disturbance and climate change (Allen et al., 2010; Christenhusz & Govaerts, 2024; Williams et al., 2020). Disturbances like wildfire remove inertia from a system by eliminating long-lived species, accelerating change in response to other stressors (Turner, 2010). It is important to study plant communities during these periods of rapid succession to understand if resilience to wildfire is impacted by modern stressors.

Plant community recovery after wildfire could be affected by ongoing climate change. Warmer temperatures favour heat adapted species, shifting plant communities toward increased dominance by more southern or low elevation species (Gottfried et al., 2012; Lenoir et al., 2008). In forests, tree canopy buffers the effects of warming climate, allowing species adapted to cooler conditions to persist. When wildfire removes canopy cover, shifts in composition towards species adapted to the current climate on the site may occur rapidly (Stevens et al., 2015; Zellweger et al., 2020). Wildfire could also trigger shifts in response to climate by removing long

lived species that established during different climatic conditions. For example, seedlings of many tree species have narrower climatic tolerances than adults, which could prevent pre-fire species from regenerating (Dobrowski et al., 2015). Instead, newly available space allows better adapted species to establish. Although warming climate may change the direction of plant community recovery, it could also promote faster vegetation regrowth and thereby faster succession via an increase in the number of growing days each year (del Moral & Chang, 2015).

Intensifying human disturbance may also change how plant communities respond to wildfire. For example, recreational trails can be a vector for the spread of exotic invasive plants and other disturbance associated species (Chisholm & McCune, 2024; Mount & Pickering, 2009). Wildfire removes many established plants, allowing space for exotic invasive plants to establish (Burke & Grime, 1996; French et al., 2025). Once present, exotic invasive plants with high competitive ability can inhibit re-establishment of native plant species (Flory & Clay, 2010; Vilà & Weiner, 2004). The rapid establishment of exotic invasive plants and other disturbance associated species is expected to accelerate revegetation of burned areas, but also shift plant communities away from their pre-fire composition.

Although many plant species have strategies to regenerate after wildfire, increasing size and homogeneity of wildfires could affect plant communities' ability to recover by limiting seed availability (Coop et al., 2020; Lyon & Stickney, 1976). Warming and drying climate conditions have increased the size and severity of wildfires over the late 20th and early 21st centuries (Collins et al., 2025; Hanes et al., 2019), and this trend is predicted to continue (Wang et al., 2020; Wotton et al., 2010). If unburned refugia are a primary source of seed for regeneration, then larger, more contiguous wildfires could decrease the speed of regrowth after wildfire by reducing seed availability. Additionally, large distances to unburned seed sources could limit re-

establishment to the subset of species with dispersal strategies that enable them to travel long distances (e.g. animal dispersed) or survive wildfire (e.g. serotinous seeds; Coop et al., 2010).

Studying plant community change after wildfire requires examining multiple drivers and properties of succession. Succession is a fundamental ecological process, defined as “the changes displayed by an ecosystem over time following a disturbance” (Poorter et al., 2023). The pattern of succession is determined by multiple drivers, including site conditions and history, species availability, and species performance (Meiners et al., 2015). These drivers can be dependent on one another and therefore are best studied holistically rather than separately (Meiners et al., 2015). Succession can also be measured in multiple ways. Possible measures include the speed of succession, the direction or trajectory of succession, and the community composition at a given point in time. Because drivers may affect aspects of succession differently, it is valuable to include multiple measures in a study of succession. For example, if increased distance to the burn edge changes the direction of succession but does not affect the rate, then combining rate and trajectory into one measure could make it difficult to determine which property of succession is most influenced by distance to the burn edge. Additionally, a lack of effect on rate could dilute the effect on trajectory so that it is not detectable.

Studies of post-fire succession are common (e.g. Grau-Andres et al., 2024; Stevens-Rumann & Morgan, 2019), but most lack pre-fire data or unburned controls. In the absence of pre-fire data, researchers often use space-for-time substitutions (called chronosequences), where nearby unburned sites are used to represent pre-fire conditions (e.g. Coop et al., 2010; Dickson-Hoyle et al., 2024; Doyle et al., 1998). These studies rely on the assumption that sites differ only in time since a disturbance, which is often not true (Johnson & Miyanishi, 2008). In addition, many studies focus on measuring only certain taxa (e.g. trees) or one aspect of succession (e.g.

rate only, or trajectory only). Some studies include pre-fire data but lack unburned controls (e.g. Downing et al., 2019; Stevens et al., 2019). Without comparison to unburned sites, it is impossible to separate successional processes that are due to fire from changes that are occurring regardless of burn status. For example, plant community shifts due to climate change may be triggered by wildfire, but comparison to shifts in similar unburned areas are required to draw this conclusion.

In this study, I use a unique dataset to assess early post-fire succession in Waterton Lakes National Park in the southern Canadian Rocky Mountains. The dataset includes pre-fire plant community composition, along with two post-fire repeat visits, in both burned and unburned plots. The plots cover a wide range of elevations and vegetation types. I evaluate the change in plant community composition in these plots over time to ask: 1) How do climate change, human disturbance, and distance to seed sources impact the trajectory and rate of succession? 2) Which plant communities are favoured by wildfire; which communities decline after wildfire; and which communities, if any, may have a decreased capacity to recover to their pre-fire state?

2.3 Methods

2.3.1 Study site

Waterton Lakes National Park (WLNP), or Paahtohmaksikimi in the Blackfoot language, is located in the southwestern corner of Alberta (Figure 1). Because of its geographical position at the narrowest point in the Rocky Mountains, WLNP is at the intersection of Pacific maritime and Arctic continental weather systems. The influences of these weather systems create a climate with frequent strong winds, and the highest amount of precipitation in Alberta (Parks Canada Agency, 2025a). Yearly precipitation amounts range from 152 cm annually on the mountainous west side of the park to 76 cm annually on grasslands at the eastern edge (Parks Canada Agency,

2025a). The varied geography and strong climate gradients in WLNP result in a high diversity of plant communities. The park contains over 1000 vascular plant species spread across four ecoregions: the foothills parkland, montane, subalpine and alpine (Achuff et al., 2002; Parks Canada Agency, 2025b).

Historically, wildfire was the primary disturbance in WLNP. However, between 1940 and 1998 there was a long wildfire free period due to fire suppression (Barrett, 1996). The historical fire regime in WLNP prior to fire suppression varied substantially depending on plant community type, and estimates of fire return intervals range from five years in fescue grasslands to 200 years in upper subalpine spruce-fir stands (Barrett, 1996). In 2017 the Kenow wildfire burned 19,303 hectares of the park (38.6%), mostly at very high severity (Parks Canada Agency, 2023). Prior to the Kenow Wildfire, the last significant wildfire was the 1998 Sofa Mountain fire which burned 1,521 hectares (Buckler, 2012). After the establishment of WLNP as a park in 1895, resource extraction was initially permitted in the form of small-scale oil drilling, mining, and grazing (MacDonald, 2000). These activities mostly ended by 1930 (MacDonald, 2000), and recreation is now the primary cause of human disturbance to plant communities in WLNP. Visitation to WLNP has been increasing, and in 2025 there were 584,977 visitors (Government of Alberta, 2026), resulting in increased pressure on park trails. There are over 200 kilometers of trails in WLNP (Parks Canada Agency, 2026), as well as off-trail travel on scrambling routes. The park has 133 known exotic plant species, which primarily grow in the low elevation foothills parkland ecoregion (Parks Canada Agency, unpublished data).

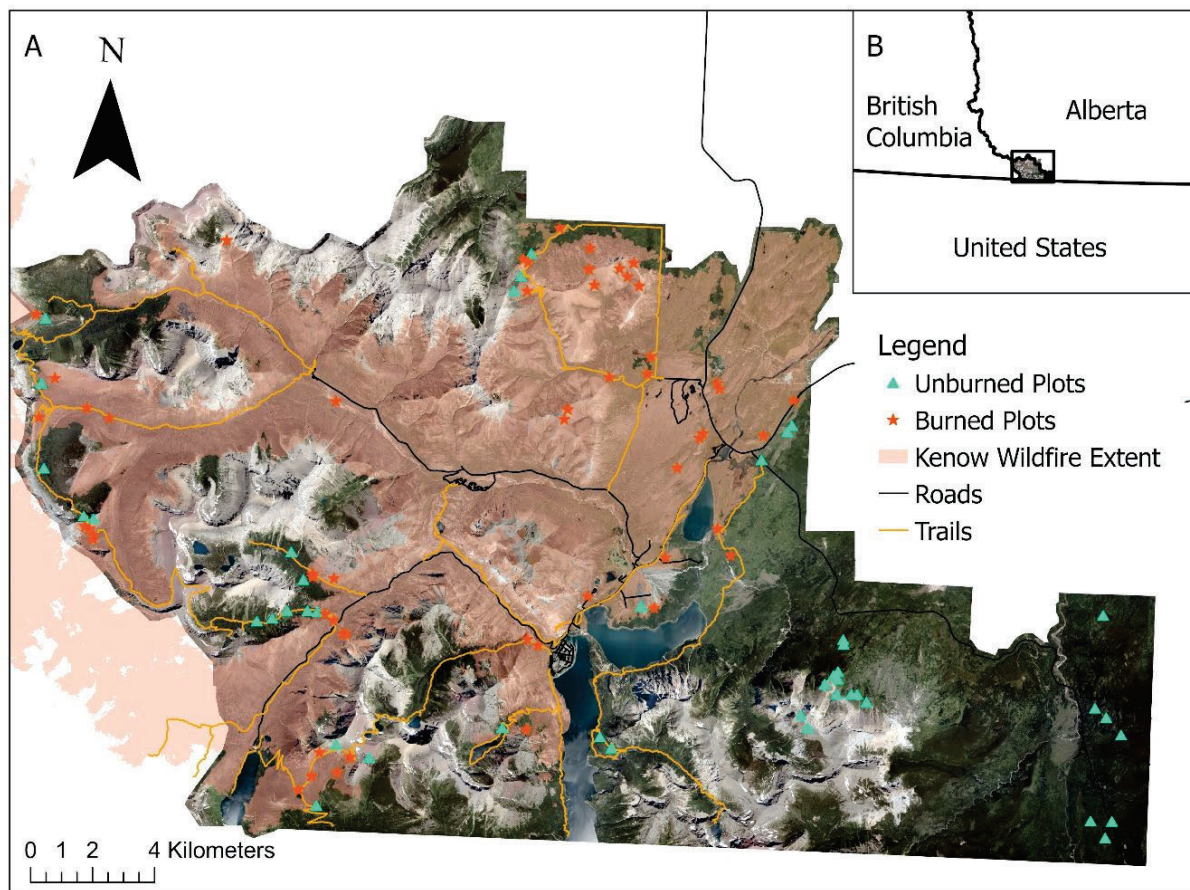


Figure 1. (A) Map of WLNP with the locations of the plots used in this study. Unburned plots are represented as blue triangles and burned plots are represented as orange stars. The extent of the 2017 Kenow wildfire is shaded in orange. (B) The location of WLNP within Alberta.

2.3.2 Data Collection

Between 1994 and 1999 Achuff et al. (2002) surveyed 277 relevé plots across Waterton Lakes National Park with the aim of classifying plant community types. They initially divided the park into polygons based on soil, vegetation and landform. Within the polygons they selected areas of homogenous vegetation that best represented the polygon for vegetation plots. They sized the plots according to vegetation type, with 20 x 20 m plots in forested areas, 15 x 15 m plots in shrublands and 10 m x 10 m plots in grasslands. Within each plot they identified all vascular plant species and estimated the percent cover of each species in four height layers.

Layer 1 includes all woody plants > 5 m tall, layer 2 is woody plants 2-5 m tall, layer 3 is woody plants 0.5-2 m tall, and layer 4 is woody plants <0.5 m and all herbaceous plants regardless of height.

Immediately after the 2017 Kenow wildfire, Parks Canada used remote sensing to map burn severity. All plots were assigned a severity rating of “unburned”, “low”, “moderate”, “high”, or “very high” based on this mapping. In 2018, the year following the wildfire, Parks Canada visited 94 burned plots to verify the accuracy of these burn severity ratings using the FIREMON Composite Burn Index (Key & Benson 2006). At the same time, they took soil samples for nutrient analysis. In 2019 and 2020 Lloren and colleagues resurveyed 98 plots across burned and unburned areas of the park (see Figure 1). Lloren chose which plots to resurvey based on accessibility and representation across an array of environmental and stress gradients (Lloren 2021; Lloren & McCune 2024). In 2024 and 2025 my field assistants and I resurveyed the same 98 plots. We identified all vascular species present and estimated the abundance of each species in each layer following the original survey methods. We also identified to species and counted all tree seedlings present in each plot (trees ≤ 1.3 m tall) to assess forest recovery potential on burned plots compared to unburned plots. In plots where seedlings were too dense to count the entire plot, we counted the north-west quadrant only. I then used these counts to estimate seedling density per hectare.

I checked all plant species for synonyms using the Taxonomic Name Resolution Service (TNRS - Taxonomic Name Resolution Service, n.d.), then standardized names using the VASCAN database (Candensys, 2026). Prior to analyses, I summed the total percent cover from the four height layers. I changed abundances of 0.1 % cover from the 2024 visit (used for species with much less than 1% cover) to 0.5 % to reflect the smallest cover class used in previous visits.

To ensure alignment between visits, I graphed species composition of all three visits to each plot and compared them visually. In some cases, there was reason to believe that species identified differently across visits to the same plot were the same, because of very similar appearances, taxonomic splits or genus-level identification at one visit, along with comparable cover estimates. In these cases, I changed the species names to reflect the most common identification (ie. two out of three visits), the new name for the species in the region, or the genus level identification. For example, in plot 4005 there was 35% cover of *Osmorhiza occidentalis* in 1994, 46% *Angelica dawsonii* in 2019 and 30% *Osmorhiza occidentalis* in 2024. Because these species are very similar in appearance, especially at the time of year the plots were measured, I corrected *A. dawsonii* to *O. occidentalis*. Where there were considerable inconsistencies within a genus, I lumped all species within the genus. In some cases, species had been lumped in previous years, so I followed this to maintain consistency. In two plots, inconsistencies between visits indicated the plots had not been accurately relocated, therefore I removed them. I used the resulting 96 plot dataset for analysis.

2.3.2.1 Response variables

Using the cleaned and harmonized plant community data from the three surveys, I calculated a metric of successional trajectory and a metric of successional rate for each plot. To quantify successional trajectory I used multivariate analyses of the changes in community composition in each plot from 1994/1999 to 2019/2020 to 2024/2025. I used the Bray-Curtis dissimilarity based on the raw species abundance matrix to measure: (1) the difference in community composition between the 1994/1999 (a) and the 2019/2020 (b) communities for each plot, and (2) the difference in community composition between the 1994 (a) and 2024/2025 (c) communities in each plot ('vegan' package; Oksanen et al., 2001). Bray-Curtis dissimilarity is an

index which ranges between 0 and 1, where 0 indicates identical community composition and 1 indicates no species in common (Bray & Curtis, 1957). I then calculated successional trajectory as follows:

$$ST = BC_{ab} - BC_{ac} \begin{cases} 1 & \text{if } ST > 0 \\ 0 & \text{if } ST < 0 \end{cases}$$

Where BC represents the Bray-Curtis dissimilarity in species composition between two visits (a vs. b, or a vs. c), and *ST* is the successional trajectory. A positive value of *ST* represents a return towards the original (1994-1999) community composition (i.e. 2024/2025 composition more similar to baseline survey composition than the 2019/2020 composition only 2-3 years post-fire) and a negative value represents a divergent trajectory. I used a binary response because the size of *ST* is influenced by the speed of community change and therefore could bias analyses towards factors that influence rate rather than trajectory.

Successional rate can also be measured in multiple ways (del Moral & Chang, 2015). Del Moral and Chang's method of estimating floristic change utilized the Euclidean distance in community composition between two surveys of the same site over time. I followed a similar approach, but substituted Bray-Curtis dissimilarity because it is a better measure of dissimilarity among ecological communities (McCune & Grace, 2002), and is consistent with the measure of successional trajectory. The equation used to calculate successional rate is as follows:

$$SR = \frac{BC_{bc}}{t_{c-b}}$$

Where BC represents the Bray-Curtis dissimilarity in species composition between the 2019/2020 and 2024/2025 visits (b vs. c), *t* is the time between visits in years, and *SR* is the successional rate.

2.3.2.2 Predictors

For each plot I measured environmental variables that are known to affect plant community composition, which I hypothesized would influence the rate and trajectory of succession (see Table 1). According to Meiners et al.'s (2015) framework, these variables primarily reflect aspects of site conditions and history, for example elevation and slope aspect. Some variables measure species availability, for example distance to the burn edge. Species performance drivers (e.g. competitive ability) have historically been the focus of many successional studies (Meiners et al., 2015). I included only broad measures of species performance, for example the relative cover of exotic invasive species, which are expected to be stronger competitors on average than native species (Vilà & Weiner, 2004).

2.3.2.2.1 Site conditions and history

I included a number of predictors that measure site conditions and history at each plot. Due to the high variability in elevation, aspect and soil characteristics of plots used in this study, these factors may have a strong influence on patterns of succession. For example, succession may proceed more slowly at higher elevations due to cooler temperatures and more stressful conditions. To measure topography, I used elevation and aspect values collected by Lloren (2021). Consistent with Lloren (2021), I converted aspect to a relative northness index using the following equation:

$$Northness = \frac{|Aspect\ in\ degrees - 180|}{180}$$

To assess the effect of substrate I measured soil depth, rock cover and soil drainage. To measure topsoil depth I followed a procedure similar to the methods used by Fuhlendorf and

Smeins (1998). My field assistants and I inserted an aluminum soil probe by hand using approximately 80 pounds of pressure and measured the stopping depth. I used the average of 12 soil depth measurements at each plot. We visually estimated the percent cover of bare rock substrate (defined as any rocks with a diameter ≥ 5 cm). I used a categorical representation of soil drainage as recorded by Achuff et al. (2002) on a 7 category scale, and collapsed these into three categories (rapidly drained, well drained, or moderately to very poorly drained) following (Lloren, 2021).

I calculated a binomial windshelter index with the intention of estimating the potential for wind-deposited soil accumulation. The index determines whether each 1 m pixel is exposed to wind or protected by upwind terrain features based on wind direction and distance from terrain features (de Leeuw et al., 2023; Veitinger et al., 2016), where zero represents erosion and one represents deposition. I used the median wind direction in degrees over the first three months after the Kenow Wildfire from the Waterton Gate Environment Canada weather station for the input wind direction. For the terrain data I used Parks Canada LiDAR data with 1 m resolution (Parks Canada, unpublished data). Because the windshelter model does not account for valley effects on wind direction, the model may be more accurate at higher elevations or more open areas. The windshelter model was originally developed to predict snow distribution due to drifting across the landscape. However, in the context of vegetation regrowth after wildfire, windshelter could also be important for the redistribution of exposed soil. To determine if the windshelter index is a reasonable proxy for nutrient distribution, I examined the correlation between nutrient content and windshelter index in the subset of plots with nutrient data. There was no significant correlation between windshelter and nutrients, therefore I considered windshelter a measure of snow drifting only.

Climate trends also influence site conditions. To quantify the effect of temperature changes, I used down-scaled trends in the change in number of frost-free days and average summer temperature from 1994 to 2019 (Kienzle, unpublished data, University of Lethbridge). This time range was chosen to align with the study period. Initially, broad scale climate trends were modeled for a 10x10 km grid across Alberta by interpolating from all Environment Canada weather stations. Within each cell in WLNP, Kienzle delineated smaller polygons based on elevation, land cover and incoming solar radiation quartile. Adjustments to the climate metrics calculated for each 10 km cell were made at the polygon scale. Air temperature was adjusted based on the difference in elevation between the polygon and the average elevation of the 10 km cell. Radiation was calculated using the Solar Analysis toolset in ArcGIS Pro. The effect of slope and aspect on solar radiation was accounted for by performing separate calculations for sloped and flat sites, then calculating a proportion for each polygon (Kienzle, 2011). Trend slopes for the 1994-2019 period were then calculated using Sen's slope test (Kienzle, 2018). The resulting climate variables represent local trends in climate during the study period that could be due to both natural and anthropogenic causes.

Burn status is an important part of site history. The majority of the Kenow Wildfire burned at very high severity, resulting in a low sample size within other burn severity categories. Therefore, I collapsed all burn severity data collected by Parks Canada into burned and unburned categories.

2.3.2.2.2 Species availability

To quantify the effect of species availability I included the distance from each plot to the burn edge, the distance to the nearest road or trail, and the resprouting ability of plants present in the pre-fire survey. Distance to the nearest road or trail and distance to burned edge values were

calculated by Lloren (2021) in ArcGIS using spatial data on road and trail locations and burn severity supplied by Parks Canada. I used the USDA Fire Effects Information System database to classify regeneration strategies for each species into the following categories: resprouting, regeneration from seed on site, regeneration from seed off site, or multiple strategies.

Regeneration strategies were available for 125 out of the 608 species found in 1994, however this accounted for 71.5% of the vegetation cover because the species with no information on regeneration strategy tend to be less common. I classified all other species as having ‘unknown’ regeneration strategy. I then used this classification to calculate the relative abundance of species known to be capable of resprouting in each plot in 1994.

2.3.2.2.3 Species performance

Successional drivers in the species performance category include measures of species life history, competitive ability and symbiotic relationships with other species (Meiners et al., 2015). I used predictors based on categories such as vegetation type to represent broad-scale differences in life-history characteristics of dominant species. Based on a qualitative assessment of the species with the highest abundance in plots prior to the wildfire, I assigned plots to the following vegetation types: coniferous, deciduous, shrub and herbaceous. Vegetation type is relevant because some types (e.g. those dominated by herbaceous species) may regrow more quickly or have better adaptations to wildfire. Because shrubs are known to have a role in facilitating tree seedling regeneration after wildfire (Collins & Roller, 2013; Crockett & Hurteau, 2022), I calculated the shrub cover on each plot using Lloren’s (2021) classification of species lifeform. Exotic invasive species are generally thought to perform differently to native species due to stronger competitive ability (Vilà & Weiner, 2004). I calculated relative exotic abundance for

plots in both 1994 and 2019 using Lloren's (2021) classification of exotic status, which was based on the Alberta Plant Lists published by the Alberta Native Plant Council.

Table 1. All variables and interactions used as candidate predictors in models of successional trajectory and/or successional rate in all plots and burned plots only.

Predictor	Predictor type	Response Variables	Hypotheses
Average soil depth	Continuous	Trajectory – all plots and burned plots	Increased probability of divergent trajectories in shallow soils due to higher stress in ongoing drought/warming conditions.
		Rate – all plots and burned plots	Faster succession in deeper soils due to increased moisture retention (less stressful conditions).
Burn Status	Binomial	Trajectory – all plots	Increased probability of divergent trajectories in the burn due to removal of established species facilitating shifts in response to stressors.
		Rate – all plots	Faster succession in the burn due to species composition changing more rapidly in response to reduced competition.
Distance to Burn Edge	Continuous	Trajectory – burned plots	Increased probability of divergent trajectories far from the burn edge due to reduced availability of seed for some species.
		Rate – burned plots	Faster succession close to the burn edge due to higher availability of seed from nearby unburned areas.
Elevation	Continuous	Trajectory – all plots and burned plots	See Burn x Elevation interaction.
		Rate – all plots and burned plots	Faster succession at lower elevations due to less stressful, warmer conditions which facilitates faster colonization and/or regrowth.
Change in frost free days 1994-2019	Continuous	Trajectory – burned plots	Increased probability of divergent trajectories with increased warming due to changing conditions favouring heat adapted species.
		Rate – burned plots	Faster succession in areas with increased warming due to longer growing seasons allowing for faster regrowth.
Northness	Proportion	Trajectory – all plots and burned plots	Increased probability of divergent trajectories on south facing slopes due to hotter/drier conditions.
		Rate – all plots and burned plots	Faster succession on south facing slopes where longer growing seasons allow for faster regrowth.
Relative Exotic Cover in 1994	Proportion	Trajectory – all plots and burned plots	Increased probability of divergent trajectories with more exotic invasive species pre-fire due to increased potential for exotic species dominance.
		Rate – all plots and burned plots	Faster succession with more exotic invasive species pre-fire due to quick regeneration times of many exotic invasive species.
Relative Cover of Resprouters in 1994	Proportion	Trajectory – all plots and burned plots	Increased probability of convergent trajectories with more resprouting plants due to their biotic legacy.
		Rate – all plots and burned plots	See Burn x Relative Cover of Resprouters in 1994 interaction.
Rock Cover in 2024	Continuous	Rate – all plots and burned plots	Slower succession with higher rock cover, which corresponds to a higher stress site.
Shrub Cover in 2019	Continuous	Rate – all plots and burned plots	Faster succession with increased shrub cover, because shrubs can facilitate regeneration by offering protective cover.

Table 1. Continued.

Predictor	Predictor type	Response Variables	Hypotheses
Soil Drainage	Categorical	Trajectory – all plots and burned plots	Increased probability of divergent trajectories on rapidly drained sites due to more moisture stress in ongoing drought conditions.
		Rate – all plots and burned plots	Faster succession on less well drained sites, because succession is known to proceed more rapidly on mesic sites.
Distance to nearest trail	Continuous	Trajectory – all plots and burned plots	Increased probability of divergent trajectories close to trails due to greater availability of exotic species.
Windshelter	Binomial	Trajectory – all plots and burned plots	Increased probability of divergent trajectories on erosion sites due to removal of soil and seeds.
		Rate – all plots and burned plots	Faster succession on deposition sites due to addition of soil and seeds.
Vegetation Type	Categorical	Trajectory – all plots and burned plots	See Vegetation Type x Burn interaction.
		Rate – all plots	Faster succession in herbaceous sites where species have shorter lifespans.
Burn x Average Soil Depth	Binomial x Continuous	Trajectory – all plots	Increased probability of divergent trajectories in shallow soil, but only in burned plots because establishing plants will be more affected by soil conditions.
		Rate – all plots	The relationship of faster succession on deeper soils will be stronger in the burn, because establishing plants will be more affected by soil conditions.
Burn x Elevation	Binomial x Continuous	Trajectory – all plots	In burned areas, higher elevations will have increased probability of divergent trajectories because they are less adapted to fire. In unburned areas lower elevations will have increased probability of divergent trajectories because they are more affected by human disturbance.
		Rate – all plots	The relationship of faster succession in low elevation sites will be stronger in the burn due to the combination of reduced competition and less stressful growing conditions.
Burn x Northness	Binomial x Proportion	Trajectory – all plots;	The increase in probability of divergent trajectories on south facing aspects will be stronger in the burn due to the removal of long-lived species.
		Rate – all plots	The relationship of faster succession on south facing slopes will be stronger in the burn due to removal of long-lived species.
Burn x Relative Exotic Cover in 1994	Binomial x Proportion	Trajectory – all plots	The increase in probability of divergent trajectories with increased exotic species will be stronger in the burn due to increased open space for invasion.
		Rate – all plots	The relationship of faster succession with increased exotics will be stronger in the burn due to increased open space for invasion.
Burn x Relative Cover of Resprouters in 1994	Binomial x Proportion	Trajectory – all plots	The increase in probability of divergent trajectories with fewer resprouting plants will be stronger in the burn due to more open space allowing different species to establish.
		Rate – all plots	In burned areas there will be faster succession where there are more resprouting species because these species can regrow faster. In unburned areas there will be faster succession where there are fewer resprouting species because there will be more species turnover.

Table 1. Continued.

Predictor	Predictor type	Response Variables	Hypotheses
Burn x Shrub Cover in 2019	Binomial x Continuous	Rate – all plots	Increased shrub cover will only facilitate faster succession in the burn because already established plants will not benefit from facilitation by shrubs.
Burn x Soil Drainage	Binomial x Categorical	Trajectory – all plots	The increase in probability of divergent trajectories on rapidly drained sites will be stronger in the burn because establishing plants will be more affected by moisture stress.
		Rate – all plots	The relationship of faster succession on less drained sites will be stronger in the burn due to reduced competition.
Burn x Distance to nearest trail	Binomial x Continuous	Trajectory – all plots	The increase in probability of divergent trajectories close to trails will be stronger in the burn due to removal of pre-existing vegetation, which increases vulnerability to invasion.
Burn x Windshelter Binomial	Binomial x Binomial	Trajectory – all plots	The increase in probability of divergent trajectories on erosion sites will only occur in the burn where soil is available for transport.
		Rate – all plots	Faster succession on deposition sites will only occur in the burn where soil is available for transport.
Burn x Vegetation Type	Binomial x Categorical	Trajectory – all plots	Increased probability of divergent trajectories in herbaceous types for unburned sites due to increased likelihood of exotic species. Increased probability of divergent trajectories in forested types for burned sites due to removal of long-lived species.
		Rate – all plots	The relationship of faster succession in herbaceous vegetation types where species have shorter lifespans will be stronger in the burn.
Change in frost free days 1994-2019 x Average Soil Depth	Continuous x Continuous	Trajectory – burned plots	The increase in probability of divergent trajectories with increased warming will only occur in shallower soils due to less moisture retention.
		Rate – burned plots	On sites with deeper soils there will be faster succession with increased warming due to plants having more resources to take advantage of longer growing seasons.
Change in frost free days 1994-2019 x Soil Drainage	Continuous x Categorical	Trajectory – burned plots	In well drained areas more warming will result in divergent trajectories due to changing conditions favouring different species. In less well drained areas warming will have less of an impact.
		Rate – burned plots	In less drained areas increased warming will result in faster succession due to longer growing seasons. In well drained areas increased warming will slow succession due to moisture stress.
Northness x Shrub Cover in 2019	Proportion x Continuous	Rate – all plots	Shrub cover will have a greater role facilitating faster succession on south facing aspects where it's protective effect will be beneficial due to hotter/drier conditions.
Northness x Soil Drainage	Proportion x Categorical	Trajectory – all plots	In well drained areas south facing aspects will have an increased probability of divergent trajectories due to hotter/drier conditions and more moisture stress. In less drained areas aspect will not have an impact.
		Rate – all plots	In less well drained areas south facing aspects will result in faster succession due to longer growing seasons. In well drained areas south facing aspects will slow succession.

Table 1. Continued.

Predictor	Predictor type	Response Variables	Hypotheses
Northness x Relative Cover of Resprouters in 1994	Proportion x Proportion	Trajectory – all plots and burned plots	South facing aspects are more likely to have a divergent trajectory if they have a low proportion of resprouting species because plants regenerating from seed will be more affected by hotter/drier conditions.
Windshelter Binomial x Elevation	Binomial x Continuous	Trajectory – all plots and burned plots	The increased probability of divergent trajectories at eroded sites will be more pronounced at higher elevations where there is more wind exposure.
		Rate – all plots and burned plots	The increased rate of succession at deposition sites versus eroded sites will be stronger at higher elevations where there is more wind exposure.
Windshelter Binomial x Relative Cover of Resprouters in 1994	Binomial x Proportion	Trajectory – all plots and burned plots	The increased probability of divergent trajectories at eroded sites will be more pronounced where there are fewer resprouting species, because resprouting species will not be wind-transported.
		Rate – all plots and burned plots	The increased rate of succession at deposition sites versus eroded sites will be stronger where there are fewer resprouting species because resprouting species will not be wind-transported.
Windshelter Binomial x Relative Cover of Resprouters x Burn	Binomial x Proportion x Binomial	Trajectory – all plots	The increased probability of divergent trajectories at eroded sites will be more pronounced where there are fewer resprouting species, but only in the burn where soil is available for transport.
Relative Cover of Resprouters x Northness x Burn	Proportion x Proportion x Binomial	Trajectory – all plots	South facing aspects are more likely to have a divergent trajectory if they have a low proportion of resprouting species, but only in burned areas where soil is available for transport.

2.3.3 Analyses

I checked all predictors for correlation using Pearson's correlation coefficient. The two relative exotic abundance measures (relative exotic cover in 1994 and 2019) and the two climate trend measures (change in frost free days and change in mean summer temperature) were correlated (Pearson's $r \geq 0.7$), therefore I selected the relative exotic cover in 1994 and the change in frost free days to include as predictors based on hypotheses and explained variance.

To examine how site conditions and history, species availability, and species performance affect successional trajectory (*ST*) and successional rate (*SR*) I built generalized

linear models with a logit link for *ST* and linear models for *SR*. I built two versions for each response variable, first for all plots and then for burned plots only. This was for two reasons. First, to examine the effect of distance to burn edge on succession. Because distance to burn edge was zero in all unburned plots I could not include it in the all plots model. Second, to determine how intensity of climate change impacts post-fire succession. The climate change variables could not be included in the all plots model because the data was not available for several unburned sites that were located outside of the 10x10 km grid squares with modelled climate trends. Climate change data was also missing from one of the burned plots, so I removed it before proceeding. This resulted in dataset of 51 plots for the burned only models. Prior to building the models I checked for outliers, and ensured there were no strong pairwise correlations between predictors (Pearson's $r < 0.70$).

I first built global models including all predictors and interactions hypothesized to affect successional trajectory or rate (see Table 1). Because the models included interactions, I standardized predictors in the global model using the 'arm' package which centers continuous predictors and divides by two standard deviations. I used an automatic model reduction process from the package 'MuMIn' (Bartoń, 2025) to build a model with every combination of 10 or fewer predictors, then rank the models by small sample size corrected AIC (AIC_c). I then selected all models within 2 AIC_c of the lowest AIC_c scoring model and averaged the predictor estimates of those models. When models in the top model set were missing a predictor, I used zero to calculate the average, resulting in predictors that were selected in few models having a smaller estimate value. I considered predictors with estimates whose 95% confidence intervals did not cross zero to be significantly associated with the response.

To visualize the relationship between the predictors and successional trajectory, I built the top model for each predictor and graphed partial regression plots ('visreg' package; Breheny & Burchett 2017), which show the effect of each predictor with all other predictors in the model held at their median (for continuous predictors) or most common category (for categorical predictors). I checked the global model for model misspecification errors using simulated residuals (package 'DHARMA'; Hartig, 2024). I also ensured no spatial autocorrelation in the residuals using spline correlograms (package 'ncf'; Bjornstad, 2022).

To visualize shifts in community composition I used non-metric multidimensional scaling (NMDS) ordinations of all plots at each visit. NMDS ordinations use ranked distances between plots to represent pairwise dissimilarity in community composition. They are generally the most suitable for analysis of ecological communities as they rely on fewer assumptions than other ordination methods and are more robust to high levels of diversity (Kenkel & Orlóci, 1986). I used Bray-Curtis dissimilarity as the distance measure for the NMDS ordination. To increase the influence of low abundance species which may be key to differentiating some plots, I square root transformed the data before calculating dissimilarity. Because many sites have no species in common, I used step-across to improve the performance of the ordination. Step-across allows the ordination to find the shortest distance between sites with no shared species by going through intermediate sites (Bradfield & Kenkel, 1987).

I tested for overall differences in plant community composition between the three visits and between burned and unburned plots using a permutational multivariate analysis of variance (PERMANOVA) with visit, burn status, and their interaction as predictors, and plot as a random effect. A PERMANOVA tests the differences in multivariate data distribution between groups, which can be due to either a shift in composition or a change in the amount of variability

between plots (Anderson, 2001). To test for differences in multivariate dispersion between the three visits and between unburned and burned plots I used a test of differences in multivariate dispersion (PERMDISP), also with visit, burn status, and their interaction as predictors and plot as a random effect. For both PERMANOVA and PERMDISP analyses I used the software PERMANOVA + for PRIMER, with 5000 permutations (Anderson et al., 2008).

Lastly, I classified the community of each plot-visit combination into types to determine how the frequency of community types changes in response to wildfire. I used a cluster analysis to categorize each plot at each visit into a community type based on species composition. The goal of cluster analysis is to group observations in a way that minimizes the variation in community composition within a group and maximizes the variation between groups (Bakker, 2026). Prior to clustering, I removed all species that occurred in less than 5% of plots to reduce the influence of rare species on cluster designation. I used C-medoids clustering, which is similar to the commonly used K-means clustering algorithm (De Cáceres & Wiser, 2025). K-means clustering builds the clusters around centroids, whose coordinates are the centre of the cluster members in Euclidean space, therefore this method is not compatible with Bray-Curtis dissimilarities. Medoids are calculated by minimizing the sum of dissimilarities between all objects in the cluster, which means they can be calculated using Bray-Curtis dissimilarities (De Cáceres & Wiser, 2025). C-medoid clustering requires the number of clusters to be pre-defined by the user. I selected 12 clusters based on examination of a silhouette plot and the sum of standard error scree plot (Charrad et al., 2014). A silhouette statistic is calculated by comparing each observation's distance to within cluster observations versus distance to outside cluster observations. The statistic ranges from -1 to 1, with 1 representing a perfect fit. The silhouette plot graphs the average silhouette statistic for each number of clusters in a specified range, so the

cluster number with the highest silhouette statistic is considered the best representation of the data. I corroborated this with the sum of standard errors scree plot, by graphing the within groups sum of standard errors for a range of possible cluster numbers and looking for a point where adding more clusters resulted in minimal error reduction.

To determine which species characterize the plant community types represented by the clusters I used an indicator analysis (package ‘indicspecies’; Cáceres & Legendre, 2009) to find species that are significantly more frequent and/or abundant in each of the 12 clusters compared to the others. I assigned names to the clusters using the results of the indicator species analysis in combination with overall community structure. To visualize the frequency of transitions between community types (i.e. shifts of plots from one community type to another) I used an alluvial plot (‘ggalluvial’ package; Brunson & Read, 2023).

I used R version 4.5.1 for all analyses (R Core Team, 2025), except for the PERMANOVA and PERMDISP tests.

2.4 Results

2.4.1 Successional Trajectory

Forty-one percent of the 44 unburned plots had a convergent successional trajectory while 63% of the 52 burned plots had a convergent trajectory. When all plots were included, nine models were within $\Delta AIC_c < 2$, including a total of 12 predictors (see Table 2). McFadden’s pseudo- R^2 for the top-ranked models ranged from 0.15 to 0.18.

Table 2. Full average of the most parsimonious models ($\Delta AIC_c < 2$) for successional trajectory across all plots. Where an individual model does not contain a predictor, zero was substituted for the estimate when calculating the average. See Table A1 for a list of models.

Predictor	Estimate	Adjusted SE	Lower 95% CI	Upper 95% CI
Burn	1.113	0.573	-0.010	2.237
Soil Depth	-0.737	0.674	-2.059	0.584
Elevation	0.336	0.558	-0.757	1.429
Northness	0.534	0.685	-0.808	1.876
Burn x Soil Depth	2.762	1.609	-0.392	5.916
Burn x Elevation	2.460	1.601	-0.678	5.598
Windshelter	0.458	0.615	-0.747	1.664
Relative Exotic Cover	0.206	0.741	-1.245	1.658
Burn x Relative Exotic Cover	-1.421	2.363	-6.052	3.209
Relative Resprouter Cover	0.064	0.311	-0.545	0.674
Windshelter x Relative Resprouter Cover	0.518	1.330	-2.089	3.125
Northness x Relative Resprouter Cover	-0.379	1.253	-2.835	2.077

The interactions between burn status and soil depth and burn status and elevation were the strongest correlates of successional trajectory, appearing in eight and seven of the top-ranked models respectively (see Table A1). In unburned plots the probability of a divergent trajectory tended to increase with deeper soils, however in burned plots this trend was opposite and weaker. The probability of divergent trajectories tended to increase with elevation in unburned sites, while in burned plots increasing elevation tended to result in more convergent trajectories. However, all predictors had 95% confidence intervals that crossed zero (see Figure 2).

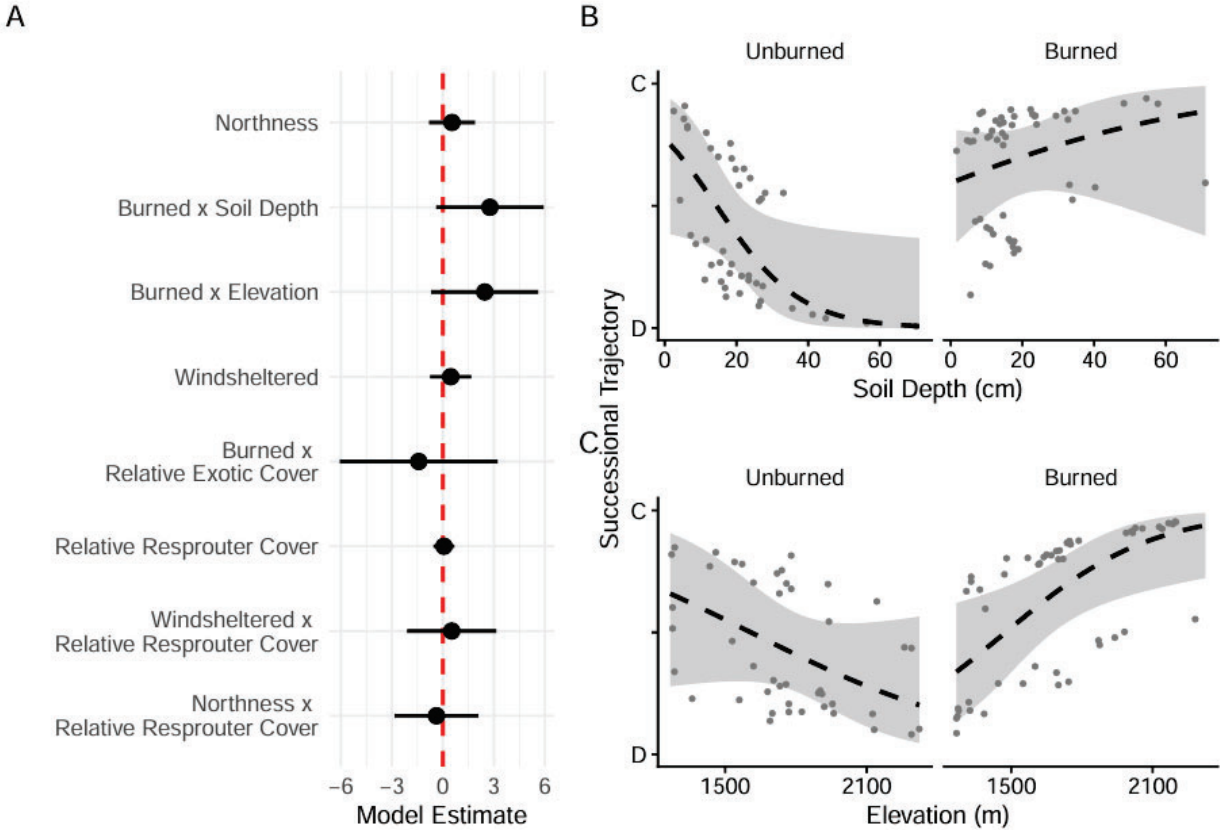


Figure 2. (A) Model averaged parameter estimates for successional trajectory (*ST*). Estimates are averaged for all 9 models within $\Delta AIC_c < 2$ of the model with the lowest AIC_c . Error bars depict 95% confidence intervals. All parameter estimates have confidence intervals that cross zero, however the elevation-burn interaction and soil depth-burn interaction were near-significant. (B) Partial regression plot depicting the effect of the interaction between soil depth and burn status on *ST*. (C) Partial regression plot depicting the effect of the interaction between elevation and burn status on *ST*. On the y-axis, “C” denotes a convergent trajectory and “D” represents divergent trajectory. Both partial regression plots were constructed using the best model that contained the parameter (see Table A1). All other parameters were held at the median value (continuous correlates) or most common category (categorical correlates). Shaded bands show the 95% confidence intervals.

In the subset including burned plots only, there were two models within a $\Delta AIC_c < 2$, including a total of 8 variables (see Table 3). McFadden’s pseudo- R^2 for the top models was 0.54 and 0.59.

Table 3. Full average of the most parsimonious models ($\Delta AIC_c < 2$) for successional trajectory across burned plots only. Where an individual model does not contain a predictor, zero is substituted for the estimate when calculating the average. Asterisks denote predictors or interactions with confidence intervals that do not cross zero. See Table A2 for a list of models within $\Delta AIC_c < 2$.

Predictor	Estimate	Adjusted SE	Lower 95% CI	Upper 95% CI
Windshelter Binomial	1.849	0.921	-2.169	5.867
Soil Depth	3.084	2.050	-0.191	6.359
Elevation*	5.331	1.671	0.762	9.901
Change in Frost Free Days*	4.291	2.331	0.671	7.911
Northness	1.914	1.847	-2.825	6.652
Relative Resprouter Cover	2.725	2.418	-1.488	6.938
Windshelter x Relative Resprouter Cover*	11.846	5.069	1.911	21.780
Soil Depth x Change in Frost Free Days*	10.763	5.470	0.041	21.485

Elevation, the interaction between soil depth and change in frost free days, and the interaction between windshelter and relative resprouter cover were the strongest correlates of successional trajectory in burned plots; all appeared in both top-ranked models (see Table A2). Successional trajectory in burned plots was more likely to be convergent at high elevations and divergent at low elevations. In plots that experience wind erosion (i.e. not windsheltered), having more resprouting species present pre-fire was more likely to result in divergent trajectories. In plots that experience deposition from wind (i.e. windsheltered), having more resprouting species present was more likely to result in convergent trajectories. In plots with deep soils, successional trajectory was more likely to be convergent as the number of frost-free days increased. In medium soils this effect was much weaker, and in shallow soils the effect was opposite and quite weak (see Figure 3).

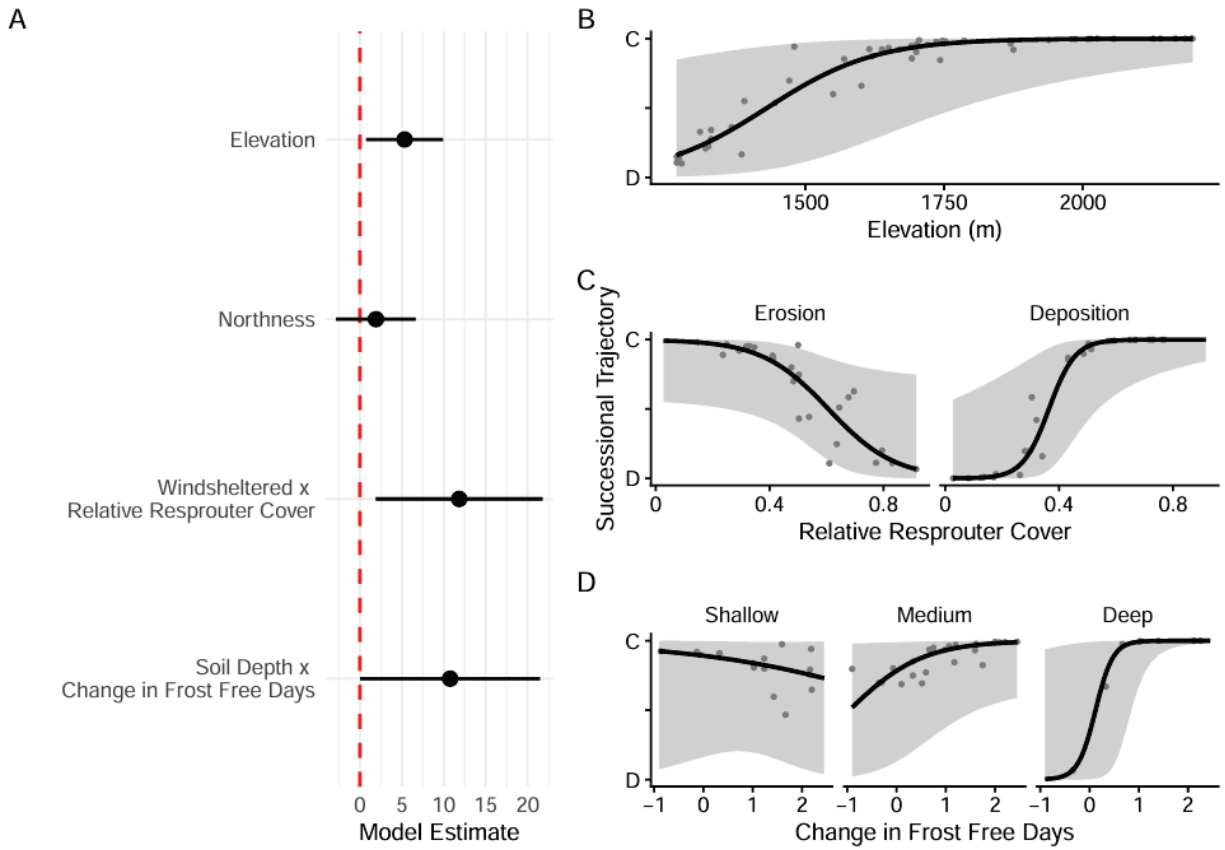


Figure 3. (A) Model averaged parameter estimates for successional trajectory (*ST*) for burned plots only. Estimates are averaged for the 2 models within $\Delta AIC_c < 2$ of the model with the lowest AIC_c . Error bars depict 95% confidence intervals. (B) Partial regression plot depicting the effect of elevation on *ST*. (C) Partial regression plot depicting the effect of the interaction between windshelter and relative resprouter cover on *ST*. (D) Partial regression plot depicting the effect of the interaction between soil depth and change in frost free days on *ST*. On the y-axis, “C” denotes a convergent trajectory and “D” represents divergent trajectory. All partial regression plots were constructed using the best model that contained the parameter (see Table A2). All other parameters were held at the median value (continuous predictors) or most common category (categorical predictors). Shaded bands show the 95% confidence intervals. Partial regression plots of predictors with estimate confidence intervals that cross zero are not shown.

2.4.2 Successional Rate

In unburned plots, successional rate ranged from 0.033 to 0.131 Bray-Curtis dissimilarity per year, with a mean change of 0.080 (SD = 0.024). In burned plots, successional rate ranged from 0.070 to 0.167 dissimilarity per year, with a mean change of 0.118 (SD = 0.027; see Figure A1).

There were five models within $\Delta AIC_c < 2$ for successional rate of all plots, including a total of 8 predictors (see Table 4). The R^2 values for the top-ranked models ranged from 0.38 to 0.40.

Table 4. Full average of the most parsimonious models ($\Delta AIC_c < 2$) for successional rate across all plots. Where an individual model does not contain a predictor, zero is substituted for the estimate when calculating the average. The asterisk denotes that confidence intervals do not cross zero. See Table A3 for a list of models within $\Delta AIC_c < 2$.

Predictor	Estimate	Adjusted SE	Lower 95% CI	Upper 95% CI
Burn	0.0190	0.0100	-0.0006	0.0386
Soil Drainage (Well)	0.0004	0.0062	-0.0116	0.0125
Soil Drainage (Moderate)	0.0111	0.0089	-0.0064	0.0285
Elevation	0.0025	0.0056	-0.0084	0.0135
Burn x Soil Drainage (Well)*	0.0328	0.0124	0.0086	0.0570
Burn x Soil Drainage (Moderate)	0.0112	0.0184	-0.0248	0.0473
Burn x Elevation	0.0226	0.0141	-0.0050	0.0501
Rock Cover	-0.0010	0.0035	-0.0078	0.0059
Relative Resprouter Cover	-0.0007	0.0027	-0.0059	0.0046
Relative Exotic Cover	0.0006	0.0028	-0.0061	0.0048

The interaction between burn status and soil drainage was the strongest correlate of successional rate, appearing in all of the top-ranked models (see Table A3). Overall, successional rate was higher in the burned plots. In burned sites, successional rate was similar across different categories of soil drainage, though slightly higher in well and moderately drained sites compared to rapidly drained sites. In unburned sites, successional rate was higher in rapidly and moderately drained sites, and lower in well drained sites (see Figure 4).

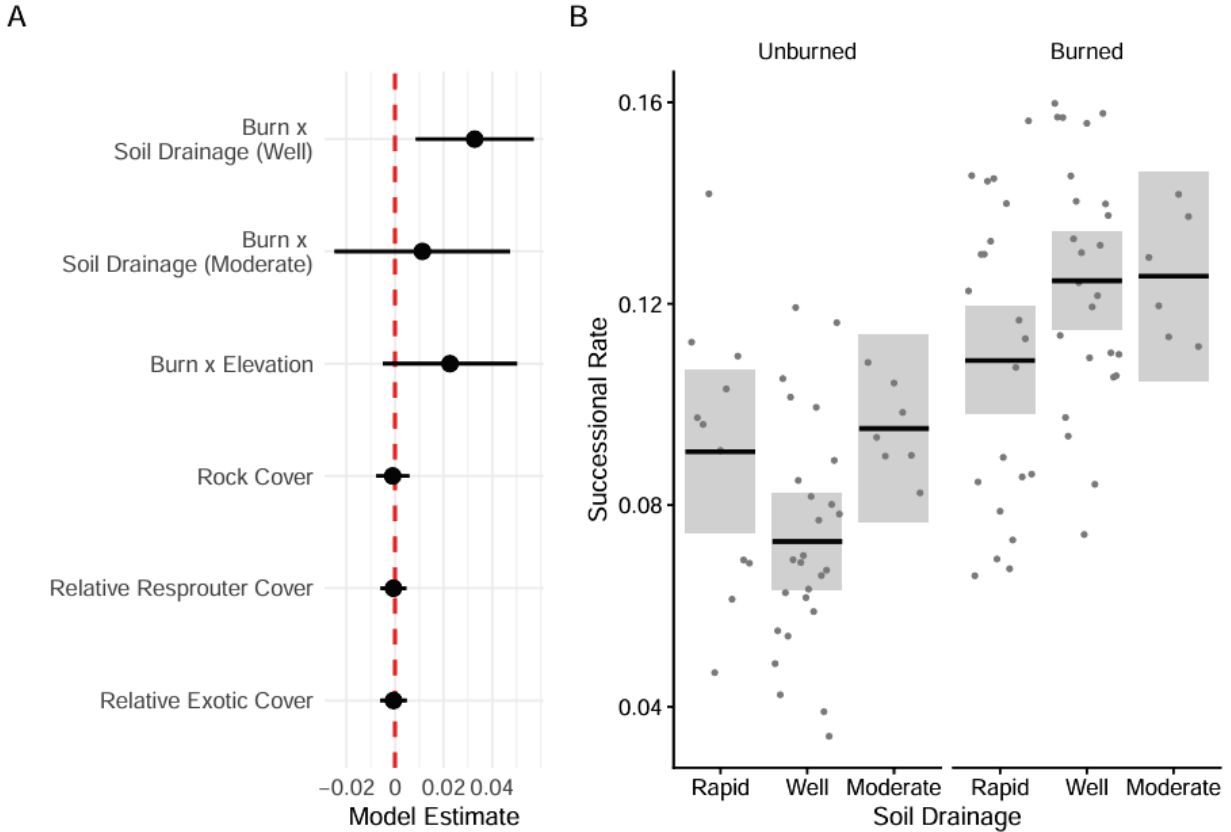


Figure 4. (A) Model averaging parameter estimates for successional rate (*SR*) on burned and unburned plots. Estimates are averaged for all 5 models within $\Delta AIC_c < 2$ of the model with the lowest AIC_c . Error bars depict 95% confidence intervals. (B) Partial regression plot depicting the effect of the interaction between burn status and soil drainage on *SR*. All partial regression plots were constructed using the best model that contained the parameter (see Table A3). All other parameters were held at the median value (continuous predictors) or most common category (categorical predictors). Shaded bands show the 95% confidence intervals. Partial regression plots of predictors with estimate confidence intervals that cross zero are not shown.

In the subset including burned plots only, there were 25 models within $\Delta AIC_c < 2$ for successional rate, including a total of 10 correlates (see Table 4). There was considerable variation in correlates within the top-ranked models (see Table A4). The R^2 values for the top-ranked models ranged from 0.01 to 0.09.

Table 5. Full average of the most parsimonious models ($\Delta AIC_c < 2$) for successional rate across burned plots only. Where an individual model does not contain a predictor, zero is substituted for the estimate when calculating the average. See Table A4 for a list of models within $\Delta AIC_c < 2$.

Predictor	Estimate	Adjusted SE	Lower 95% CI	Upper 95% CI
Change in Frost Free Days	-0.0046	0.0076	-0.0194	0.0103
Soil Drainage (Well)	0.0045	0.0085	-0.0121	0.0211
Soil Drainage (Moderate)	0.0040	0.0095	-0.0146	0.0226
Elevation	0.0059	0.0086	-0.0109	0.0227
Distance to Burn Edge	0.0035	0.0068	-0.0098	0.0168
Soil Depth	0.0001	0.0018	-0.0034	0.0036
Soil Depth x Change in Frost Free Days	0.0013	0.0070	-0.0124	0.0150
Shrub Cover	-0.0018	0.0051	-0.0118	0.0082
Rock Cover	-0.0007	0.0035	-0.0076	0.0062
Relative Exotic Cover	-0.0002	0.0017	-0.0035	0.0031
Relative Resprouter Cover	-0.0002	0.0016	-0.0034	0.0030

Although a number of variables and interactions were included in the best models for successional rate, the intercept only model was also among the best models. Additionally, all predictors had 95% confidence intervals that crossed zero (see Figure 5).

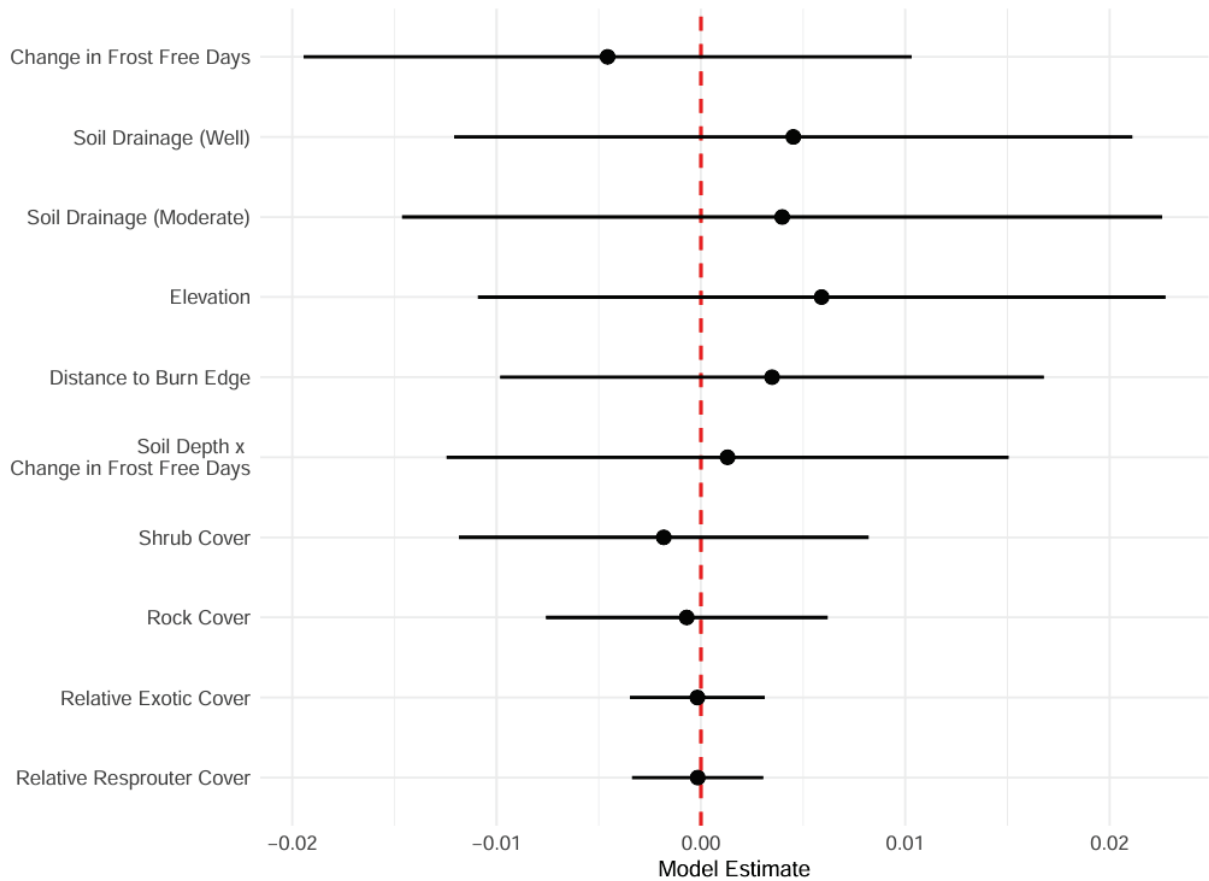


Figure 5. Model averaging parameter estimates for successional rate (*SR*) of burned plots. Estimates are averaged for all 25 models within $\Delta AIC_c < 2$ of the model with the lowest AIC_c . Error bars depict adjusted standard error. No partial regression plots are shown because all predictors have estimates with 95% confidence intervals that cross zero.

2.4.3 Plant Community Successional Outcomes

The NMDS ordination shows that there is less variability in community composition across plots in the post-fire surveys than before the fire (see Figure 6).

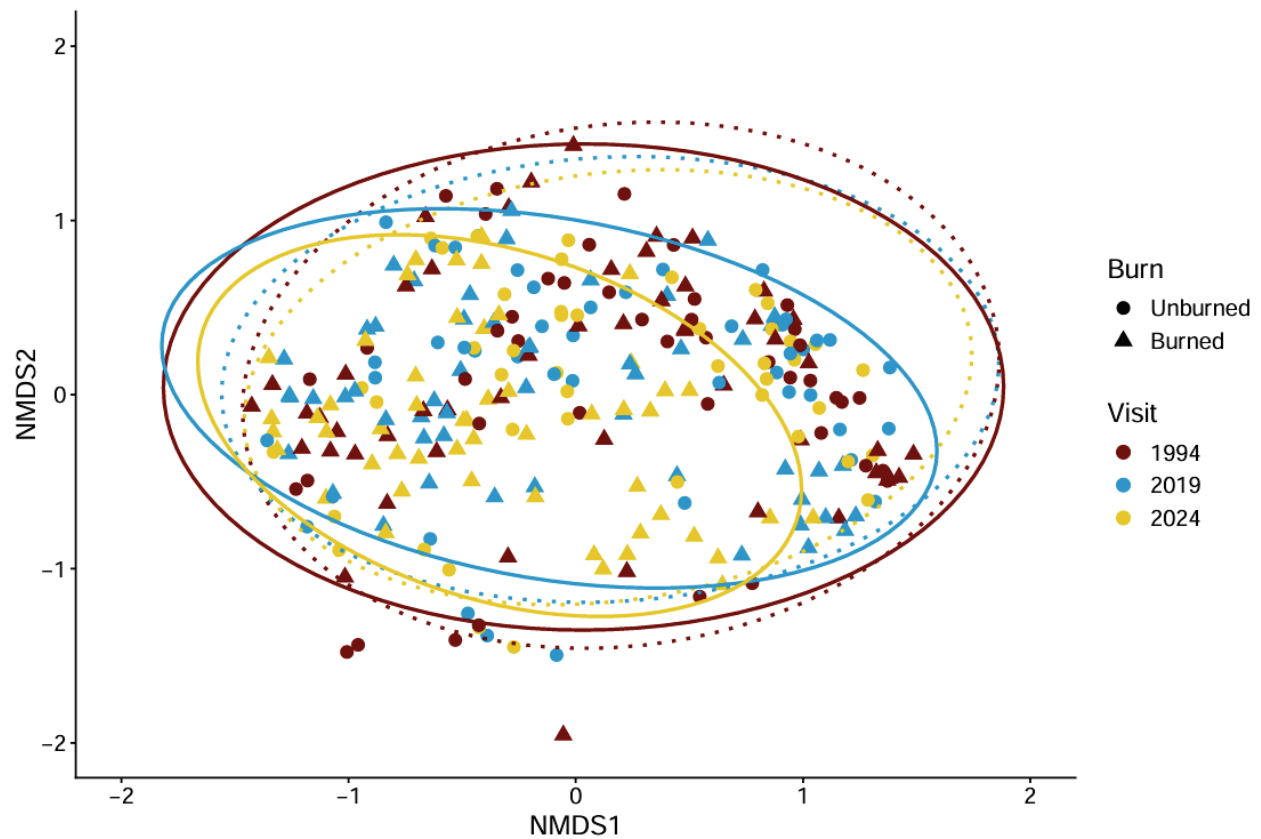


Figure 6. Non-metric multidimensional scaling ordination of community composition for all plots. Stress is 0.16 in 3 dimensions. Symbols represent visits to individual plots; plots belonging to the unburned subset are depicted as circles and plots belonging to the burned subset are depicted as triangles. Ellipses represent the 90% confidence interval for each combination of burn status and year. Note that in 1994 the ‘burned’ plots were those eventually to be burned. Both points and ellipses are coloured by visit (1994 is red, 2019 is blue, 2024 is gold). Ellipses for burned plots are solid lines and ellipses for unburned plots are dotted lines.

There was a significant difference in community composition between the three visits, and between burned and unburned plots (see Table 6).

Table 6. Results of PERMANOVA comparing visit and burn status in terms of plant species composition, with a random effect for plot. Bray-Curtis dissimilarity is used to calculate differences in composition. The test statistic is calculated using Type III sum of squares, and significance is based on 5000 permutations.

Factor	df	SS	MS	Pseudo-<i>F</i>	<i>p</i> (perm)
Visit	2	26533	13267	8.7568	0.0002
Burn	1	32151	32151	4.0273	0.0004
Plots (random effect)	94	750430	7983.3	5.2695	0.0002
Visit x Burn	2	15860	7930.2	5.2345	0.0002
Residuals	188	284820			
Total	287	1112200			

There was a significant difference in community composition between burned and unburned plots in both 2019 and 2024, but not in the 1994 pre-fire visit. Within the unburned plots only, all pairwise comparisons between visits were significantly different. This was also true within the burned plots only. There was no significant difference in beta diversity between unburned and burned plots at any visit, or between visits for the unburned plots. In the burned plots only, there was significantly lower beta diversity in the 2019 and 2024 visits as compared to the 1994 visit.

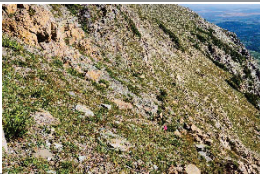
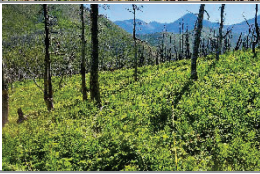
The beta diversity in 2024 tended to be lower than in 2019 and was close to significant (see Table 7).

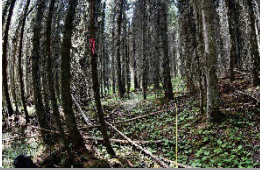
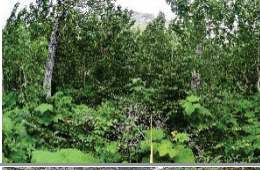
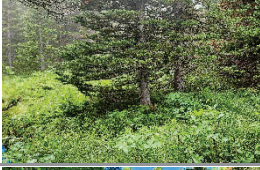
Table 7. Results for pairwise PERMANOVA and PERMDISP tests comparing burn status within each visit, and visits within each burn status. Type III sum of squares is used to calculate the pseudo *t* statistic and significance is based on 5000 permutations.

Pairwise Comparison	Within Level	PERMANOVA		PERMDISP	
		Pseudo <i>t</i>	<i>p</i> (perm)	Pseudo <i>t</i>	<i>p</i> (perm)
Burned vs. Unburned	1994	0.945	0.5609	0.3762	0.7401
	2019	2.598	0.0002	0.2602	0.8086
	2024	2.406	0.0002	0.7811	0.4633
1994 vs. 2019	Burned	3.130	0.0002	2.3198	0.0269
	Unburned	1.767	0.0002	1.4224	0.2064
1994 vs. 2024	Burned	3.262	0.0002	4.2756	0.0002
	Unburned	1.896	0.0002	1.8983	0.0952
2019 vs. 2024	Burned	3.106	0.0002	2.0631	0.0534
	Unburned	1.996	0.0002	0.4923	0.6737

The best definition of community types used 12 clusters, which explained 43% of plant community variation (PERMANOVA, Pseudo-F = 18.95, p (perm) = 0.001). Within each community type there was usually a consistent dominant species and characteristic lifeform (see Table 8). Four of the community types were primarily herbaceous, three community types were shrub-dominated, and five community types were forested. The number of significant indicator species varied based on community type and ranged from 4 to 33 species (see Table A5).

Table 8. Characteristics of the 12 community types. Cover values for dominant species and each life form are averaged across all plots within the community type. Cover values of the most abundant lifeform for each community are bolded. Gram stands for graminoid.

Representative Plot	Community Type	Tree Cover (%)	Shrub Cover (%)	Gram. Cover (%)	Forb Cover (%)	Dominant Species (% Cover)	Average Rate	Convergent Trajectory (proportion)
	Forb Meadow	0.3	8.9	22.9	39.2	<i>Lupine spp.</i> (5.2%)	Unburned: 0.118 Burned: 0.111	Unburned: 1/1 Burned: 1/5
	Fescue Grassland	1.9	29.1	36.5	31.3	<i>Festuca campestris</i> (22.9%)	Unburned: 0.076 Burned: 0.099	Unburned: 1/3 Burned: 8/9
	Alpine Tundra	1.4	1.8	2.8	11.7	<i>Senecio triangularis</i> (1.4%)	Unburned: 0.079 Burned: 0.123	Unburned: 3/5 Burned: 1/4
	Disturbance Followers	2.8	15.5	6.6	47.4	<i>Chamaenerion angustifolium</i> (23.3%)	Unburned: NA Burned: 0.105	Unburned: NA Burned: 0/1
	Huckleberry-Sedge	0.7	14.4	5.2	6.8	<i>Vaccinium myrtillus</i> (6.9%)	NA – not present in 1994	NA – not present in 1994

Representative Plot	Community Type	Tree Cover (%)	Shrub Cover (%)	Gram. Cover (%)	Forb Cover (%)	Dominant Species (% Cover)	Average Rate	Convergent Trajectory (proportion)
	Willow Shrubland	0.8	45.5	10.3	27.8	<i>Salix spp.</i> (34.2%)	Unburned: 0.087 Burned: 0.100	Unburned: 0/3 Burned: 0/1
	Spiraea Shrubland	7.8	37.3	10.6	21.8	<i>Spiraea betulifolia</i> (23.1%)	NA – not present in 1994	NA – not present in 1994
	Aspen Forest	37.9	34.2	13.7	80.1	<i>Populus tremuloides</i> (29.6%)	Unburned: 0.082 Burned: 0.113	Unburned: 4/7 Burned: 2/6
	Spruce-Subalpine Fir Forest	61.9	29.6	3.4	40.6	<i>Abies bifolia</i> (32.2%)	Unburned: 0.079 Burned: 0.125	Unburned: 1/7 Burned: 5/7
	Mixed Forest	40.0	28.0	4.1	65.8	<i>Thalictrum spp.</i> (13.7%)	Unburned: 0.087 Burned: 0.131	Unburned: 3/6 Burned: 7/8
	Subalpine Fir-Beargrass Forest	38.4	29.0	6.7	59.1	<i>Xerophyllum tenax</i> (44.3%)	Unburned: 0.061 Burned: 0.131	Unburned: 2/6 Burned: 6/7
	Lodgepole Pine Forest	64.6	27.3	5.4	43.8	<i>Pinus contorta</i> (37.9%)	Unburned: 0.086 Burned: 0.115	Unburned: 3/6 Burned: 3/4

Seedling densities in previously forested communities varied substantially depending on community type and burn status (see Table 9). Aspen Forest, Spruce-Subalpine Fir Forest and Lodgepole Pine Forest all had higher seedling densities of some dominant tree species in burned plots than in unburned plots (*Populus tremuloides*, *Picea engelmannii* and *Pinus contorta*

respectively). However, burned Spruce-Subalpine Fir Forest plots had low densities of another dominant tree species, *Abies bifolia*, as compared to unburned plots. Burned Subalpine Fir-Beargrass plots in the burn had very low seedling densities of their dominant tree species, *A. bifolia*. The dominant tree species in the Mixed Forest, *Pseudotsuga menziesii*, had low regeneration densities across burned and unburned plots.

Table 9. Seedling densities per hectare in forested communities in 2024, organized by community type pre-fire in burned and unburned plots. The median, lower and upper quartiles are shown. The highest median density for each community type and species is bolded to show whether that species is more prevalent in burned or unburned areas.

Community in 1994	Species	Burned Plots				Unburned Plots			
		n	Median	Q1	Q3	n	Median	Q1	Q3
Aspen Forest	<i>Abies bifolia</i>	6	0	0	0	7	0	0	63
	<i>Populus tremuloides</i>		225	25	5188		100	0	983
	<i>Populus trichocarpa</i>		0	0	581		0	0	0
Spruce- Subalpine Fir Forest	<i>Abies bifolia</i>	7	100	0	163	7	2375	1213	3200
	<i>Picea englemannii</i>		222	0	450		0	0	0
	<i>Pinus contorta</i>		89	25	1700		0	0	0
	<i>Populus tremuloides</i>		0	0	125		0	0	0
	<i>Pseudotsuga menziesii</i>		25	0	470		0	0	0
Mixed Forest	<i>Abies bifolia</i>	8	0	0	0	6	1275	444	1975
	<i>Picea englemannii</i>		0	0	0		0	0	75
	<i>Populus tremuloides</i>		363	0	1481		0	0	38
	<i>Pinus contorta</i>		100	56	356		0	0	0
	<i>Pseudotsuga menziesii</i>		0	0	6		0	0	0
Subalpine Fir -Beargrass Forest	<i>Abies bifolia</i>	7	25	0	63	6	2650	2200	4075
	<i>Picea englemannii</i>		0	0	0		25	0	88
	<i>Populus tremuloides</i>		0	0	38		0	0	0
Lodgepole Pine Forest	<i>Abies bifolia</i>	4	0	0	150	6	1700	450	2950
	<i>Picea englemannii</i>		0	0	75		50	0	119
	<i>Pinus contorta</i>		963	813	2400		0	0	0
	<i>Pseudotsuga menziesii</i>		0	0	0		100	6	494

Q1 = lower quartile; Q3 = upper quartile

Overall, unburned plots tended to stay within the same community type over the course of the three visits, with some transitioning to similar community types between the 1994 and 2019 visits (see Figure 7). For example two plots were Spruce-Fir Forest in 1994 and shifted to the Subalpine Fir-Beargrass community type in 2019. Both community types have abundant

subalpine fir, but the Subalpine Fir-Beargrass community type is more open and dominated by beargrass. The most common shift in the unburned sites was towards the Subalpine Fir-Beargrass Forest, with plots in both the Mixed Forest and the Spruce-Subalpine Fir Forest transitioning to this community type.

Burn status strongly influenced community type (see Figure 7). The burned plots saw considerably more movement between community types, especially between the 1994 and 2019 visits. The Disturbance Follower community type increased in prevalence from one plot in 1994 to 18 plots in 2019, gaining plots that had been spread across several forested community types as well as the Forb Meadow and Fescue Grassland community types prior to wildfire. However, this community type was short-lived and the 2024 visit saw a decrease in the prevalence of the Disturbance Follower community type down to 9 plots. A number of burned plots with Disturbance Follower communities in 2019 transitioned to Spiraea Shrubland or Huckleberry-Sedge community types by 2024.

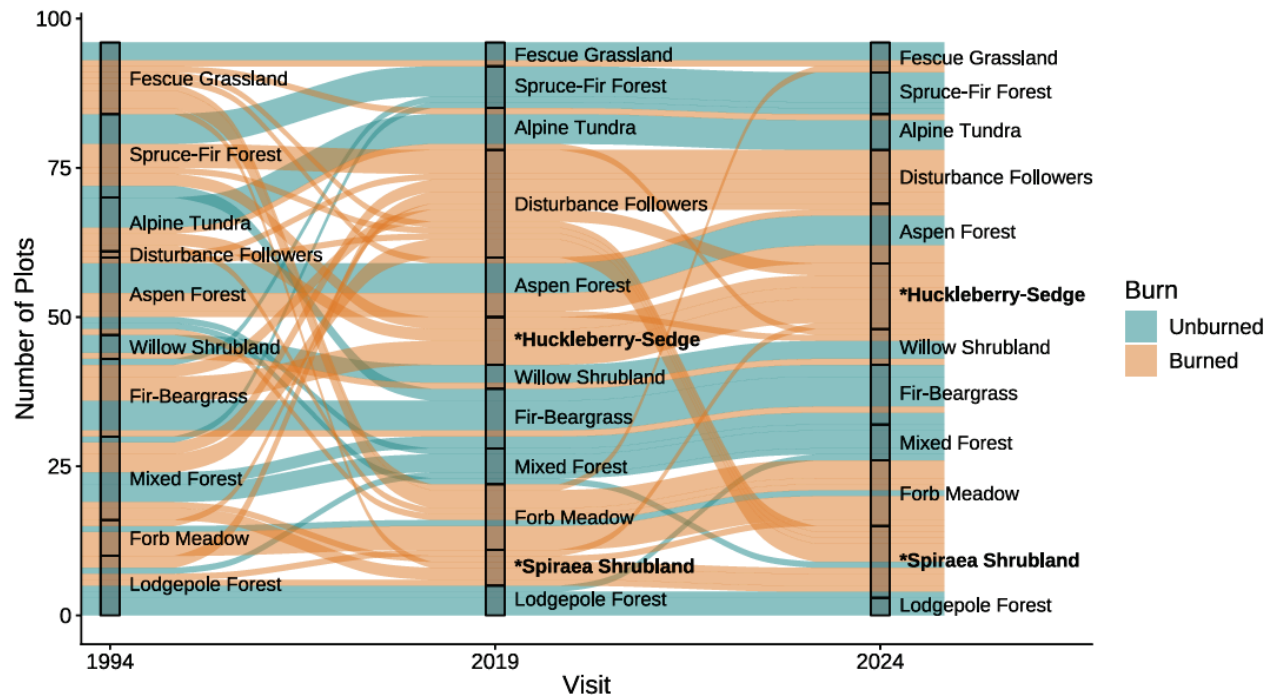


Figure 7. Flow diagram showing the movement of plots between community types over the three visits. Community types were defined using C-medoid clustering with 12 clusters. The width of the lines is proportional to the number of plots taking a given pathway between community types, and the height of the vertical bar sections at each visit shows the number of plots in each community type at that visit. New community types post-fire are labeled in bold with asterisks.

Two of the 12 community types were not present in WLNP prior to the fire. These were Spiraea Shrubland (8 plots in 2019 and 11 plots in 2024), and Huckleberry-Sedge (6 plots in 2019 and 12 plots in 2024; see Figure 8), both of which are shrub dominated. The Spiraea Shrubland community type generally occurs at mid elevations and is dominated by *Spiraea betulifolia*. The Huckleberry-Sedge community type occurs at higher elevations and is dominated by multiple *Vaccinium* species as well as the sedges *Carex rossii* and *Carex geyeri*. There were no burned plots classified as Spruce-Subalpine Fir Forest, Mixed Forest or Lodgepole Pine communities. In contrast, other community types were highly resilient to fire; 50% of Aspen Forest plots and 80% of Forb Meadow plots returned to these community types immediately post-fire.

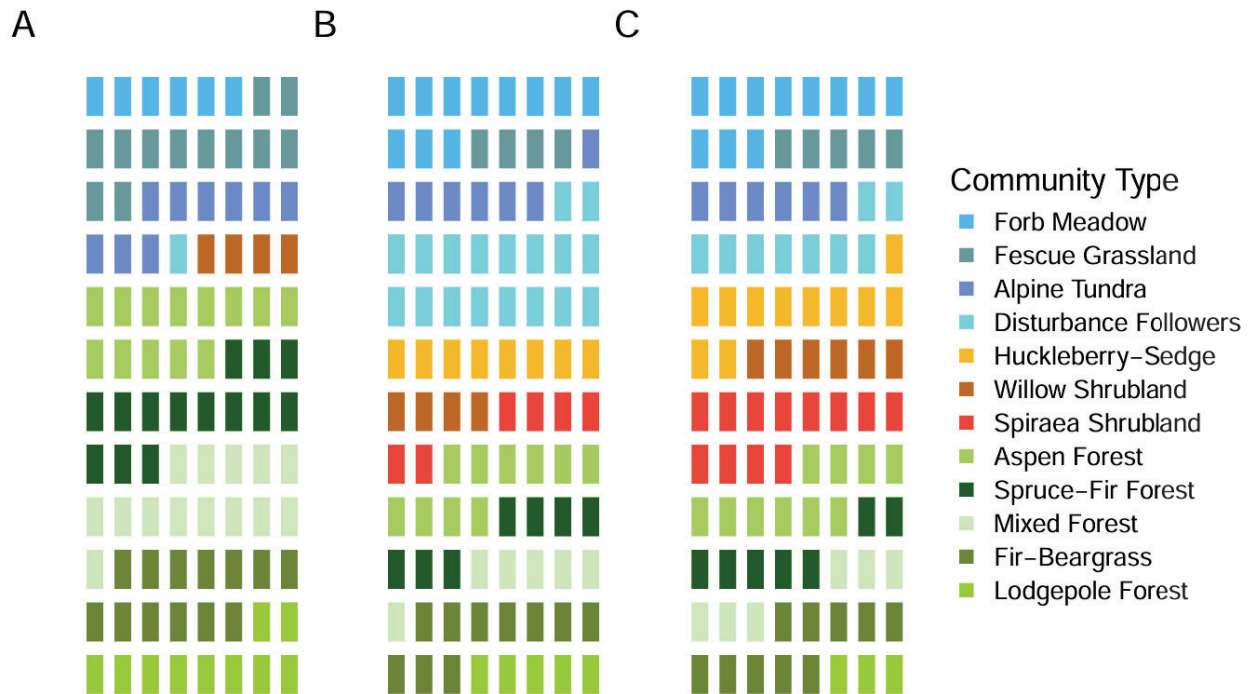


Figure 8. Number of plots in each community type at the A) 1994, B) 2019 and C) 2024 visits. Each rectangle represents a plot. Herbaceous communities are represented by the blue colour family, shrub communities are represented by the orange colour family and forested communities are represented by the green colour family.

2.5 Discussion

As large fires become increasingly frequent in many ecosystems, there is growing concern that plant communities may not be able to recover to their pre-fire state. In this study, I show that the early stages of plant succession are resilient to wildfire despite human disturbance and climate change. Although many plant communities are returning towards pre-fire composition, lack of regeneration of key tree species in some communities indicates that regrowth of these forests will be slow to occur and is perhaps uncertain. My study ties together two seemingly contradictory bodies of literature. Classic post-fire studies of whole plant communities elsewhere in the Rocky Mountains show that pre-fire species quickly regenerate in

burned areas (Doyle et al., 1998; Lyon & Stickney, 1976; Turner et al., 1997). However, a rapidly growing body of work on tree seedling regeneration post-fire raises concern that trees are not regenerating sufficiently to regrow forests (Stevens-Rumann et al., 2018a). I show that even as some forested communities could become more open due to reduced tree regeneration, the understory is converging towards a pre-fire state.

There are a large variety of response variables used in the successional literature, yet studies often fail to define clearly which properties of succession they are measuring. This makes interpreting and comparing successional studies challenging because the relative importance of different drivers may vary depending on which property is studied. I found different drivers for successional trajectory and rate, highlighting the value of investigating the drivers of these two measures separately. The primary drivers of successional trajectory were site condition and history factors, along with an interaction between site condition and species availability. In contrast, successional rate was more difficult to predict, and highly variable even in unburned plots. If these two measures were combined, the challenges with modelling rate may have obscured the trajectory results. Defining and separating the measures of these two properties could improve theoretical frameworks for succession by showing how drivers act to propel succession forward.

2.5.1 Successional Trajectory and Rate

Most burned areas in WLNP are returning towards their pre-fire community composition. This is consistent with other studies of post-fire succession in the Rocky Mountains which found that post-fire communities were mostly composed of species that were on site pre-fire (Doyle et al., 1998; Lyon & Stickney, 1976). On the other hand, unburned areas generally diverged over the course of my study.

Although more subtle than wildfire, there are likely multiple forces causing succession in unburned areas. For a plot to have a convergent trajectory, a temporary disruption that shifts species composition away from the original composition is required. Examples of this in unburned areas could be a windstorm, flood or short-lived insect outbreak. Additionally, to be measured as convergent in my study, the shift away from original community composition must roughly coincide with the post-fire visit. Within the time scale of my study, causes of succession in unburned areas are more likely to be continuous pressures resulting in “divergent” succession. For example, Lloren (2021) found that woody, taller and shade tolerant species increased in unburned areas in WLNP between 1998 and 2019. This trend has been ongoing since the late 1800s, resulting in forest densification and encroachment of grasslands (Levesque, 2005). These changes are consistent with fire suppression. Insects and disease could also be continuous pressures on the time scale of my study. Whitebark and limber pine have been declining over the course of the study period due to white pine blister rust (Shepherd et al., 2025), while western balsam bark beetle has been causing increasing subalpine fir mortality (Parks Canada, unpublished data). Although some of these pressures could represent threats to a particular ecosystem, a divergent successional trajectory itself is not a concern. Ecological communities are adaptive systems that change over time (Carroll et al., 2023), and I am measuring only one portion of a long-term cycle.

2.5.1.1 Effects of climate and climate trends

Trends in climate influenced successional trajectory in unexpected ways. Sites with an increasing number of frost-free days had an increased likelihood of a convergent successional trajectory in the burn, but only in plots with deep soils. This is consistent with my prediction for successional rate; I expected that a longer growing season would facilitate more regrowth and

therefore turnover. However, it is an unexpected result for trajectory. I expected that a changing climate would result in a divergent trajectory because warmer conditions should favour species with greater temperature tolerances. It is difficult to explain why this interaction affects trajectory but not rate, and it may be that trend in frost free days is correlated with another underlying factor that affected trajectory. Although not significant, communities on north facing (i.e. cooler) slopes were more likely to have convergent trajectories than those on south facing slopes. It may be that regardless of trends in temperature change (e.g. as represented by the change in the number of frost-free days), hotter and drier conditions on south-facing slopes create stressful conditions, thereby increasing the likelihood of divergent trajectories. Northness was not retained in either rate model.

Studies of the impact of climate trends on regeneration post-fire have mixed results. In Oregon, Downing *et al.* (2019) examined the effect of several climate variables on ponderosa pine regeneration and did not find a clear trend. In contrast, a meta-analysis of seedling regeneration after wildfire in the U.S. Rocky Mountains found that drier conditions have significantly reduced seedling regeneration in the 21st century (Stevens-Rumann *et al.*, 2018). Studies of the effects of changing climate on understory species post-fire were more consistent. Fire tended to shift species composition towards lower elevation or more southern species, indicating a divergent trajectory in response to warming climate (Stevens *et al.*, 2015; Wilson *et al.*, 2024). It is possible that individual species in WLNP could have shifted in distribution, but the effect on community composition was negligible because more abundant species that were not impacted by climate had greater influence on the whole community measure.

The timespan of this study may have been too short to observe the effects of climate trends on plant communities. Measuring climate trends from 1994 to 2019 may have resulted in

capturing short-term fluctuations rather than long-term trends. Additionally, there could be lags in plant community responses to climate trends, meaning that additional visits will be required to observe an impact.

2.5.1.2 Effects of human disturbance proxies

Human disturbance did not appear to have an impact on the rate or trajectory of succession. Proximity to trails or roads was not retained in any of the top models for trajectory or rate. Earlier work by Lloren & McCune (2024), found that the dissimilarity between 1994 and 2019 visits to the unburned plots was greater when plots were more distant from trails or roads. Therefore, the amount of change in community composition after the fire was influenced by the proximity of roads and trails, but not the subsequent rate or direction of succession.

The introduction and spread of exotic invasive species is expected to be one of the primary impacts of human disturbance on plant communities. Relative exotic cover pre-fire was retained in the successional trajectory model for all plots, however the confidence intervals overlapped zero. In both of the rate models, relative exotic cover pre-fire was retained, however the estimate was very close to zero. Lower elevations were significantly correlated with increased probability of divergent trajectories, which could be driven by human disturbance as there is greater human use at lower elevations. However, this cannot be disentangled from other potential drivers of elevational gradients such as changing soil properties, precipitation patterns and wind levels.

Although the relative abundance of exotics in 1994 was not an important predictor of succession patterns, both abundance and species richness of exotic species increased in burned plots post-fire. Exotic species richness continued to increase from 2019 to 2024, while relative abundance increased at higher elevations, but began to decline at lower elevations. The increase in abundance and richness post-fire is consistent with the results of Prev  y *et al.* (2024) who

found that burned areas across the western U.S. had higher richness and cover of exotic species compared to unburned areas. Despite increases, both exotic richness and abundance were low throughout the study period. The greatest mean richness was 2 species per plot in 2024 (median 1, max 13), and the greatest mean relative abundance was 3.5% per plot in 2019 (median 0.5%, max 46%). Communities may be able to handle some level of increase in exotic species without an impact to the successional trajectory or rate. For example, in Yellowstone National Park, exotic thistles increased in absolute abundance over time, but decreased in relative abundance (Wright & Tinker, 2012). Therefore, although exotics were present, they did not impact the overall communities' ability to regenerate.

2.5.1.3 Effects of species availability

The rate and trajectory of succession were not influenced by the distance to unburned seed sources. Herbaceous and shrub species were the dominant cover during the early stages of succession measured in my study, and these lifeforms may be less dependent on unburned seed sources than trees. Other studies have found varying impacts of distance to the burn edge depending on the species studied. A large body of research has focused on the impacts to presence and density of tree seedlings; finding a decline in tree seedling regeneration with increasing distance to unburned seed sources in most species (Boag et al., 2020; Chambers et al., 2016; Coop et al., 2010; Stevens-Rumann et al., 2018). Tree species with alternative regeneration strategies were the exception to this rule; Coop *et al.* (2010) found that limber pine which is bird dispersed and aspen which resprouts did not decline in density with distance to the burn edge. In Yellowstone, Turner *et al.* (1997) found that increased distance to unburned areas was not associated with reduced vegetation cover or species richness. Several species from the Yellowstone study were also common in burned areas in my study, including *Carex rossii* which

Turner et al. (1997) found was more abundant farther from the burn edge. Although dominant early successional species are not affected by lack of nearby unburned seed sources, the reason they play an important early successional role may be due to adaptations to dispersal after fire, such as long-distance dispersal, resprouting or a fire tolerant seedbank (Doyle et al., 1998; Turner et al., 1997).

2.5.1.4 The strongest correlates of successional change

The variables most strongly correlated with rate and trajectory of succession were primarily related to site conditions and history. Elevation was retained as a predictor in all models, and was significant in the model for trajectory in burned sites. I predicted that high elevation sites would be more likely to have divergent trajectories, because fire is less frequent at high elevations and therefore I expected communities to be less adapted. In contrast, my results show that the probability of divergent trajectories is greater at lower elevations. It is possible that different successional rates between the fire and the initial visit post-fire affected the calculation of trajectory. Higher elevations tend to have slower initial rates of succession because harsher conditions limit species establishment until facilitation from initial colonizers moderates the environment (Anderson, 2007). This was true in WLNP where there was very little regeneration at higher elevations in 2019. For example, plots in the upper subalpine had a mean total vegetation cover of 30% in 2019. Therefore, gaining species in the second post-fire visit likely increased similarity to pre-fire community composition, resulting in a convergent trajectory. On the other hand, low elevation sites had already experienced considerable regrowth by the first visit, resulting in the 1994 and 2019 visits having relatively more similar species composition compared to high elevation sites. The low elevation plots in the foothills parkland had a mean

total vegetation cover of 125% in 2019. This means that changes in species composition at low elevations had a greater chance of registering as a divergent trajectory.

Elevation could also be correlated with another underlying driver. For example, lower elevations which tend to be farther from the continental divide receive less precipitation (Parks Canada Agency, 2025a), and regeneration there could have been moisture limited. Different species of herbivores occupy different elevational ranges in the park. Elk (*Cervus elaphus* L. 1758) tend to be concentrated at low elevations in the park. Elk density in WLNP has previously been estimated at 1200/100 km²; higher than surrounding regions (Eisenberg et al., 2014). Some of the key grass species in WLNP's grasslands (*Festuca campestris*, *Festuca idahoensis* and *Pseudoroegneria spicata*) are sensitive to elk grazing (Thrift et al., 2013). These species may have been particularly vulnerable to damage when initially establishing, resulting in shifts in plant community composition where elk densities are high.

The interaction between the relative abundance of resprouting species pre-fire and windshelter was also a significant correlate of successional trajectory on burned plots. I predicted that in areas of high erosion, soil and the seedbank would be removed and therefore increased presence of resprouting species would increase the likelihood of a convergent trajectory. However, the effect was contrary to my prediction, and erosion sites with high resprouter cover were more likely to diverge. At deposition sites, high resprouter cover increased the probability of convergence. This could be caused by snow drifting rather than soil and seed movement. Snow accumulation affects vegetation composition through mechanisms like shorter growing season and protection from desiccation and moisture runoff during melting (Billings & Bliss, 1959; Knight et al., 1977; Weaver & Collins, 1977). Species that resprout are perennials, and therefore more likely to overwinter. Therefore, this interaction could be due to the protective

nature of snowdrifts. In erosion sites where there is no protective snow cover, resprouter species may have been exposed to more winter desiccation and therefore did not recover towards their pre-fire abundance as well as resprouters in plots protected with snow deposition. Both the elevation and windshelter variables illustrate a major challenge with using observational studies to study succession in natural environments: environmental variables are complex and can be representative of multiple underlying processes.

Depending on burn status, soil drainage affected successional rate. In unburned areas, the rate was lower in well drained plots compared to rapidly or moderately drained plots. This may be due to changes in precipitation levels between 1994 and 2024. WLNP has experienced a strong drying trend over recent decades (Kienzle & Clark, 2019), and areas that are either wet or dry may be more sensitive to changes in precipitation than intermediate sites. Species on moderately drained sites may be more adapted to moisture, while very dry sites may have already been the limit of some species tolerances. In both cases there could be faster shifts in community composition as a result of the significant reduction in moisture from precipitation.

2.5.1.5 Challenges of measuring succession

Separating trajectory and rate of succession proved more challenging than expected, and difficulties with these measures may have influenced my results. Because the magnitude of the successional trajectory value is influenced by rate of change, I converted the trajectory metric to a binomial. This separates the measures of trajectory and rate, but it is possible there is still an influence. On sites with a fast rate of succession, the signal for convergent versus divergent trajectory should be strong. On sites with a slow succession rate (e.g. unburned sites), it will be weaker and there is a higher chance of the trajectory being classified incorrectly due to unavoidable noise in the data. However, any misclassification is likely to be random relative to

the hypothesized drivers and therefore not result in bias. Converting trajectory to a binomial measure introduces some additional issues. Using a binomial means that sites with very little change were classified as either converging or diverging when the best categorization may have been no trajectory.

Despite these potential issues with the trajectory measure, the best models for trajectory explained more variability compared to the best models for rate. The inability of the hypothesized predictors to explain variability in successional rate could indicate the existence of additional drivers of successional rate that I did not measure. For example, a more detailed categorization of the traits and regeneration strategies of the pre-fire community may have improved rate predictions since many post-fire species regenerate from species present pre-fire (Doyle et al., 1998; Lyon & Stickney, 1976), and the presence of rapidly growing species may shift community composition faster. Additionally, a measure of changing precipitation patterns over the study period may have been valuable for modelling successional rate, as other studies have found that the rate of succession increases with more available moisture (del Moral & Chang, 2015; Donnegan & Rebertus, 1999). On the western edge of the park, precipitation levels were lower post-fire compared to average levels between the 1998 visit and the fire (Aspinall et al., 2025), so moisture could have limited the rate of succession during the post-fire period.

The trajectory measure may have been subject to some noise because it incorporates data from the first visit. The plots were not permanently marked until the second visit. Prior to that, they were located with GPS coordinates which means plots likely shifted in location slightly from the first to second visit, possibly affecting the recorded community composition. Additionally, the plots were measured roughly two decades prior to the fire. If a burned plot experienced major change in that time, a divergent trajectory could be driven by factors other

than fire. For this reason, it is valuable to be able to compare drivers of change in burned sites to drivers in the unburned sites. If a predictor had the same effect on successional trajectory or rate across both burned or unburned sites, I would be able to infer that the effect was not specific to post-fire succession.

Assessing rate and trajectory across diverse communities and a large elevational range provides opportunities to identify successional drivers that are influential across a wide range of community types, however it also creates challenges. Some drivers of succession may be specific to certain communities and therefore obscured in a study of multiple community types. For example, on a harsh site the rate of colonization could be slow at first and then speed up due to facilitation by initial colonizers, whereas on a site that is not limited by dispersal or resources the rate of successional change could be fast initially and decline over time (Anderson, 2007). Therefore, we could be sampling some sites during a period of increased successional rate, while at other sites the rate may have already slowed during our sampling period (see Figure 9). Using the 2019/2020 visit as a starting point from which to assess the subsequent five year trajectory of recovery may have created issues when comparing across communities. Two to three years into succession is very different in an alpine community versus a grassland community that is adapted to a short fire return interval and may have completed most of its successional pathway in that time period.

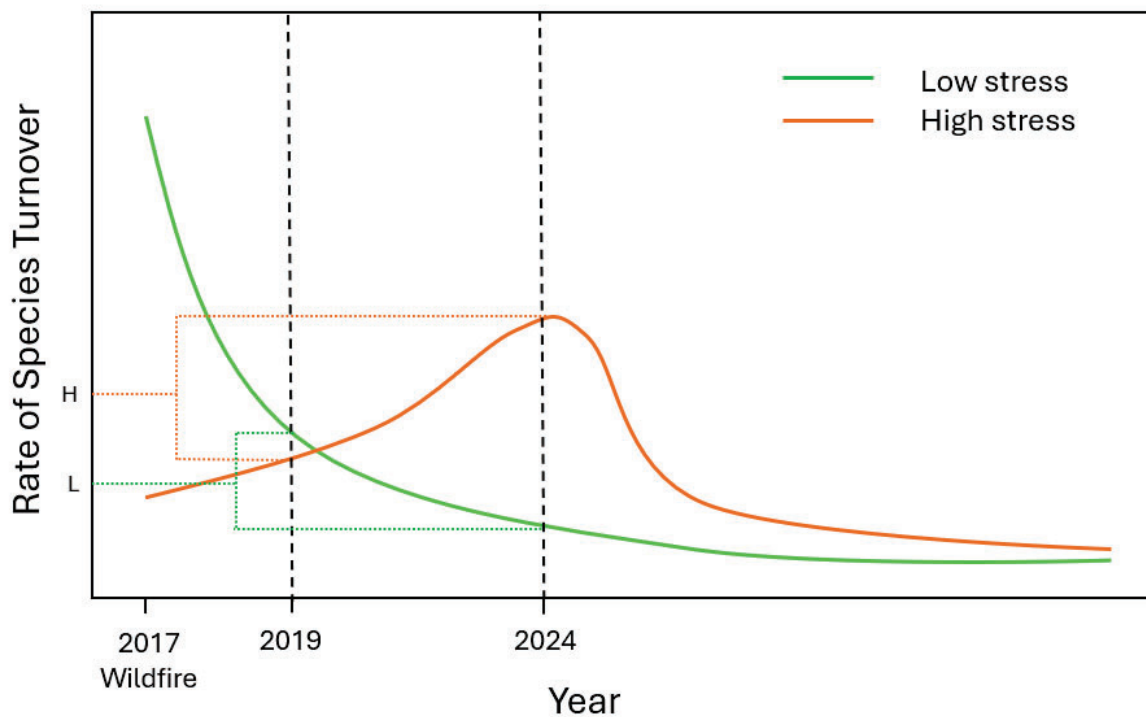


Figure 9. Example patterns of species turnover that could affect successional rate. The average rate of succession over my sampling period (from 2019 to 2024) in the hypothetical high stress scenario is denoted by H, while L denotes the average for low stress. In the low stress site species turnover is fastest immediately post-fire then slows as species establish because there are fewer available resources. In the high stress site, initial species turnover is slow, then increases as some species establish and facilitate others. In this scenario, successional rate measured from 2019 to 2024 is lower in the low stress site because most of the change occurred immediately post-fire. Actual shapes and timespans of species turnover are unknown. Figure is adapted from Anderson (2007).

2.5.2 Community shifts

The burn caused significant shifts in the community composition across all plots, and a tendency towards homogenization over time. Burned plots generally shifted towards species adapted to open areas and away from species that prefer a closed canopy. This trend is expected given that the fire effectively removed all or nearly all of the mature trees. Because fire creates more homogenous habitat and promotes fire follower species, a post-fire reduction in beta diversity is expected. However, it is surprising that homogenization appeared to continue in the

2024 visit, despite communities being further along in succession and increasing in species richness.

Ongoing changes to composition and beta diversity could be due to multiple waves of fire followers. According to Lyon & Stickney (1976), post-fire species in the Rocky Mountains tend to be largely the same as pre-fire species, but their relative abundances change over time. My study only partially supports this conclusion. Some species remained relatively consistent in their frequency of occurrence across visits, while other species appeared or disappeared. In the 2019 post-fire visit, several ephemeral species that were not present pre-fire appeared. By the 2024 visit, these species had declined in distribution. For example, *Dracocephalum parviflorum* (American dragonhead) was present in 13 burned plots in 2019 and 6 plots in 2024; *Descurainia sophia* (flixweed) was present on 5 burned plots in 2019 and 1 plot in 2024. Both species regenerate quickly after fire from a soil seedbank and *D. parviflorum* has fire activated seeds that ensure germination is timed with its preferred conditions (Akinsoji, 1988; Lyon & Stickney, 1976). Subsequently, a group of secondary post-fire followers became increasingly widespread. These include species such as *Calamagrostis rubescens* (pinegrass), which was present on 4 of the pre-fire plots in 1994, 1 plot in 2019 and 12 plots in 2024, and *Carex rossii* (Ross's sedge) which increased from 0 plots in 1994, to 1 plot in 2019, to 30 of the 52 burned plots in 2024. These species have adaptations to regeneration after fire from rhizomes or the soil seedbank (USFS, 2025). The secondary fire followers are likely partially responsible for the ongoing shift and homogenization of communities, as they are not only more widespread but also generally more abundant than the initial post-fire species.

Cosmopolitan species likely also influenced the trends in overall species composition. This group was already common before fire, but became increasingly widespread post-fire. For

example, *Achillea boreale* (Boreal yarrow) was present in 21 of the pre-burn plots in 1994, in 31 plots in 2019 and 43 of 52 burned plots in 2024. *Poa pratensis* (Kentucky bluegrass) a competitive grass with both native and exotic subspecies, was present on 1 plot in 1994, 15 plots in 2019 and 20 plots in 2024. There are few comparable examples of sustained biotic homogenization in the post fire literature. In the Sierra Nevada mountains of northern California, Weeks *et al.* (2023) also found that initial trends in homogenization became stronger over time. Sites that burned at high and very high severity increasingly shifted in composition and became more similar to one another.

2.5.2.1 Response of community types to fire

Shrub and forb dominated communities were the most successful in the burn. Three pre-existing community types became more common post-fire: the Forb Meadow, Disturbance Follower, and Willow Shrubland communities. In addition, two new community types, both shrub dominated, formed only after the burn. These were the Huckleberry-Sedge and Spiraea Shrubland communities. The formation of a Huckleberry-Sedge community type is consistent with the results of other post-fire studies, which have found that the dominant species of this community type are common post-fire (Doyle *et al.*, 1998; Turner *et al.*, 1997). The Spiraea Shrubland community type was not present in the 1994 visit, however interestingly two unburned plots transitioned to this community type in 2024 (along with 10 burned plots). One of the unburned plots is located in an avalanche path, while the other plot appeared to be affected by a windstorm. This suggests that disturbance in general rather than fire specifically promotes the formation of the Spiraea Shrubland community type.

The frequency of community types dominated by long-lived species tended to decline the most in response to fire. Seven communities declined in frequency after the fire; these were

forested communities as well as the Fescue Grassland and Alpine Tundra community types. Spruce-Fir and Subalpine Fir-Beargrass forests generally transitioned to the Huckleberry-Sedge community type, one of the new post-fire community types. Some Alpine Tundra communities also transitioned to Huckleberry-Sedge. Burned Fescue Grassland sites most commonly transitioned to Forb Meadow communities. Other studies have found a decrease in dominant rough fescue community grass species, coupled with an increase in forbs post-fire. However, these studies also found more rapid recovery times, with partial or complete recovery in 2 to 4 years (Antos et al., 1983; Bork et al., 2002). The burns in these studies may have been less severe than the Kenow wildfire as they occurred in June and December while the Kenow wildfire occurred in September. The Aspen Forest community type was less affected by fire than other forested communities, with half of the burned Aspen Forest plots remaining in that community type. Aspen Forest plots that did transition to another community type did not follow a consistent pathway and split into several different community types. The relative stability of aspen forest post-fire is consistent with other studies which have found that aspen forests are promoted by fire (Kulakowski et al., 2006; McKenzie & Tinker, 2012).

2.5.2.2 Anticipated community resilience

The ability of communities to return to their pre-fire state may be predictable based on early establishment of species characteristic of pre-fire community composition. In the Rocky Mountains, the majority of tree seedlings establish within the first six years post-fire (Harvey et al., 2016; Turner et al., 1997; Urza & Sibold, 2017). High elevation tree species have short-term seed viability (e.g. 3 years in Englemann spruce and 1 year in subalpine fir), therefore tree seedling regeneration from onsite seed sources needs to happen quickly (Turner et al., 1997). Turner *et al.* (2016) found that 24 years after fire, early patterns of seedling regeneration were

still the main determinants of stand structure. This may be true for other plant lifeforms as well, unless species are adapted to long distance dispersal or have a long-lived seed bank.

Based on seedling regeneration at the 2024 visit, some forest communities are likely to recover to their pre-fire composition relatively quickly. Burned Lodgepole Pine and Mixed Forest community types generally transitioned to either Disturbance Follower, Huckleberry-Sedge, or Spiraea Shrubland community types. However, the transition is probably temporary as plots with the Lodgepole Pine community type pre-fire had a mean lodgepole pine regeneration density of 2250 seedlings per hectare. This is comparable to an area in Yellowstone National Park which had 2300 lodgepole pine seedlings per hectare following wildfire, with other Yellowstone areas ranging from 600 to 111,000 lodgepole pine seedlings per hectare (Turner et al. 1997). Turner et al. (2016) revisited the same sites 24 years after the Yellowstone fires and found that early lodgepole pine densities were a good predictor of long-term establishment. Other post-fire studies in the Rocky Mountains have shown that lodgepole pine is favoured by fire (McKenzie & Tinker, 2012; Urza & Sibold, 2017). Urza & Sibold (2017) found that mixed forests tended to shift to dominance by a single tree species post-fire. In my study 5 out of 8 burned Mixed Forest community plots had multiple species of tree seedlings, so most plots appear to be returning to a mixed forest community.

Other communities appear less likely to return to pre-fire composition. Many species declined in abundance in response to the wildfire, however only a few declined in frequency and occurred in fewer plots in 2024 than 1994. These were the tree species *Abies bifolia*, *Picea engelmannii* and *Pinus albicaulis*, as well as understory species such as *Goodyera oblongifolia*, *Moneses uniflora* and *Osmorhiza occidentalis*. Regeneration of *A. bifolia* was especially low in the burned Subalpine Fir-Beargrass community type, where it was previously a dominant

species. Although some ongoing establishment of *A. bifolia* is expected, regeneration of this species peaked six years post-fire in a study immediately south of WLNP (Harvey et al., 2016). With the exception of *P. albicaulis*, these tree species do not have long-lived seed banks or adaptations to long distance dispersal (Southern Regional Extension Forestry, n.d.; USFS, 2025), therefore recolonization is likely to be very slow.

If a return to the pre-fire community type is the desired outcome, planting of subalpine fir may be required in the Subalpine Fir-Beargrass and Spruce-Subalpine Fir community types. However, the pre-fire community may not always be the desired state. Prior to the Kenow wildfire, the proportion of the landscape that was forested was much higher than it was 100 years ago, a trend that was likely driven in part by fire suppression (Levesque, 2005). Therefore, a typical historical state for WLNP may lie somewhere between the highly forested pre-fire landscape, and the widespread early successional communities now present.

2.5.3 Conclusion

In this study, I did not find strong evidence that climate trends and human disturbance impact the ability of plant communities to recover after wildfire. Although change in the number of frost-free days influenced succession, the effect was not as predicted, and there was no evidence for influence from human disturbance or distance to the burn edge. Plant communities have transitioned to new community types post-fire, and two communities that did not exist pre-fire formed, however overall successional trajectory in burned areas tended to be convergent. Because of the tendency toward convergent trajectories and widespread distribution of many pre-fire species, most communities will likely return to a pre-fire state with time. Limitations to recovery are more likely to be species specific, rather than on a whole community scale. In contrast, unburned communities were more likely to have divergent successional trajectories.

This demonstrates that successional processes independent of wildfire are also shaping plant communities. Although current community trajectories provide an indication of the future, it is unknown how long these trajectories will be maintained. Further study will be valuable to understand the stability of trajectories over time.

CHAPTER 3: CONCLUSION

Despite over a century of research, much remains to be learned about both theoretical and practical aspects of succession. This is partially because the context of succession is changing in many ecosystems due to novel disturbance and increasing human-caused stress (Turner & Seidl, 2023). Additionally, succession as a result of natural disturbance is difficult to study due to the long time frames involved, low replication, and lack of true controls (Poorter et al., 2023; Wiens & Parker, 1995). These challenges are compounded by a multitude of competing theoretical frameworks and lack of consistent terminology for what is being measured, making it difficult to synthesize research and conduct meta-analyses (Meiners et al., 2015; Poorter et al., 2023).

In this study I clearly defined and measured two properties of succession: trajectory and rate. By measuring successional trajectory and rate separately, I demonstrated that these properties of succession are influenced by different drivers. Successional rate was influenced by site conditions and history factors only; while successional trajectory was influenced primarily by site conditions and history factors, along with a species availability factor. The site conditions and history factors that were most important were different for trajectory and rate. Burned communities tended to have a faster rate of succession and more convergent trajectory as compared to unburned communities. Neither rate nor trajectory was impacted by the degree of change in climate, proximity to corridors of human disturbance, or the distance to an unburned seed source.

Despite the theoretical benefits, measuring rate and trajectory came with practical challenges. This was especially true when comparing across a wide range of plant communities spanning a large elevation gradient. The first visit post-fire occurred during the second growing season, at which point significant regrowth had occurred in some communities while in others

there was almost none. Successional rate varies over time (Anderson, 2007), so I may have been measuring a period of faster rate in some communities versus others. In order to remove the influence of rate from the trajectory measure, I converted trajectory into a binomial. However, this meant that all trajectories were categorized as either convergent or divergent, when in some cases sites may have had no trajectory due to minimal change.

Future studies of succession would benefit from continuing to clearly define and separate the properties of succession that are measured. Multiple strategies could then be used to quantify each property. My measure of successional trajectory has flaws, however it is simple and intuitive to use. It could be measured alongside other metrics to understand how consistently individual metrics perform. Improving how succession is measured will make it easier to compare across studies and test the various theoretical frameworks for succession.

To determine how the wildfire affected different plant community types, I classified communities into 12 types using a cluster analysis and examined the transitions in community types over time. For land managers, understanding the responses of particular types of plant communities to wildfire is more useful than modelling rate and trajectory. Although less quantitative, it is simpler to understand and apply. Managers can use the information from this analysis to understand which communities are most affected by wildfire. Despite a tendency towards convergent trajectories in burned areas, communities generally transitioned to a different community type as a result of the fire. There was an overall shift away from forested and other communities dominated by long-lived species towards forb and shrub dominated communities. This is unsurprising given that trees take longer to regrow as compared to other lifeforms. By assessing seedling densities in burned forest communities and comparing to their unburned counterparts, I am able to determine that most forest communities are likely to regrow. The

exception is the Subalpine Fir-Beargrass community type. This high elevation forest community type is missing subalpine fir seedlings which are its dominant tree species, meaning recovery may be slow or uncertain. If this is a concern for park management, tree planting could be explored. Prior to planting, regeneration patterns in this community should be explored further to determine if seedlings are limited by seed source, climate or other factors (Larson et al., 2022). This will enable planting strategies to be more effective. For example if climate is limiting, cool moist sites with a greater likelihood of survival could be targeted for planting; if dispersal is limiting, the creation of regeneration islands could be prioritized.

This study took place in the very early stages of succession, especially for slow growing communities like forests. It would be valuable to continue to revisit the plots used in this study to determine if early trends are sustained long term. Information on changing precipitation patterns could be incorporated into rate and trajectory models. Many of the strongest correlates of successional rate and trajectory (e.g. soil depth and soil drainage) are moisture linked, indicating that a measure of precipitation trends could explain more of the variability in successional trends. Other studies that encompass a wide range of community types would benefit from visiting sites the first year post-disturbance, to reduce the issue of different communities being at different successional stages when the study begins. It would also be beneficial to have enough replicates to determine if rate and trajectory vary by community type. Different drivers may have been important depending on community type, or even had opposite effects. For example, a steeper increase in the number of frost-free days could have increased successional rate in communities where plant growth is limited by growing season, and slowed it in communities that are already hot and dry. Despite these challenges, it is worthwhile to include multiple community types in successional studies as it allows overarching patterns to be identified. In addition, measuring

unburned sites along with burned sites allowed me to clearly demonstrate how the drivers of succession after wildfire are different from causes of community shifts in unburned areas. I recommend that future studies also include measurements of unburned sites over time.

Succession continues to be an important field of study as wildfires and other climate-related disturbances become increasingly frequent. Understanding which drivers and stressors affect the properties of succession can help identify where recovery may be impeded, or as is the case in my study, alleviate concerns about the resilience of plant communities. Clear definitions of the properties of succession and categorization of drivers (e.g. using Meiners *et al.* (2015) framework) will assist in comparison across studies and improve theoretical understanding of succession as this body of literature continues to grow.

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APPENDIX: SUPPLEMENTAL TABLES AND FIGURES

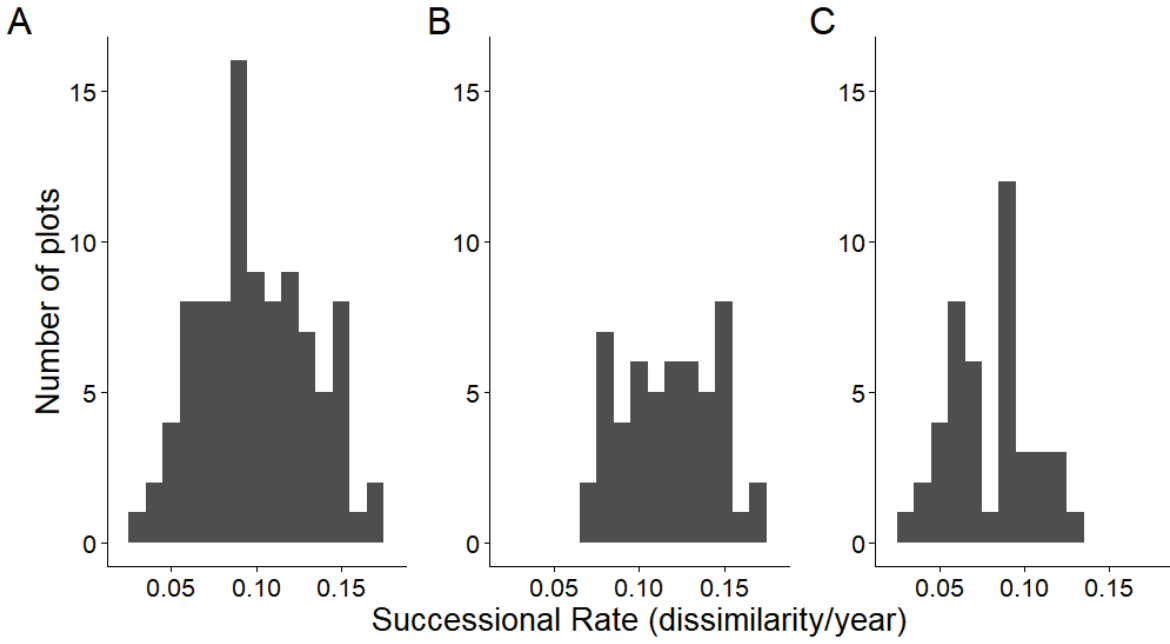


Figure A1. Distribution of the successional rate variable for A) all plots, B) burned plots only and C) unburned plots only.

Table A1. Summary of models within $\Delta AIC_c < 2$ of the lowest AIC_c for successional trajectory of all plots

Model Estimates												df	logLik	AIC_c	ΔAIC_c	Weight	Pseudo R^2
Burn status	Windshelter	Soil Depth	Elevation	Northness	Relative Exotic Cover	Relative Resprouter Cover	Burn status x Soil Depth	Burn status x Elevation	Burn status x Relative Exotic Cover	Windshelter x Relative Resprouter Cover	Northness x Relative Resprouter C						
1.36		-0.73	0.50	1.04			3.03	3.01				7	-55.82	126.9	0.00	0.206	0.16
1.02	0.94	-0.87	0.30				3.06	3.29				7	-56.09	127.4	0.54	0.157	0.15
0.91	0.97	-0.90	0.28		0.43		3.30	2.63	-2.93			9	-54.09	128.3	1.36	0.105	0.18
1.24		-0.77	0.45	1.00	0.41		3.26	2.41	-2.64			9	-54.12	128.3	1.42	0.101	0.18
0.61	0.79			-0.08	1.08	0.08			-5.34	3.80	-3.84	9	-54.14	128.4	1.47	0.098	0.18
1.25	0.49	-0.81	0.44	0.70			3.07	3.17				8	-55.51	128.7	1.77	0.085	0.16
1.06		-0.72		0.85	0.17		2.24		-3.87			7	-56.72	128.7	1.80	0.083	0.15
1.39		-0.77	0.63	1.15		0.39	3.08	2.89				8	-55.53	128.7	1.82	0.083	0.16
1.00	1.09	-1.05	0.27			0.30	3.44	3.63		1.74		9	-54.32	128.7	1.82	0.083	0.18

Table A2. Summary of models within $\Delta AIC_c < 2$ of the lowest AIC_c for successional trajectory of burned plots only

Windshelter	Soil Depth	Elevation	Change in Frost Free Days	Northness	Relative Resprouter Cover	Windshelter x Relative Resprouter Cover	Soil Depth x Change in Frost free days	df	logLik	AIC_c	ΔAIC_c	Weight	Pseudo R^2
1.15	3.30	5.89	4.29	3.42	3.30	13.34	11.57	9	-13.575	49.5	0.00	0.56	0.59
2.74	2.74	4.62	4.29		1.99	9.95	9.73	8	-15.295	50.0	0.48	0.44	0.54

Table A3. Summary of models within $\Delta AIC_c < 2$ of the lowest AIC_c for successional rate of all plots

Burn status	Soil Drainage	Elevation	Relative Exotic Cover	Relative Resprouter Cover	Rock Cover	Burn status x Soil Depth	Burn status x Soil Drainage	Burn status x Elevation	df	logLik	AIC_c	ΔAIC_c	Weight	Pseudo R^2
0.018	+	0.0028					+	0.026	9	-218.735	457.6	0.00	0.384	0.40
0.019	+	0.0057			-0.0057		+	0.026	10	-218.330	459.2	1.69	0.165	0.40
0.018	+	0.0017		-0.0043			+	0.028	10	-218.405	459.4	1.83	0.154	0.40
0.023	+						+		7	-222.086	459.4	1.88	0.150	0.38
0.018	+	0.0016	-0.0043				+	0.026	10	-218.454	459.5	1.93	0.146	0.40

Table A4. Summary of models within $\Delta AIC_c < 2$ of the lowest AIC_c for successional rate of burned plots only

Soil Drainage	Soil Depth	Distance to burn edge	Elevation	Change in frost free days	Relative Exotic Cover	Relative Resprouter Cover	Rock Cover	Shrub Cover	Soil Depth x Change in frost free days	df	logLik	AIC_c	ΔAIC_c	Weight	Pseudo R^2
				-0.013						3	113.04	-219.6	0.00	0.067	0.03
+			0.013							5	115.39	-219.4	0.13	0.062	0.08
		0.012	0.014							4	114.12	-219.4	0.19	0.060	0.05
		0.010		-0.013						4	113.97	-219.1	0.50	0.052	0.05
										2	111.65	-219.0	0.53	0.051	NA
			0.011							3	112.76	-219.0	0.55	0.051	0.02
+										4	113.92	-219.0	0.60	0.049	0.05
		0.012	0.011	-0.010						5	115.03	-218.7	0.84	0.044	0.07
	0.0028								0.030	5	115.01	-218.7	0.88	0.043	0.07
+				-0.011						5	114.95	-218.6	1.00	0.040	0.07
				-0.011				-0.010		3	112.53	-218.6	1.02	0.040	0.01
										4	113.70	-218.5	1.05	0.039	0.04
			0.0088	-0.010						6	116.20	-218.5	1.09	0.039	0.09
+		0.0094	0.015							3	112.49	-218.5	1.10	0.038	0.01
		0.0099								4	113.65	-218.4	1.13	0.038	0.04
			0.017				-0.011			5	114.78	-218.2	1.35	0.034	0.06
+								-0.0096		4	113.47	-218.1	1.51	0.031	0.03
				-0.011				-0.0071		5	114.65	-218.0	1.60	0.030	0.05
		0.011	0.018				-0.0088			4	113.40	-217.9	1.63	0.029	0.03
				-0.014	-0.0061			-0.010		4	113.36	-217.9	1.71	0.028	0.03
+			0.0105	-0.0075						6	115.87	-217.8	1.74	0.028	0.08
				-0.014		-0.0058				4	113.32	-217.8	1.80	0.027	0.02
		0.012	0.012					-0.0070		5	114.55	-217.8	1.80	0.027	0.05
+			0.011					-0.0070		6	115.83	-217.7	1.82	0.027	0.08
			0.0093					-0.0076		4	113.25	-217.6	1.94	0.025	0.02

Table A5. Significant indicator species for the community types identified through the cluster analysis. Fidelity is the probability of finding the indicator species in a plot of the specified community type. Specificity is the probability that a plot belongs to a community type given that the indicator species is present.

Species	p value	Fidelity	Specificity
Fescue Grassland			
<i>Festuca campestris</i>	0.005	0.952	0.905
<i>Rosa spp.</i>	0.005	0.905	0.271
<i>Dasiphora fruticosa</i>	0.005	0.857	0.625
<i>Arctostaphylos uva-ursi</i>	0.005	0.667	0.783
<i>Pulsatilla nuttalliana</i>	0.005	0.667	0.429
<i>Allium cernuum</i>	0.005	0.619	0.347
<i>Antennaria parvifolia</i>	0.005	0.524	0.748
<i>Sedum lanceolatum</i>	0.005	0.476	0.408
<i>Anemone multifida</i>	0.005	0.476	0.430
<i>Silene parryi</i>	0.005	0.381	0.606
<i>Penstemon confertus</i>	0.005	0.381	0.370
<i>Drymocallis pseudorupestris</i>	0.005	0.381	0.519
<i>Erigeron speciosus</i>	0.005	0.381	0.658
<i>Eriogonum umbellatum</i>	0.005	0.381	0.452
<i>Juniperus communis</i>	0.005	0.286	0.688
<i>Potentilla gracilis</i>	0.01	0.381	0.427
<i>Primula spp.</i>	0.01	0.286	0.683
<i>Danthonia spp.</i>	0.01	0.238	0.409
<i>Erigeron compositus</i>	0.015	0.524	0.239
<i>Lomatium triternatum</i>	0.015	0.429	0.368
<i>Arabis nuttallii</i>	0.025	0.286	0.382
Aspen Forest			
<i>Symphoricarpos spp.</i>	0.005	0.970	0.691
<i>Amelanchier alnifolia</i>	0.005	0.879	0.486
<i>Viola canadensis</i>	0.005	0.818	0.908
<i>Populus tremuloides</i>	0.005	0.788	0.793
<i>Bromus inermis</i>	0.005	0.727	0.767
<i>Prunus virginiana</i>	0.005	0.727	0.651
<i>Vicia americana</i>	0.005	0.727	0.623
<i>Heracleum maximum</i>	0.005	0.697	0.587
<i>Lathyrus ochroleucus</i>	0.005	0.667	0.470
<i>Osmorhiza occidentalis</i>	0.005	0.576	0.736
<i>Prosartes spp.</i>	0.005	0.576	0.521
<i>Urtica dioica</i>	0.005	0.515	0.834
<i>Maianthemum racemosum</i>	0.005	0.485	0.413
<i>Berberis repens</i>	0.005	0.455	0.405

Species	p value	Fidelity	Specificity
<i>Symphyotrichum ciliolatum</i>	0.005	0.455	0.558
<i>Sanicula marilandica</i>	0.005	0.424	0.735
<i>Cirsium arvense</i>	0.005	0.394	0.519
<i>Geranium richardsonii</i>	0.005	0.394	0.807
<i>Maianthemum stellatum</i>	0.005	0.394	0.432
<i>Phleum pratense</i>	0.005	0.394	0.627
<i>Poa pratensis</i>	0.005	0.394	0.567
<i>Rubus idaeus</i>	0.005	0.333	0.479
<i>Taraxacum officinale</i>	0.01	0.606	0.193
<i>Moehringia lateriflora</i>	0.015	0.364	0.275
<i>Geranium viscosissimum</i>	0.05	0.424	0.274
Huckleberry-Sedge			
<i>Vaccinium myrtillus</i>	0.005	0.895	0.266
<i>Carex rossii</i>	0.005	0.579	0.456
<i>Vaccinium scoparium</i>	0.005	0.421	0.653
<i>Phacelia hastata</i>	0.005	0.368	0.355
<i>Carex geyeri</i>	0.01	0.579	0.285
Willow Shrubland			
<i>Salix spp.</i>	0.005	1	0.963
<i>Equisetum spp.</i>	0.005	0.786	0.897
<i>Cornus sericea</i>	0.005	0.571	0.475
<i>Calamagrostis canadensis</i>	0.005	0.429	0.822
Subalpine Fir - Beargrass			
<i>Abies bifolia</i>	0.005	1	0.352
<i>Xerophyllum tenax</i>	0.005	0.97	0.823
<i>Vaccinium membranaceum</i>	0.005	0.879	0.741
<i>Luzula hitchcockii</i>	0.005	0.455	0.569
<i>Pinus albicaulis</i>	0.01	0.485	0.262
<i>Arnica spp.</i>	0.035	0.212	0.496
Mixed Forest			
<i>Thalictrum spp.</i>	0.005	1	0.447
<i>Ribes lacustre</i>	0.005	0.808	0.555
<i>Angelica dawsonii</i>	0.005	0.769	0.61
<i>Pedicularis bracteosa</i>	0.005	0.769	0.768
<i>Clematis occidentalis</i>	0.005	0.692	0.368
<i>Veratrum viride</i>	0.005	0.654	0.4
<i>Valeriana sitchensis</i>	0.005	0.5	0.53
<i>Acer glabrum</i>	0.005	0.462	0.504
<i>Castilleja miniata</i>	0.005	0.423	0.484
<i>Erigeron glabellus</i>	0.005	0.308	0.605
<i>Lonicera involucrata</i>	0.005	0.308	0.596

Species	p value	Fidelity	Specificity
<i>Pseudotsuga menziesii</i>	0.005	0.308	0.588
<i>Erythronium grandiflorum</i>	0.005	0.231	0.649
<i>Actaea rubra</i>	0.01	0.423	0.395
<i>Eucephalus engelmannii</i>	0.01	0.423	0.385
<i>Anticlea occidentalis</i>	0.01	0.385	0.381
<i>Populus trichocarpa</i>	0.01	0.231	0.584
<i>Rubus parviflorus</i>	0.02	0.654	0.221
<i>Aquilegia flavescens</i>	0.025	0.577	0.266
<i>Sorbus spp.</i>	0.045	0.346	0.261
<i>Antennaria racemosa</i>	0.045	0.192	0.462
Forb Meadow			
<i>Achillea borealis</i>	0.005	1	0.318
<i>Gaillardia aristata</i>	0.005	0.964	0.363
<i>Galium boreale</i>	0.005	0.964	0.331
<i>Festuca idahoensis</i>	0.005	0.857	0.682
<i>Koeleria macrantha</i>	0.005	0.857	0.725
<i>Lupinus spp.</i>	0.005	0.821	0.574
<i>Lithospermum ruderae</i>	0.005	0.714	0.714
<i>Cerastium arvense</i>	0.005	0.643	0.656
<i>Pseudoroegneria spicata</i>	0.005	0.643	0.458
<i>Erigeron caespitosus</i>	0.005	0.607	0.818
<i>Boechera spp.</i>	0.005	0.536	0.287
<i>Comandra umbellata</i>	0.005	0.536	0.698
<i>Monarda fistulosa</i>	0.005	0.536	0.629
<i>Heterotheca villosa</i>	0.005	0.429	0.651
<i>Artemisia campestris</i>	0.005	0.393	0.429
<i>Oxytropis splendens</i>	0.005	0.393	0.79
<i>Allium textile</i>	0.005	0.357	0.855
<i>Oxytropis sericea</i>	0.005	0.357	0.502
<i>Packera cana</i>	0.005	0.357	0.326
<i>Potentilla hippiana</i>	0.005	0.357	0.42
<i>Androsace septentrionalis</i>	0.005	0.321	0.713
<i>Eriocoma nelsonii</i>	0.005	0.286	0.598
<i>Castilleja lutea</i>	0.005	0.25	0.591
<i>Poa compressa</i>	0.005	0.25	0.529
<i>Erysimum inconspicuum</i>	0.005	0.214	0.661
<i>Poa interior</i>	0.005	0.214	0.759
<i>Agoseris glauca</i>	0.01	0.714	0.232
<i>Linum lewisii</i>	0.01	0.286	0.466
<i>Hedysarum sulphurescens</i>	0.015	0.607	0.319
<i>Solidago spp.</i>	0.025	0.25	0.44
<i>Calochortus apiculatus</i>	0.04	0.357	0.239

Species	p value	Fidelity	Specificity
<i>Poa secunda</i>	0.04	0.143	0.521
<i>Bromus pumpellianus</i>	0.05	0.25	0.423
Spiraea Shrubland			
<i>Spiraea betulifolia</i>	0.005	1	0.535
<i>Phacelia sericea</i>	0.005	0.667	0.424
<i>Agoseris glauca</i>	0.005	0.556	0.272
<i>Penstemon albertinus</i>	0.005	0.5	0.46
<i>Ribes viscosissimum</i>	0.005	0.5	0.405
<i>Draba aurea</i>	0.005	0.444	0.453
<i>Eurybia sibirica</i>	0.005	0.444	0.37
<i>Agrostis scabra</i>	0.005	0.333	0.325
<i>Tragopogon dubius</i>	0.005	0.333	0.391
<i>Campanula alaskana</i>	0.01	0.833	0.213
<i>Elymus lanceolatus</i>	0.015	0.167	0.555
<i>Sabulina rubella</i>	0.025	0.333	0.284
<i>Symphyotrichum laeve</i>	0.04	0.556	0.19
<i>Penstemon lyallii</i>	0.04	0.333	0.287
Lodgepole Pine Forest			
<i>Pinus contorta</i>	0.005	1	0.855
<i>Chimaphila umbellata</i>	0.005	0.611	0.893
<i>Calamagrostis rubescens</i>	0.005	0.556	0.455
<i>Clintonia uniflora</i>	0.01	0.556	0.478
<i>Osmorhiza depauperata</i>	0.015	0.278	0.48
<i>Hieracium umbellatum</i>	0.015	0.222	0.356
<i>Pyrola asarifolia</i>	0.02	0.222	0.324
<i>Pyrola chlorantha</i>	0.025	0.278	0.38
<i>Alnus alnobetula</i>	0.035	0.333	0.427
Englemann Spruce-Subalpine Fir Forest			
<i>Picea engelmannii</i>	0.005	0.929	0.62
<i>Arnica cordifolia</i> or <i>latifolia</i>	0.005	0.929	0.364
<i>Orthilia secunda</i>	0.005	0.714	0.376
<i>Goodyera oblongifolia</i>	0.005	0.643	0.37
<i>Galium triflorum</i>	0.005	0.571	0.352
<i>Menziesia ferruginea</i>	0.005	0.571	0.456
<i>Viola orbiculata</i>	0.005	0.571	0.296
<i>Osmorhiza berteroi</i>	0.005	0.393	0.52
<i>Tiarella trifoliata</i>	0.005	0.286	0.867
<i>Lonicera utahensis</i>	0.04	0.464	0.321
Alpine Tundra			
<i>Saxifraga austromontana</i>	0.005	0.636	0.772
<i>Potentilla glandulosa</i>	0.005	0.545	0.423

Species	p value	Fidelity	Specificity
<i>Penstemon ellipticus</i>	0.005	0.455	0.565
<i>Carex raynoldsii</i>	0.01	0.227	0.76
<i>Cystopteris fragilis</i>	0.015	0.273	0.363
Disturbance Followers			
<i>Chamaenerion angustifolium</i>	0.005	1	0.645
<i>Dracocephalum parviflorum</i>	0.005	0.5	0.919
<i>Geranium bicknellii</i>	0.005	0.5	0.945
<i>Sambucus racemosa</i>	0.01	0.286	0.679
<i>Elymus glaucus</i>	0.03	0.286	0.388