QUANTIFYING PLANT COMMUNITY CHANGE AT WATERTON LAKES NATIONAL PARK OVER THE PAST 25 YEARS

JED IMMANUEL LLOREN
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Dr. J.L. McCune Thesis Supervisor	Assistant Professor	PhD
Dr. L. Flanagan Thesis Examination Committee Member	Professor	PhD
Dr. E. Schultz Thesis Examination Committee Member	Professor	PhD
Dr. L. Chasmer Thesis Examination Committee Member	Assistant Professor	PhD
Dr. R. Laird Chair, Thesis Examination Committee	Associate Professor	PhD

DEDICATION

This thesis is dedicated to those that battle with mental illness. May you find the strength within yourself to keep pushing forward and achieve everything you desire.

ABSTRACT

Plant communities are changing in response to natural and anthropogenic drivers. However, we know little about how different drivers have affected Rocky Mountain plant communities over the past few decades. In 2017, a wildfire burned 50% of the vegetation at Waterton Lakes National Park, located in Canada's southern Rocky Mountains. Using re-surveys of vegetation plots established in the 1990s, I quantified changes in plant community diversity and composition over the past two decades. I found that fire severity interacted with human disturbance to affect species richness and community composition. I also found that burned and unburned plots are experiencing diverging trajectories. Herbaceous and short-lived species have become more prominent in burned plots, whereas unburned plots are becoming increasingly characterized by woody species. Ecologists should continue conducting legacy studies as they have the potential to expand our theoretical understanding of community assembly and inform management decisions.

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CHAPTER 1: INTRODUCTION

1.1 Background

At a global scale, plant diversity is declining (Corlett 2016; IUCN 2020). It is estimated that 40% of the world's plant species are currently at risk of extinction (Royal Botanic Gardens Kew 2020). Humphreys et al. (2019) found that 315 plant species have gone extinct from 1900 to 2018, and an additional 256 disappeared prior to 1900. However, at the local scale (i.e. scales less than $1000m^2$) plant species richness has often stayed constant, or even increased (Vellend et al. 2013a). These patterns have been revealed by so-called *legacy studies*: re-surveys of previously established and spatially referenced plots to measure local changes in plant communities over time. Thus, by conducting legacy studies, we can determine plant community baselines and more accurately track changes over time.

Legacy studies from around the world have shown that, at the plot-level, plant communities can exhibit a wide range of trajectories. For example, Beauvais et al. (2016) found that understory plant species richness tripled between 1977 and 2013 in a suburban protected area near Montreal. This gain resulted from an increase in both native and exotic plant species, driven by stand maturation and forest regeneration after a canopy-disrupting disturbance. In contrast, Damschen et al. (2010) found sharp declines of about 75% in herbaceous species richness in mountain forest plant communities over 60 years in Oregon. The authors linked their findings to a warming climate, as the species that declined the most were those not tolerant of warm or dry conditions. Hale et al. (2008) found that a decrease in (1) pioneer and (2) historically dominant species was offset by the colonization of new species, resulting in no significant change in local scale species richness in temperate floodplains in Wisconsin over a span of 50 years. However, although there was no net change in species richness, species composition changed quite dramatically over that period. When considering the evidence provided by these legacy studies, it is clear that we cannot assume that local species richness is also declining over time even if we know that global diversity is decreasing. They also show that major changes in community composition may be occurring at local sites, even if species richness has remained stable over time. These changes in community composition may reveal even more information about the effects of drivers of community change than simply counting the number of species.

In addition to shifts in species composition at the local scale, the beta diversity of plant communities in a region can change over time. Whittaker (1972) describes beta diversity as the degree of differentiation between local communities. A region with high beta diversity will feature communities that differ greatly from each other in terms of community composition. In contrast, a region with low beta diversity will feature communities that have many of the same species in common. Biotic homogenization, or a loss in beta diversity, occurs when local plant communities within a region become more similar to each other in terms of their species composition (Olden and Rooney 2006). Biotic homogenization has been found in many legacy studies, including some in Canada. For example, Savage and Vellend (2015) resurveyed 48 forest plots in southern Quebec, finding that the average species richness at each plot increased by about 6.5 species, 42 years after the original surveys. However, they noted that significant biotic homogenization had occurred due to plant communities at higher elevations converging towards similar compositions as low elevation plant communities over time. Biotic homogenization is an important concept to include in studies of plant community change because it can reveal the loss of unique and specialist species at the regional scale even while diversity is increasing at local scales.

Our ability to measure changes at the local scale depends on the availability of data from previous years to determine changes over time. We can then link these changes to potential drivers and determine possible mechanisms for plant community change. Legacy studies in Canada have linked drivers such as climate change and human disturbance to changes in plant communities. For example, using re-surveys of three sites in Quebec, Becker-Scarpitta et al. (2019) compared changes in plant community composition over a 40-year period. They found that increases in species richness and shifts in composition were greatest at the site that experienced the strongest degree of warming over the study period. Another study conducted by McCune and Vellend (2013) on Vancouver Island linked human disturbance to an increase in plant species richness over a 40-year study period. Like the legacy studies conducted in Quebec, the authors found a significant decrease in beta diversity, in this case caused by an increase in disturbance associated species. However, across many more parts of Canada, like the southern Rocky Mountains, we still have no information regarding how local plant communities have changed over time. Plant communities in these areas have experienced many potential stressors over the past century and decades. For example, the lengthening of fire return intervals in some parts of the southern Rocky Mountains has been found to cause forest encroachment – the movement of forests into grassland areas (Levesque 2005; Stockdale et al. 2019). In addition, these areas have experienced increased human disturbance due to rising amounts of recreation use. At Waterton Lakes National Park, visitor numbers have doubled between 1994 and 2016 (Parks Canada 2008; Parks Canada 2019a). Finally, recent catastrophic wildfires that have occurred after long periods of fire suppression can cause significant changes in plant communities (Crawford et al. 2001; Tuner et al. 1997).

In this study, I investigated the effects of natural drivers, anthropogenic factors, and the interactions between them on plant communities in Waterton Lakes National Park (WLNP) over the past 20 to 25 years using a dataset which incorporates repeat field surveys at previously established sites. Because about 50% of the vegetation at WLNP was burned in the high-severity 2017 Kenow Wildfire (Greenaway et al. 2018), I was able to contrast the responses to changes due to succession and increased human pressures in unburned plots to the immediate changes seen in burned plots. Since my surveys were conducted soon after the Kenow fire, they will also serve as a new baseline for documenting the trajectory of plant community change following a severe wildfire in this region.

1.1.1 Drivers of plant community change

Climate change is an important driver of plant community change. Warming temperatures and drier summers have caused more severe and frequent wildfires (Miller et al. 2009). In some cases, wildfires can increase species richness and cause a divergence in species composition from nearby unburned sites (Mehlman 1992). However, this may not occur in all vegetation types. For example, Foster et al. (2017) describe a positive correlation between fire frequency and species richness in woodlands, a negative response in heaths, and no effect in forests. The changing climate has also been linked to shifts in species ranges allowing species to colonize new areas and invade established communities. Chen et al. (2011) found that warming temperatures were causing terrestrial species to shift in elevation at a rate of 11.0m per decade and to higher latitudes at a rate of 16.9km per decade. Tracking changes over the long-term using historical data and repeated surveys will help strengthen our theories about how plant communities respond to these changes.

Although a warming climate has increased fire frequency and severity in some regions, fire suppression by humans, which was prominent in North America during the early and mid-20th century, caused intervals between fire events to lengthen compared to pre-settlement baselines (Stockdale et al. 2019). Prior to the 1900s, fire return intervals in montane ecosystems in southern Alberta were estimated to be between 26 to 35 years. Since the introduction of intense fire suppression and the abolishment of fire use by First Nations in the 1900s, fire intervals in those areas are now estimated to range from 84 to 104 years (Rogeau 2016). Similarly, the upper foothills region of south-western Alberta has seen fire return intervals lengthen from about 39 years prior to the 1900s to 104 years after the introduction of fire suppression in the 1900s (Rogeau 2016). Fire suppression leads to an increase in woody species density as trees and shrubs reproduce and grow without interference by fire. As canopies densify, a decrease in shade intolerant herbaceous species follows (Lydersen et al. 2013), as less light reaches the understory. In turn, there is an increase in shade tolerant species (Cole 1981). Fire suppression has also been known to reduce the proportion of species that are adapted to fire, resulting in a shift in composition towards fire intolerant species (Cole 1981; Keane et al. 2002). These findings illustrate the importance of assessing changes in plant communities long unaffected by fire.

Landscape change by humans also causes changes in plant communities. For example, deforestation to make way for trails and roads can change landscape context – the amount and configuration of vegetation on the landscape. The landscape context of a plant community, such as the distance to the forest edge, can affect species richness and composition. For instance, in a protected park in France, forest edges were found to host larger numbers of forest and grassland specialist species compared to adjacent habitats, resulting in greater species richness and diversity at these sites (Burst et al. 2016). Using legacy data in the Saanich Peninsula, McCune and Vellend (2015) found that disturbance associated, annual, exotic plants species were more likely to colonize areas with greater road density on the surrounding landscape. As humans continue to change landscapes, we must incorporate measures of landscape context when studying the responses of plant communities over time.

In addition, there can be interactions between the effects of natural disturbances, landscape context, and other environmental factors in driving plant community change. For example, landscape context can influence the responses of plant communities after a wildfire. Burned plots near trails may have a higher likelihood of invasion by exotic plant species because of unintentional transportation of plant propagules by recreational users (Daniels et al. 2019). In a study of plant communities in Ottawa, Canada, Lloren et al. (2020) found that plots which were more severely damaged by an ice storm saw a greater decrease in species richness than lightly damaged plots after 20 years, but only if they were far from the edge of the forest. Therefore, because of interactions between changing natural disturbance regimes, environmental factors, and anthropogenic pressures, studying their effects on plant communities simultaneously will help us better predict future plant assemblages in response to these disturbances.

1.1.2 Documenting winners and losers

While understanding how drivers of change affect plant communities can be useful, those studies focus more on the changes that can occur on a broader scale. They do not provide much information on how certain species are directly affected over time. Therefore, it is also important to determine which species are increasing or declining over time. Doing so will allow us to test whether these “winners” and “losers” are associated with certain traits, which may indicate which types of species are likely to persist in the future. In addition, identifying the traits of winners and losers can help to further identify drivers of change. For example, the proliferation of exotic and disturbance associated plant species implicates human disturbance as a major driver of change (McCune and Vellend 2013). Similarly, after natural disturbances like wildfires, plants with short lifespans, shorter height at maturity, and smaller seed size tend to succeed because these traits allow them to quickly colonize disturbed habitats (Shyrock et al. 2014). Abella and Fornwalt (2015) observed a surge in short-lived forbs after a large wildfire in Colorado. Evaluating plant traits can also lead to rejecting hypotheses about the drivers of change. In Great Britain, Smart et al. (2003) hypothesized that greater nutrient availability would lead to a shift towards nutrient-loving plant species from the 1960s to the 1990s. However, they found that this pattern did not occur in all habitats. Once winner and loser species are determined, we will be able to create and implement conservation efforts more effectively. For example, we will be able to highlight which groups of species could be at greater risk of declining in the future. For example, shade tolerant, native species could be more at risk than shade intolerant exotics after a wildfire.

1.1.3 The Study Site

Waterton Lakes National Park (WLNP; 49.0833^{o}N, 113.9167^{o}W) is located in southwestern Alberta, Canada, bordered by British Columbia and Montana to its west and south, respectively. It is unique in that it encompasses foothills parkland, montane, subalpine, and alpine ecoregions all in a relatively small area (505km^2). The park has experienced natural disturbances (e.g. the 1998 Sofa and 2017 Kenow Wildfires), and increasing human disturbance (trails, development, recreational use) over the past few decades. Therefore, it is an ideal place to study the effects of these factors on plant communities. From 1994-99, Parks Canada established 330 vegetation plots for the Ecological Land Classification (ELC) project (Achuff et al. 2002). The purpose of the project was to compile an inventory of landforms, soils, and vegetation within the park. In September 2017, the Kenow Fire burned 50% of the park's vegetation, affecting 138 of the ELC plots (Greenaway et al. 2018). By conducting re-surveys at a subset of plots within the previously established network of vegetation sites, I am able to quantify changes in the species richness of each plot and shifts in species composition over the past two decades.

1.2 Objectives

The overarching goal of this research project is to quantify changes in plant community diversity and composition in WLNP over the past 25 years, and to determine the mechanisms driving these patterns. This project has the following objectives:

1. Quantify the magnitude of change in the diversity and species composition of plant communities in Waterton Lakes National Park over the past 25 years.

2. Determine whether patterns of change are predictable based on fire history, environmental factors (i.e. elevation, slope, aspect, soil drainage), or proximity to anthropogenic disturbance.
3. Test for interactions between environmental factors (e.g. elevation, slope, fire severity) and anthropogenic disturbance on the measured changes in diversity or species composition over time.
4. Determine which species have increased or declined over time and whether this is predictable based on species' traits.

1.3 Thesis organization

This thesis contains four chapters. The two chapters following the introductory chapter are prepared as standalone manuscripts which aim to address the thesis objectives.

In Chapter 2, I quantify the changes in plant species richness and composition in WLNP since the mid-1990s and test the role of wildfire, edaphic conditions, topography, and anthropogenic disturbance in driving these changes. I test the hypotheses that humans or natural pressures are the main drivers of plant community change at WLNP. I predict that plots located at lower elevations and near roads and trails would see greater change if humans have been the primary driver of change. If natural pressures drive changes in these communities, then I expect to see a smaller influence of trails and roads and greater change in areas that were affected by the 2017 Kenow Fire. This chapter incorporates objectives 1-3.

In Chapter 3, I use an indicator species analysis to determine which species have significantly increased ("winners") or declined ("losers") since the original surveys. I then test whether disturbances (i.e. 2017 Kenow Fire and humans) or natural succession have been the main driver of change over time. If disturbances are the main driver of plant change, then plant traits that are associated with high colonization ability (e.g. lighter seed mass, shorter maximum height, shade intolerance) and association with disturbance (e.g. exotic species) should characterize the winners, especially in post-fire communities. If natural succession has been the main driver of change over time, then plants with traits associated with greater competitive ability (e.g. taller maximum height, shade tolerance) should have increased over the past 25 years in unburned plots. As such, the chapter addresses objective 4.

Chapter 4 ties together the findings of this thesis in a conclusion. Here, I also discuss the limitations of my study and suggest possible avenues for future research.

CHAPTER 2: THE ROLES OF WILDFIRE, ENVIRONMENTAL FACTORS, AND HUMAN DISTURBANCE ON PLANT COMMUNITY CHANGE OVER 25 YEARS

2.1 Abstract

Although plant diversity is declining at the global scale, legacy studies have shown varying trends in plant community change at the local scale. However, there have been relatively few legacy studies in Canada. Due to changing fire regimes and increasing human recreational activity, these natural and anthropogenic pressures may be driving changes at the local scale in the southern Canadian Rocky Mountains. In 2017, about 50% of the vegetation at Waterton Lakes National Park (WLNP) was affected by wildfire, which allows me to compare how the trajectory of these burned communities differs from unburned areas. Comparing plant community data from surveys conducted in WLNP in the 1990s to re-surveys in 2019 and 2020, I measured changes in plot-level species richness, species composition, and beta diversity over time, and tested for correlations between human disturbance, wildfire, environmental variables, and their interactions on these changes. Across all plots, I found that the total number of species present at WLNP increased from 403 in the original surveys to 426 in the re-surveys. Plot-level species richness significantly increased by an average of 12% over the study period. There was a significant shift in composition across all plots, but beta diversity declined significantly only among burned plots. Plots at higher elevations tended to lose species over time, especially those that burned in the Kenow Fire. There was also a significant interaction between fire severity and human disturbance: changes in local community composition were greater farther from trails in unburned areas but increased closer to trails in

moderately burned plots. This study emphasizes the need to consider the effects of human disturbance and natural pressures in unison to accurately predict trajectories of plant community change.

2.2 Introduction

Globally, plant diversity is declining (Corlett 2016; IUCN 2020). In 2007, the International Union for Conservation of Nature reported that 8,457 plant species (or 2% of all plants) were listed as threatened. At the time, only 4% of all plant species had been evaluated (IUCN 2007), which suggests that the true number of threatened plants is much higher. In 2020, it was estimated that 40% of all plant species are threatened by extinction (Royal Botanic Gardens Kew 2020). However, at the local scale, different patterns have emerged. A meta-analysis conducted by Vellend et al. (2013a) examined changes in species richness at plots which were re-surveyed at least five years apart. They found that at the local scale (i.e. less than $1000m^2$), the distribution of changes in species richness centered around zero. This means that although there is a global decline in plant species diversity, at smaller scales, it is possible to see communities increase, decrease, or exhibit no net change in species richness over time.

However, species richness is just one aspect of plant communities. A community that shows no net change in species richness over time does not indicate that there has been no turnover in the species present. For example, a wildfire may cause fire-sensitive species to be extirpated from a local site, causing species richness to go down. However, if new fire adapted species from nearby communities can move into these burned areas and replace the extirpated species, it is possible for that community to show no change in richness over time, even though the composition is vastly different (Turner et al. 1997). In addition, the distinctiveness of local communities within a region can change over time. Beta diversity is a measure of the degree of differentiation between local communities within a region. Biotic homogenization – a decrease in beta diversity – can occur when unique species are lost or common species colonize many sites (Olden and Rooney 2006). Biotic homogenization is a key concept to include in studies of plant communities because it can indicate the loss of unique species at a regional scale, despite potential species gains at the local scale.

One way that we can track changes in plant communities over time is by conducting legacy studies. These are studies which re-survey previously established and spatially referenced plots to determine changes over time (Vellend et al. 2013b). A handful of legacy studies have examined plant community changes in Canada. Beauvais et al. (2016) conducted re-surveys of 133 vegetation plots in Mont-Saint-Bruno National Park, near Montreal, 36 years after the original surveys. While they found that a large increase in native species caused understory species richness to triple, the increase also led to biotic homogenization. Savage and Vellend (2015) re-surveyed 48 forest plots in southern Quebec 42 years after the original surveys. They found that the average species richness at each plot increased by about 6.5 species, representing a 27% gain on average. They also noted significant biotic homogenization across the study area as plant communities at higher elevations converged towards similar compositions as plant communities at lower elevations. A study by Becker-Scarpitta et al. (2019) later expanded on these results by comparing trends in community change from three protected parks in Quebec (Gatineau Park, Forillon National Park, and Mont Mégantic National Park). While there was no significant change in species richness at Forillon, the Mont Mégantic and Gatineau surveys revealed significant increases in species richness of 27% and 38%, respectively. There was no significant reduction in beta diversity over time. However, the authors did note a significant shift in community composition at all three locations driven by warming temperatures. Interestingly, they found that greater degrees of change in both species richness and community composition occurred at the site that experienced the greatest warming in temperature. Finally, on southern Vancouver Island, British Columbia, McCune and Vellend (2013) conducted re-surveys of 184 plots about 40 years after the original surveys. They found that although species richness tended to increase at the plot-level, similar species established across many plots resulting in biotic homogenization. The authors identified human disturbance as the main driver of change in this area because exotic and disturbance associated species had increased the most over time.

These legacy studies have all documented an increase in local species richness and biotic homogenization. Biotic homogenization was mainly driven by the spread of common species, warming temperatures, and human disturbance. However, these studies represent a very small sample of the plant communities and environments in Canada. For parts of Canada such as the southern Rocky Mountains, the magnitude of local scale changes in plant communities over the past few decades, and the main drivers of those changes, are unknown. It is important that we conduct long-term studies that investigate local scale changes in these plant communities. Doing so will allow us to identify areas that are more susceptible to invasion by exotic species or encroachment by woody species, and therefore may require more immediate and intense treatment to protect sensitive or culturally valued native plant species. It will also add to our current knowledge regarding community assembly, and help ecologists better predict the potential trajectories of plant communities as the influences of the warming climate and humans continue to grow.

In this study, I re-surveyed a subset of plots first established in the 1990s as part of the Ecological Land Classification project at Waterton Lakes National Park (WLNP), in the southern Rocky Mountains of Alberta, Canada. The Park is notable as it features four distinct ecoregions (foothills parkland, montane, subalpine, and alpine), within a relatively small area (505km^2). As a result, large environmental gradients (i.e. elevation, aspect, soil type) are present at the Park, which support a diverse range of plant communities. It has also experienced wildfires in its recent history (1998 Sofa and 2017 Kenow Wildfires) and has a moderate level of human disturbance (trails, development, recreational use), making it an ideal location to study the long-term changes in plant communities in response to natural and human disturbances.

Due to the protected nature of WLNP (i.e. relatively little development and landscape fragmentation), wildfires, climate change, and successional processes could be the main drivers of community change. If this hypothesis is correct, I predict an increase in species richness in burned plots, as wildfires have been shown to result in an increase plant species richness even just 2-3 years after the disturbance (Crawford et al. 2001; Reilly et al. 2006). In addition, I expect to see pronounced shifts in local community composition and biotic homogenization at burned plots as a set of fire adapted species establish in these affected areas (Strand et al. 2019). There may also be an increase in species richness at higher elevations if warming temperatures are allowing more species to colonize plots at higher elevations (Savage and Vellend 2015). In unburned plots, I expect that the ongoing encroachment of trees into grassland areas, due to lengthening fire return intervals as described by Stockdale et al. (2019), will lead to a decrease in local species richness due to a reduction of resources (i.e. light) being provided to the understory. Finally, if forest encroachment is in fact driving change in unburned plots, then I expect to see a decrease in beta diversity as common shade tolerant species persist while a more diverse suite of shade intolerant herbs and grasses decline (Beauvais et al. 2016).

Although WLNP is a protected area, it is possible that increasing visitor numbers and recreation use has caused human disturbance to be the main driver of plant community change over the past two decades. If this is true, then I expect to see an increase in local species richness due to an increase in exotic and disturbance associated species in most plots, as has been found elsewhere in Canada (e.g. Beauvais et al. 2016, McCune and Vellend 2013). In addition, I predict that increases in local species richness and shifts in community composition will be greater in plots closer to roads and trails, and at lower elevation, because the influences of human disturbances should be greatest in these areas (Queiroz et al. 2014, McCune and Vellend 2015). A widespread increase of common exotic and disturbance associated species would also result in biotic homogenization at WLNP.

It should be noted that natural and human disturbances are not mutually exclusive as the effects of natural drivers and anthropogenic disturbance can interact (Chazdon 2003; Hermy and Verheyen 2007; Lloren et al. 2020). For example, plant communities that have recently been severely burned may be more susceptible to colonization by exotic species facilitated by human disturbance (Daniels et al. 2019). As such, I hypothesize that interactions between natural and human disturbances will influence community change at WLNP. I predict that the greatest degree of change in species richness and composition will be found in areas that were burned in the Kenow Fire and close to human activity (i.e. plots closer to trails and roads and at lower elevation).

2.3 Methods

2.3.1 Study area

Waterton Lakes National Park (WLNP; 49°08’N 113°92’W; Figure 1), located in southwestern Alberta, Canada, was designated a National Park in 1930 (Parks Canada 2020a). In 1979, the United Nations Educational, Scientific and Cultural Organization (UNESCO) designated WLNP as a biosphere reserve. In 1995, UNESCO also designated the Park as a World Heritage Site based on its biological significance within the Western Cordillera region (Parks Canada 2020b).

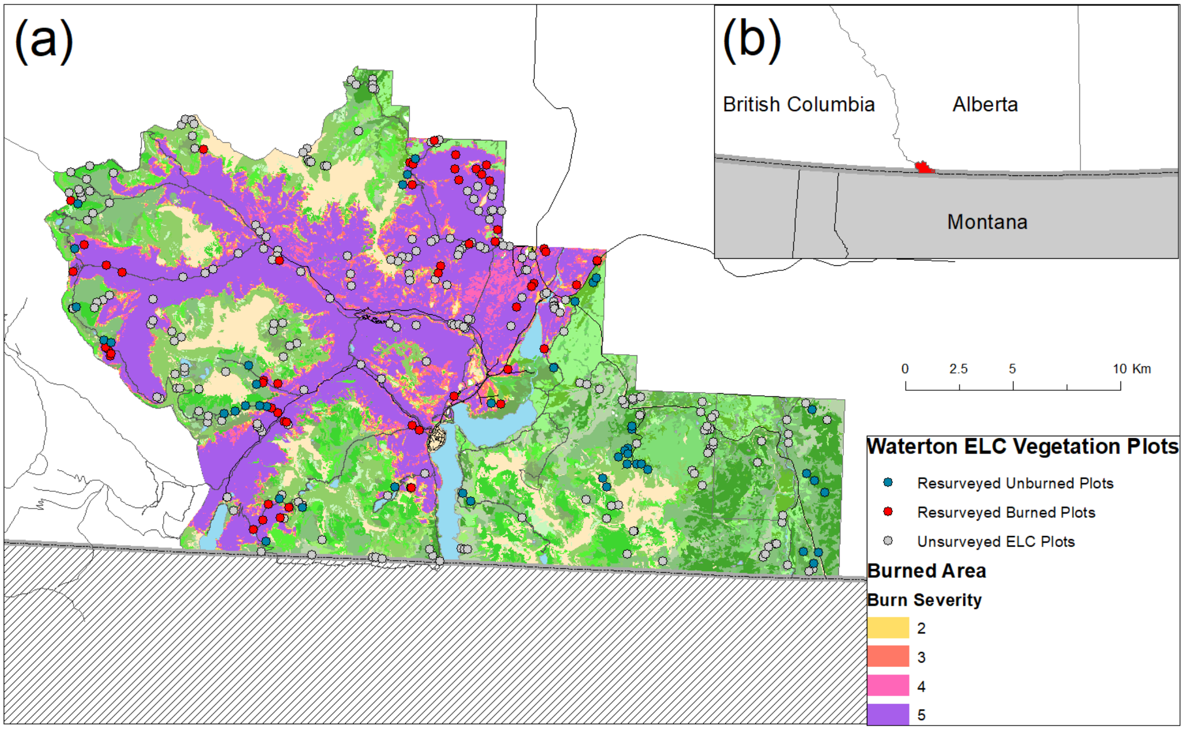

Figure 1 (a) Map outlining the boundaries of Waterton Lakes National Park. Vegetation within the park (green shading), mountainous areas (cream), waterbodies (blue), and surrounding areas within Alberta (white) and the United States (hatched) are included. Areas burned in the 2017 Kenow Fire are indicated in yellow, orange, pink, and purple. The points show the locations of all plots, including those not resurveyed. (b) The location of the study area (red) within the province of Alberta, and in relation to the nearby areas in Canada (white) and the United States (grey).

WLNP contains four ecoregions (foothills parkland, montane, subalpine, and alpine), and lies within the Montane Cordillera ecozone (Parks Canada Agency 2017). The ecoregions vary greatly in their climatic conditions. For example, the foothills parkland ecoregion, the portion of the park found at the lowest altitude (lowest point = 1280m above sea level), experiences the least growing season precipitation (GSP; annual mean = 377mm) and the warmest temperatures (mean annual temperature (MAT) = 3°C). In contrast, the alpine ecoregion, found at the highest altitude (highest point = 2940m above sea level), has an annual mean GSP of 472mm and a MAT of -2.4°C (Natural

Regions Committee 2006). This variation in climatic conditions over a relatively small area results in a correspondingly diverse range of plant communities. In general, as altitude increases plant species must be tolerant of more extreme conditions (e.g. increased winds and colder temperatures), leading to decreasing plant diversity but also an increase in plant species that are more resilient to harsh conditions (Parks Canada 2018a). The observed decrease in plant diversity at higher elevations occurs because there are fewer plant species that are adapted to these intense alpine conditions.

The vegetation in the foothills parkland ecoregion features fescue grasslands and aspen (*Populus tremuloides*) groves. The montane and subalpine ecoregions are characterized by coniferous forests and vegetation dominated by lodgepole pine (*Pinus contorta*). However, the subalpine forests are differentiated by the co-dominance of Engelmann spruce (*Picea engelmannii*). The alpine ecoregion vegetation is mainly composed of low-laying shrubs (e.g. *Dasiphora fruticosa*; Strong and Leggat 1992). Over 1000 species of vascular plants are recorded in WLNP. These include more than 175 provincially rare, 50 nationally rare, and 2 globally rare plant species. Over 20 plant species are endemic to the Waterton area (Parks Canada 2018b).

Wildfires are the most prominent natural disturbance in WLNP. Two large lightning-ignited, non-intersecting wildfires (1998 Sofa Fire and 2017 Kenow Fire) have occurred over the past three decades. In southern Alberta, wildfires are estimated to occur in intervals of about 100 years (Stockdale et al. 2019). The most recent wildfire known to have occurred near the study area, prior to those two wildfires, was the 1910 southern Alberta wildfire (Arthur 2014). The 2017 Kenow Wildfire burned approximately 35,000 hectares including about 50% of the vegetation at WLNP (Figure 1). Of that, 75% burned at extreme severity (Greenaway et al. 2018). Occasionally, prescribed burns are conducted in WLNP to reduce aspen encroachment, improve grassland condition, and prepare areas for whitebark pine planting. In 2006, Parks workers ignited the largest prescribed fire at WLNP burning 1,600 hectares of prairie (Parks Canada 2019b).

Recreational use accounts for most of the human disturbance at WLNP. In 2016, 536,864 visitors came to WLNP over the course of the year, compared to 346,573 visitors in 1996 (Parks Canada 2008; Parks Canada 2019a). WLNP contains the hamlet of Waterton Park, which had a year-round population of about 100 inhabitants in 2016 (Statistics Canada 2017). Although logging is prohibited in the Park, WLNP occasionally provides permits to the Kainai and Piikani nations to make harvest of trees for traditional use. However, these harvests are very small and selective in nature and are very unlikely to have affected the vegetation plots included in this study (*G. Alger pers. comm.*).

2.3.2 Data collection

From 1994-1999, Achuff et al. (2002) established 330 plots for the purpose of classifying the vegetation of WLNP for integration into the Ecological Land Classification (ELC) project. This project was conducted to create an inventory of resources (i.e. landforms, soils, vegetation) present at WLNP. As such, they divided areas of the Park into mapped polygons based on landform features, identifiable by aerial photographs, and non-randomly selected plots in areas of relatively homogenous vegetation that represented the predominant vegetation of each polygon area. The goal was to capture an accurate representation of the plant community types present in all areas of the Park. They surveyed 20m x 20m plots in forested areas, 15m x 15m plots in shrublands, and 10m x 10m plots in grasslands. The surveyors delineated the plots by pacing, after calibration with a metre tape, and recorded the coordinates of the plot centres using a handheld Global Positioning System (GPS). In 2000, WLNP workers corrected these coordinates using differential correction (*P. Achuff pers. comm.*). Differential correction is a method of correcting GPS coordinates that were scrambled by the U.S. Military prior to the year 2000 (Trimble Navigation 2004). The surveyors identified all vascular plant species found within the plots and visually estimated the approximate percent cover of each species in seven different height layers. Although visual estimates of plant cover could provide less accuracy in moderate ranges (i.e. 30 to 70 percent), this method is widely used by ecologists and has been shown to be a reliable measure of plant abundance in a variety of plant community types (Schulz et al. 2009). The seven layers were later compressed into the following four layers, as presented in the final ELC report: (1) all trees taller than five metres, (2) trees 2-5m tall, (3) trees and shrubs 0.5m to 2m tall, and (4) trees and shrubs less than 0.5m and all herbaceous species regardless of height. For each plot, the surveyors also used an altimeter, clinometer, and compass to record elevation, slope, and aspect, respectively. They also dug and examined soil pits in the field according to the guidelines given in the Canada Soil Information System to determine soil type and drainage (Day 1983). Plots were then classified into seven different drainage classes where 1 = very rapidly drained, 2 = rapidly drained, 3 = well drained, 4 = moderately well drained, 5 = somewhat drained, 6 = poorly drained, and 7 = very poorly drained.

In October 2017, WLNP workers used satellite imagery to map the burned area after the Kenow fire (Eagle Mapping Ltd 2018). To create the burn rating classes, they used Normalized Burn Ratio (NBR) values as published by Key and Benson (2006). This is based on satellite data where near-infrared (R4) and mid-infrared (R7) reflectance of vegetative areas is compared pre- and post-fire. First NBR is calculated separately for pre- and post-fire vegetation, as follows (Equation 1).

$$NBR = \frac{(R4 - R7)}{(R4+R7)} \qquad \text{Equation 1}$$

Healthier vegetation areas will have much greater near-infrared reflectance and low mid-infrared reflectance whereas recently burned areas will have low near-infrared reflectance and high mid-infrared reflectance. Then, the difference in infrared radiance (dNBR; Equation 2) from pre- and post-fire conditions is used to establish burn classes, as shown below:

$$dNBR = NBR_{prefire} - NBR_{postfire} \qquad \text{Equation 2}$$

Following the published values in Key and Benson (2006), burn classes in this study are defined using the following dNBR ranges: 1 (low severity) = -0.10 to +0.09, 2 = +0.10 to +0.269, 3 = +0.27 to +0.439, 4 = +0.44 to +0.659, and 5 (high severity) = +0.66 to +1.30.

In the summer of 2018, Parks Canada researchers visited 105 of the affected ELC plots and assessed burn severity to ground truth the satellite-based burn ratings. To do this, researchers followed the FIREMON Composite Burn Index protocol, which is based on observational assessments of fire damage (Key and Benson 2006). They established a 30m x 30m area at each of the visited ELC plots and divided the vegetation into five layers: (1) substrates, (2) herbs, low shrubs and trees (<1m in height), (3) tall shrubs and trees (1-5m), (4) intermediate trees (>5m), and (5) large trees (>20m). They then examined each layer for different indicators of fire damage (e.g. duff layer depth, % canopy mortality, char height) and recorded the appropriate score for each criterion, where the maximum score was 3 (high severity) and the minimum was 0 (unchanged).

For each layer, surveyors averaged these 0 to 3 values to determine the burn severity for that layer. The surveyors then averaged the scores across all layers, at the respective plot, to determine the plot's overall burn rating where the minimum score was 0 (unburned/unaffected) and the maximum was 3 (high severity). These final burn ratings were indexed and compared to the satellite layers constructed previously. These comparisons showed that the dNBR estimations were accurate, and I used those burn rating classifications in this study.

Using GPS coordinates and field notes, I re-located and re-surveyed 72 of the original plots from June to August 2019 and 32 plots between June and August 2020, for a total of 104 plots. The handheld GPS units used in the re-surveys have an accuracy of 3m to 5m. This means that some changes in terms of species gains or losses since the original surveys may be due to errors in plot re-location but, because I am examining change across all plots, I do not expect these re-location errors to bias the data in one direction or the other. It has also been shown that the use of GPS coordinates and/or field notes to re-survey semipermanent plots allows for robust analysis of decadal changes in vegetation despite modest errors in re-location (Kopecký and Macek 2015). Because six of the plots surveyed in the 2019 and 2020 seasons contained plant communities that did not match those given in the original surveys (i.e. a meadow instead of a forest in an unburned area), I excluded these from the study due to likely errors in the original coordinates. Of the 98 plots included in this study, 53 were burned in the Kenow Fire and 45 were not. I chose which plots to survey based on their accessibility, while also ensuring that the selected plot locations represented a wide range of elevation, slope, vegetation type, and distance from recreational trails. I delineated plots and conducted the re-surveys following the protocol from the original surveys. However, my protocol differed from the original surveys in that I always used measuring tapes to delineate the plot area, rather than pacing, and the layers I used during the vegetation surveys corresponded to the layers presented in the final ELC report. In addition, I placed a permanent marker at the plot centres so that future surveys can relocate the plots more precisely. On two occasions, I conducted surveys with Dr. Peter Achuff – one of the original surveyors – allowing me to better ensure consistency between the original survey and my re-surveys with respect to plot re-location, set up, and cover estimates.

I standardized plant species names across all surveys according to the Integrated Taxonomic Information System (https://www.itis.gov/). I lumped some species to the genus level where identification to species is difficult (e.g. *Danthonia sp*. includes *D. californica*, *D. intermedia*, and *D. parryi;* Supplementary Table 1). I collapsed the four vegetation layers into a single layer by summing the estimated percent cover of each species in all four layers prior to analysis.

2.3.3 Analyses

1. Regional scale responses

I first quantified changes in total species richness, average species richness, and community composition across all plots. For simplicity, I refer to the original survey period (1994,1995, and 1999) as “1994” and the re-survey years (2019 and 2020) as “2019”. I tallied the total number of species across all plots in each survey period, the total present in 2019 but not in 1994, the total present in 1994 but not in 2019, the total number of exotic species across all plots in each period, and the average number of exotic species in 1994 and 2019 per plot. I also calculated the proportion of species found at each plot in 1994 that were still present at the same plot in 2019. I then conducted tests for significant changes in local species richness (alpha diversity) and beta diversity across all survey plots between the two survey periods. To test for significant differences in species richness, exotic species richness, and relative abundance of exotic species between 1994 and 2019, I used Wilcoxon signed rank tests (Wilcoxon 1945). I repeated these tests for burned and unburned plots separately.

To test for changes in overall community composition and beta diversity, I conducted a permutational multivariate analysis of variance with 5,000 permutations (PERMANOVA; Anderson 2001) which tests for significant shifts in overall community composition across all plots and/or changes in variability in community composition among all plots between years. I included interactions between (1) year and burn status and (2) year and ecoregion to test if changes in community composition varied with burn status or in different ecoregions. A significant PERMANOVA test cannot differentiate between shifts in composition, changes in beta diversity, or both. Therefore, I also conducted a test for homogeneity of multivariate dispersions (PERMDISP; Anderson et al. 2006) which tests for differences in the variability in composition among plots (a measure of beta diversity) *only* in each group. I included year, burned status, and their interaction as predictors in the PERMDISP test. This test used 5,000 permutations. I ran the PERMANOVA and PERMDISP tests on a matrix of Bray-Curtis dissimilarities for each pair of plots based on the square-root transformed abundances of all species in each plot (Bray and Curtis 1957).

2. Plot-level responses

I built models to test the influence of burn severity, environmental conditions, and proximity to human disturbance on plot-level changes in species richness and composition between 1994 and 2019. The response variables were (1) net change in total species richness at each plot from 1994 to 2019 and (2) the shift in community composition within each plot as measured by the Bray-Curtis dissimilarity between each plot in 2019 and the same plot in 1994. Using the Bray-Curtis dissimilarity metric, a 0 indicates that the plot in 2019 has identical species composition as it did in 1994 (same species present, in the same abundances). A Bray-Curtis dissimilarity of 1 would indicate that the plot in 2019 has none of the species that were present in 1994. To analyse the net change in total species richness, I used a linear model. I used a generalized linear model with a beta binomial distribution to model dissimilarities at each plot because the response variable varies from 0-1 and is not binomial (i.e. not a measure of successes out of a number of trials).

I included six predictor variables and two covariates which represent different factors that could drive changes in species richness and composition (Table 1). I included starting species richness (i.e. species richness at each plot in 1994) to account for the tendency of species richness to revert to the mean over time (Bormann and Likens 1979). I included the difference in survey date between the original and re-survey to account for the fact that seasonal timing of vegetation surveys can influence whether certain species are detected (Burrows 2004). Due to logistical constraints, I was not able to re-survey every plot at the exact same time of year as in the original surveys. To represent the effects of the fire, I collapsed the burn severity ratings from the five categories given previously to two (1 to 4 = moderate, 5 = severe) and designated all unburned plots as fire severity = none. To represent environmental conditions that could influence the degree of change over time, I included elevation, slope, aspect, and soil drainage. I determined the aspect of each plot based on a 25m Digital Elevation Model (Alberta Environment and

Parks, Government of Alberta). Then I calculated the northness index using following function:

$$Northness = \frac{|(Aspect\ in\ degrees - 180)|}{180} \qquad \text{Equation 3}$$

Plots facing north will have a value of 1, south-facing plots will have a value of 0, and east or west facing plots will both have a value of 0.5.

I collapsed soil drainage from seven categories to three (1 and 2 = well drained, 3 = moderately well drained, 4 to 7 = poorly drained) to avoid categories with few or no plots. I also included the distance of each plot to the nearest trail or road to represent proximity to human disturbance. I used the *near* function in ArcGIS (ESRI 2020), which determines the nearest straight-line distance from a point of interest to the target feature (i.e. official and unofficial trails and roads at WLNP). I obtained the road and trail shapefiles from Parks Canada workers. They created the trail shapefiles based on GPS points taken in 2008 and manual corrections using aerial photographs. Before building the models, I checked for correlations between predictors (Pearson's r ≥ 0.70; Supplementary Table 2). I did not include ecoregion as a predictor because it was very highly correlated with elevation.

I also included four interactions between these predictors in each model. Because trails and roads can act as vectors for seed transport and well-drained soils have been shown to be ideal for plant development, I included an interaction between soil drainage and distance to the nearest trail or road. I also included an interaction between burn severity and distance to trails because previous studies have found trails to be a possible predictor of seedling establishment (e.g. Daniels et al. 2019), which may allow plots that were severely burned and close to trails to change in species richness or composition more significantly after the Kenow fire. I included the interaction between elevation and burn severity because previous studies have found that plant regeneration decreases with increasing elevation and that this response is amplified by burn severity where lower elevations gain more species and higher elevations tend to experience greater losses (e.g. Coop et al. 2010). Finally, I added an interaction between elevation and the distance to the nearest trail or road because while previous studies have found that roads can facilitate colonization (especially of disturbance-tolerant species; McCune and Vellend 2013), few species are able to survive at higher elevations. In addition, lower elevations are more heavily trafficked, thus the influence of human disturbance should be less evident at higher elevations. Therefore, if there is a significant interaction, the effects of trails and roads should be lower at higher elevations.

Table 1 Predictor variables used to model changes in species richness and community composition from 1994 to 2019.

Response variable	Predictor variable	Variable type (units/categories)	Predictor type
Change in species richness (2019-1994)	Species richness 1994	Continuous (count)	Covariate
	Difference in survey date (2019-1994)	Continuous (days)	
	Elevation	Continuous (metres)	Environmental
	Northness	Continuous (index)	
	Slope	Continuous (degrees)	
	Soil drainage	Categorical (poor, medium, well)	
	Burn severity	Categorical (unburned, moderate, severe)	Fire effects
	Distance to the nearest trail or road	Continuous (metres)	Human effects
	Soil drainage x distance to nearest trail or road	Categorical x continuous	Interaction
	Burn severity x distance to nearest trail or road	Categorical x continuous	
	Burn severity x elevation	Categorical x continuous	
	Distance to nearest trail or road x elevation	Continuous x continuous	
Bray-Curtis dissimilarity (2019-1994)	Difference in survey date (2019-1994)	Continuous (days)	Covariate
	Elevation	Continuous (metres)	Environmental
	Northness	Continuous (index)	
	Slope	Continuous (degrees)	
	Soil drainage	Categorical (poor, medium, well)	
	Burn severity	Categorical (unburned, moderate, severe)	Fire effects
	Distance to the nearest trail or road	Continuous (metres)	Human effects
	Soil drainage x distance to nearest trail or road	Categorical x continuous	Interaction
	Burn severity x distance to nearest trail or road	Categorical x continuous	
	Burn severity x elevation	Categorical x continuous	
	Distance to nearest trail or road x elevation	Continuous x continuous	

Before building the models, I standardized the predictor variables in both models by subtracting the mean and dividing by twice the standard deviation. For each response variable, I built a model containing all potential predictors and the four interactions described above. I then performed backward stepwise model selection using AIC to determine the minimum adequate model for each response variable (Venables and Ripley 2002). I ensured that residuals were not spatially autocorrelated using spline correlograms (Bjørnstad and Falck 2001) and checked for overdispersion in the beta binomial model using scaled residuals (Hartig 2020). Once I determined the minimum adequate model, I used marginal fitting of terms (drop1 test) to drop each term from the minimum adequate model to determine which predictors and interactions had a significant effect on the model once all other variables were accounted for. I used partial regression plots to show the relationships between the significant predictors of each model and the two response variables. These plots illustrate the conditional effect of each predictor on the response variable while holding all other predictors at their median, or at the value of the most common category for categorical predictors (Breheny and Burchett 2017). I report R^2 to describe the explanatory power of the linear model and pseudo-R^2 for the beta binomial GLM (McFadden 1973).

I conducted all tests in R version 3.5.0 and PRIMER v7.0.17 (Clarke and Gorley 2008; R Core Team 2018). I used the "arm" package to standardize the predictor variables in the linear models (Gelman and Su 2018). I fit the glm using the "betareg" and "glmmTMB" packages (Cribari-Neto and Zeileis 2010, Brooks et al. 2017). I created scaled residuals for fitted linear models using the "DHARMa" package to test for typical model misspecification problems (i.e. overdispersion; Hartig 2020). I used the "ncf" package to check for spatial autocorrelation (Bjørnstad and Falck 2018). I conducted stepwise model selection using the "MASS" package (Venables and Ripley 2002). I used the "visreg" package to graph the partial regression plots (Breheny and Burchett 2017). I conducted the PERMDISP and PERMANOVA tests using PERMANOVA+ for PRIMER (Anderson et al. 2008).

2.4 Results

2.4.1 Response across all plots

There were 403 species recorded across all 98 plots in the 1994 vegetation surveys, and 426 species in 2019. Of the species recorded in 1994, 77 were not found in 2019. 109 species were found in the 2019 surveys but not in the 1994 surveys (Supplementary Table 3, 4). The mean species richness per plot in 1994 was 25.89, compared to 29.09 in 2019. This difference in mean species richness between 1994 and 2019 was significant (Wilcoxon signed rank test, $p < 0.05$; Figure 2). On average, 49% of the species recorded in each plot in 1994 were still present in the same plot by 2019. There were 11 exotic species found in these plots in the original surveys, compared to 33 in the re-surveys. Of the 11 exotic species found in 1994, two were not found in 2019 (*Festuca ovina, Hypericum perforatum*). It should be noted that the record of *F. ovina* in this area is doubtful as other *Festuca* species may have been misidentified as *F. ovina* previously.

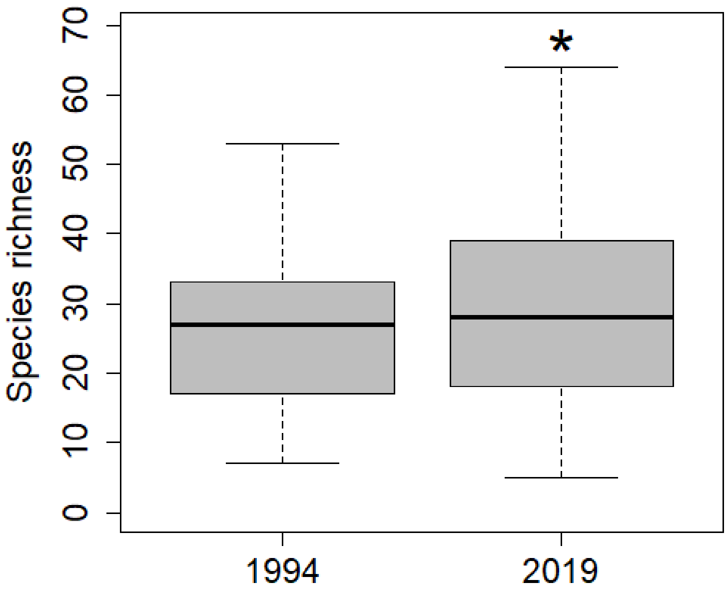

Figure 2 The distribution of species richness at each plot during the original and 2019 re-surveys. The black line indicates the median species richness for that survey. Whiskers are 1.5 times the interquartile range. * indicates $p < 0.05$ according to a Wilcoxon signed rank test.

Species richness at each plot varied greatly within each survey group. In 1994, the maximum species richness was 53 and the minimum was 7. This compares to a maximum species richness of 64 in 2019, and a minimum of 5. From 1994 to 2019, unburned plots significantly increased by 5.49 species on average (22.4%; Wilcoxon signed rank test, $p < 0.01$; Figure 3a), while burned plots experienced a non-significant average gain of 1.26 species (4.7%; Wilcoxon signed rank test, $p = 0.574$; Figure 3b). There was a significant increase in exotic species per plot between 1994 and 2019, from a mean of 0.6 exotic species per plot, to a mean of 1.6 exotic species per plot (Wilcoxon signed rank test, $p <0.01$). Burned plots experienced a significant increase of 1.55 exotic species per plot from 1994 to 2019 (Wilcoxon signed rank test, $p <0.01$), compared to a significant increase of 0.47 exotic species per plot in unburned plots (Wilcoxon signed rank test, $p <0.01$). There was a significant 2% increase in average relative abundance of exotic species per plot from 1994 to 2019 (from 1.03% in 1994 to 3.09% in 2019; Wilcoxon signed rank test, $p < 0.05$).

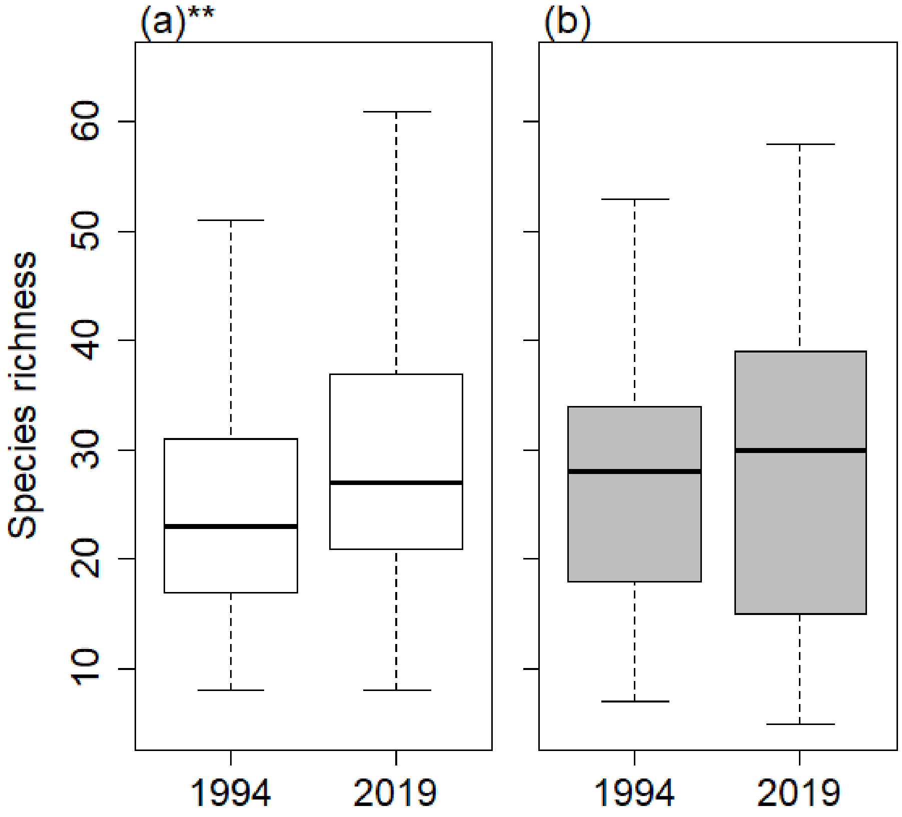

Figure 3 The distribution of species richness at each plot during the original and 2019 re-surveys in (a) unburned and (b) burned plots. The black line indicates the median species richness for that year. Whiskers are 1.5 times the interquartile range. ** indicates $p < 0.01$ according to a Wilcoxon signed rank test.

Across all plots, there was a significant shift in composition between 1994 and 2019 (PERMANOVA, $p < 0.01$). There was also a significant interaction between year and burn status (PERMANOVA, $p < 0.001$). A pairwise PERMANOVA test examining the interaction between year and burn status showed that only burned plots experienced a significant shift in composition (Pairwise PERMANOVA test, $p < 0.001$). There was also an interaction between year and ecoregion (PERMANOVA, $p < 0.05$; Table 2). The pairwise tests examining the interaction between year and each ecoregion showed that the montane, lower subalpine, and upper subalpine ecoregions experienced significant shifts in species composition between 1994 and 2019, whereas the foothills and alpine ecoregions did not.

Table 2: Pairwise PERMANOVA tests between 1994 and 2019 within each ecoregion.

Ecoregion	P-value
Foothills (n=18)	0.147
Montane (n=21)	< 0.05
Lower subalpine (n=30)	< 0.05
Upper subalpine (n=25)	< 0.01
Alpine (n=4)	0.448

Across all plots, there was no significant change in beta diversity between 1994 and 2019 (PERMDISP, $p = 0.589$). However, there was a significant interaction between year and burn status. Pairwise PERMDISP tests revealed a significant decrease in beta diversity for burned plots between 1994 and 2019 (Pairwise PERMDISP test, $p < 0.05$; Figure 4), but not for unburned plots (Pairwise PERMDISP test, $p = 0.215$).

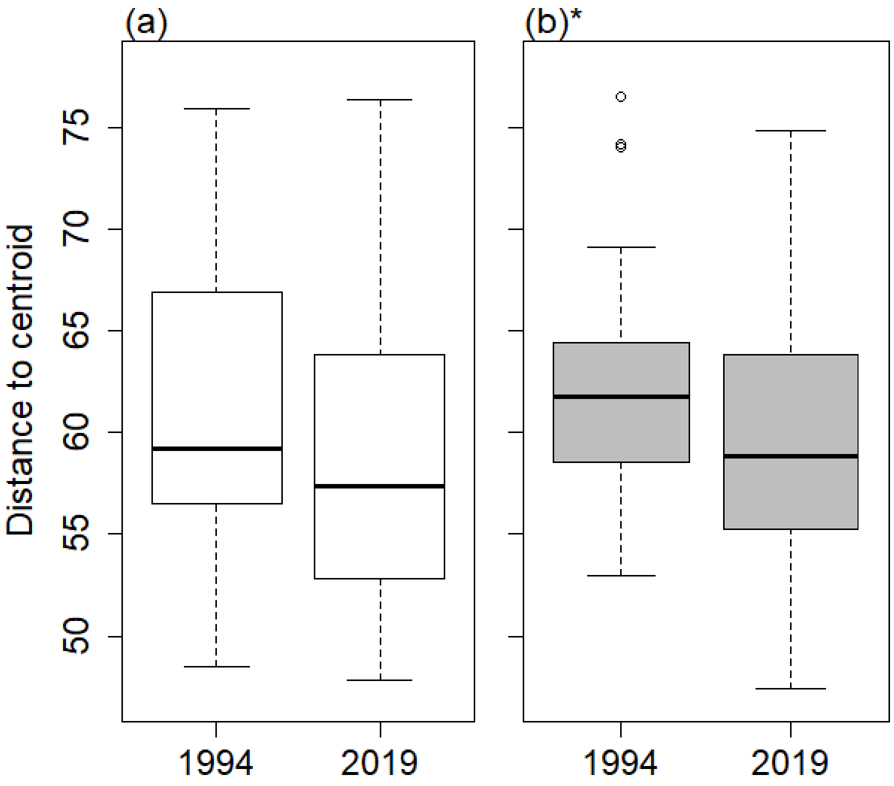

Figure 4 The distance to the multivariate centroid (a measure of beta diversity) of plots in 1994 and 2019 for plots that (a) did not burn in the 2017 Kenow fire and (b) plots that did burn in the 2017 Kenow fire. The black lines indicate the median distance to centroid for that survey group. Whiskers are 1.5 times the interquartile range. * indicates $p < 0.05$ in pairwise PERMDISP comparison.

2.4.2 Plot-level responses

The minimum adequate model for net change in species richness at each plot included species richness in 1994, distance to the nearest road or trail, and the interaction between burn severity and elevation (Figure 5). Of these, species richness in 1994 and the interaction between burn severity and elevation were significant predictors once all other factors in the model were accounted for, according to marginal fitting of terms (drop1 test; Table 3). The model explained about 22% of the variation in net change in species richness. Plots that had fewer species in 1994 were more likely to have a net gain in species compared to plots with higher starting species richness (Figure 5a). There was a significant negative correlation between change in species richness and elevation, and this correlation was steeper in moderately burned plots and even steeper in severely burned plots (Figure 5c).

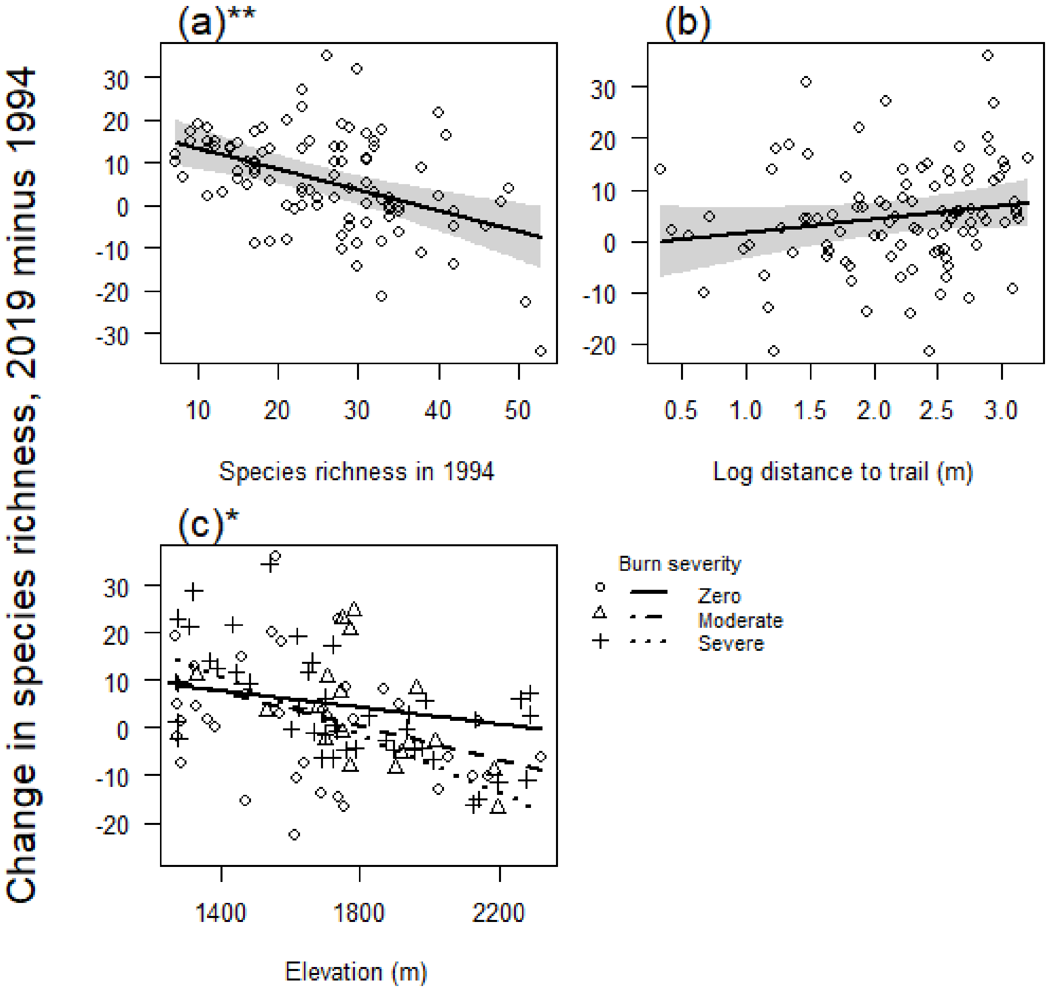

Figure 5 Partial regression plots based on the minimum adequate model for the net change in species richness from 1994 to 2019 showing the effect of (a) species richness in 1994, (b) distance to nearest trail or road, and (c) the interaction between elevation and burn severity. For all panels, all other variables are held at the median or the most common category for categorical predictors. Legend for panel (c) given to the right of the plot. *indicates $p < 0.05$ in drop1 test, **indicates $p < 0.001$ in drop1 test. Confidence intervals in the interaction are omitted for clarity.

Table 3: Results of the models assessing potential predictors of changes in species richness and composition at Waterton Lakes National Parks ELC vegetation plots from 1994 to 2019. P-values refer to the significance of each predictor after marginal fitting of terms.

Response	Predictor	Coefficient	SE	AIC*	P-value
Change in species richness	Intercept	-0.5755	3.9453	469.82	N/A
	Species richness in 1994	-0.5755	2.4848	484.66	<0.001
	Distance to the nearest trail/road	2.6205	1.6686	470.47	0.119
	Elevation x burn severity† (moderate)	-5.2608	5.7437	472.59	0.044
	Elevation x burn severity† (severe)	-12.5914	4.9628		
Change in composition	Intercept	0.325532	0.156467	-127.034	N/A
	Elevation	0.222794	0.062200	-116.638	<0.001
	Northness	0.262062	0.061287	-111.830	<0.001
	Soil drainage‡ (moderate)	-0.260952	0.171002	-126.058	0.08
	Soil drainage‡ (well)	0.006865	0.183049		
	Distance to trail/road x burn severity† (moderate)	-0.401985	0.143121	-123.394	< 0.05
	Distance to trail/road x burn severity† (severe)	-0.208389	0.137302		

*AIC of the model including all factors except the one being tested. Main effects which are included in an interaction were excluded during marginal fitting of terms.
†Coefficients for burn severity are compared to the reference category ‘unburned’
‡Coefficients for soil drainage are compared to the reference category ‘poor’

The minimum adequate model for the change in plot-level community composition included elevation, northness, soil drainage, and the interaction between burn severity and distance to the nearest trail or road (Figure 6). Of those, elevation, northness, and the interaction between burn severity and the distance to the nearest road or trail were significant predictors once all other factors in the model were accounted for, according to marginal fitting of terms (drop1 test; Table 3). The minimum adequate model explained approximately 49% of the variation in composition shifts. Plots at lower elevations tended to see smaller shifts in species composition compared to plots found at higher elevations (Figure 6a). Plots that are more north-facing tended to have greater shifts in composition than south-facing plots (Figure 6b). Finally, there was an interaction between burn severity and distance to the nearest trail or road (Figure 6d). Plots that were not burned in the Kenow Fire saw increasing shifts in composition as distance from the nearest trail or road increased. This differs from moderately burned plots, which experienced smaller shifts in composition farther from trails and roads and severely burned plots which tended to see large shifts in composition regardless of distance to trails and roads.

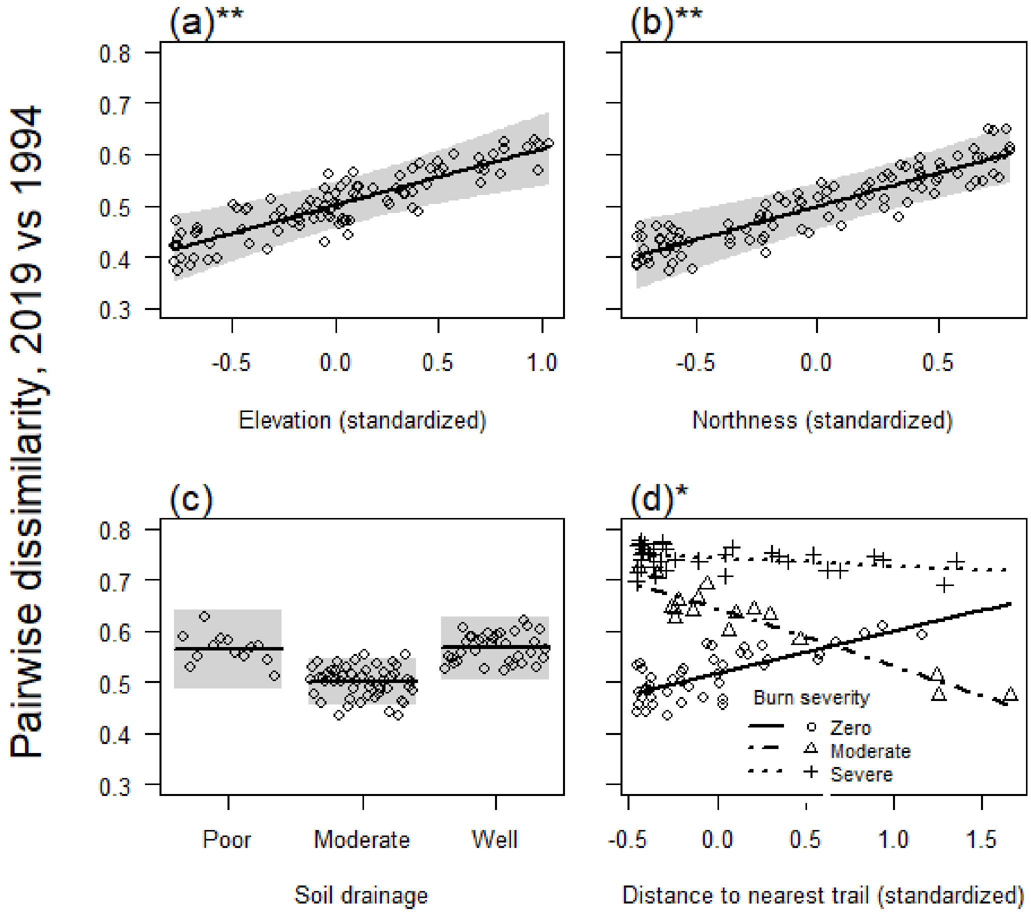

Figure 6 Partial regression plots based on the minimum adequate model for the change in plot-level community composition from 1994 to 2019 showing the effect of (a) elevation, (b) northness, (c) soil drainage, and (d) the interaction between the distance to the nearest trail or road and burn severity. For all panels, all other variables are held at the median or the most common category, for categorical predictors. * indicates $p < 0.05$ in drop1 test, ** indicates $p < 0.001$ in drop1 test. Confidence intervals in the interaction are omitted for clarity.

2.5 Discussion

My results show that the 2017 Kenow Fire has been a major driver of change at WLNP. I found that the effects of the fire have led to shifts in composition and biotic homogenization among burned plots. I also found an increase in exotic species at WLNP, which is consistent with findings of studies on the effects of human disturbance on plant community composition (e.g. McCune and Vellend 2013; Lázaro-Lobo and Ervin 2021). Most importantly, I show that these two drivers of change can interact. For example, severely burned plots at low elevations (where human disturbance is greatest) experienced the greatest gains in species richness. Therefore, monitoring of burned plots should prioritize areas that are severely affected by fire and heavily used by humans, to see if these drastic changes will persist over time or if these communities will be able to return to pre-fire compositions.

2.5.1 Natural pressures as drivers of community change: the role of the Kenow wildfire

I hypothesized that burned plots would see an increase in species richness due to the opening of the canopy layer, allowing previously suppressed, herbaceous, shade intolerant species to colonize after the fire. The Kenow Fire resulted in a 4.7% increase in species richness at burned plots, however this difference was not significant. Burned plots experienced a wide range of changes in species richness compared to the 1994 baseline. For example, one burned plot at WLNP had 26 more species in 2019 compared to the original ELC survey, whereas another burned plot had 35 fewer species. The result at each plot depends on the balance between the number of species gained and lost since the disturbance. Increases in species richness after a wildfire result from the clearing of the canopy layer, which creates favourable growing conditions for many herbaceous species which were previously suppressed due to a lack of light (Bolton and D’Amato 2019). In addition, high severity fires reduce vegetation density, which facilitates the immigration of herbaceous species via wind-dispersed seeds (Reilly et al. 2006). This can result in an increase in species richness if new species are able to reach burned areas. On the other hand, species lost due to the killing of trees and other fire-sensitive species are not always replaced by an equal or greater number of new species. This can happen because of a lack of viable seeds at burned plots after a wildfire. After high severity fires, much of the seed bank is lost (Pinno and Errington 2016), resulting in fewer opportunities for species in pre-fire communities to return after the disturbance. In cases where few seeds are able to survive, vegetation regeneration will depend on long-distance dispersal from areas containing viable seeds. Therefore, burned plots farther from viable seed sources may see weaker post-fire regeneration (Downing et al. 2019), resulting in only small gains in species richness, or even a net loss.

Colonization of new species after a wildfire is also related to the topography surrounding a site. Peeler and Smithwick (2020) showed that seed source pattern (i.e. terrain) can mediate post-fire regeneration in mountainous environments. For example, it is easier for seeds to disperse onto plots found below seed sources, resulting in greater vegetation regeneration compared to plots found above seed sources. This may explain why my model of net change in species richness showed that severely burned communities at high elevations had greater net losses of species since the 1994 surveys, even though severely burned plots at lower elevations tended to have a net gain of species compared to 1994 levels. In addition, it may be difficult for the few seeds that do manage to reach higher elevations to persist, due to the harsher growing conditions making establishment more difficult (Sánchez-González and López-Mata 2005). This compares to plots at lower elevations which feature more favourable growing conditions for a wider range of species. Finally, there tend to be more fire adapted woody (i.e. *Acer glabrum*, *Berberis repens*, *Populus tremuloides*) and herbaceous (i.e. *Carex interior*, *Eucephalus engelmannii*) species at lower elevations. The ability of these species to return after the fire event would minimize species loss at lower elevations. At higher elevations, where vegetation is dominated by fire-sensitive species (i.e. conifers), it can be expected that greater losses will follow, as seen in this study.

As previous legacy studies have shown, species richness is not the only measure that should be considered when assessing changes in plant communities over time. This study also shows that the 2017 Kenow Fire has led to significant shifts in species composition across all burned plots and a significant decline in beta diversity. Mehlman (1992) notes that plots receiving similar burn treatments may end up having species compositions more similar to each other than was observed in pre-fire communities due to the creation of similar, homogenous habitats favouring the same species across different sites. Many of the burned sites in my study were colonized by the same fire-followers including *Chamerion angustifolium*, *Chenopodium album*, and *Dracocephalum parviflorum*, which likely caused the biotic homogenization among burned plots (see also Chapter 3). Another explanation for the decrease in beta diversity among burned plots is that many species which occurred in only a few plots at WLNP in 1994 seem to have been lost by 2019. Examples include *Botrychium spp.*, *Larix lyallii*, *Lilium philadelphicum*, and *Pedicularis contorta*. The loss of unique species resulting in a decrease in beta diversity has also been observed in previous wildfire studies (e.g. Turner et al. 1997; Nowak et al. 2002).

Interestingly, overall shifts in community composition were significant only in the montane and subalpine ecoregions. This is mostly likely a result of the different species that characterize each ecoregion. At WLNP, communities in the montane and subalpine ecoregions tend to be dominated by fire intolerant conifer species such as *Pinus contorta* and *Picea spp.* (Strong and Leggat 1992). After the Kenow Fire, communities found in burned plots in these two ecoregions became dominated by herbaceous species which may have previously been suppressed by the closed canopy, resulting in a large shift in composition. Shyrock et al. (2014) found similar results after a wildfire in the Mojave Desert, where tall, long-lived, woody species were replaced by small, short-lived, herbaceous species. In contrast, pre-fire communities in the foothills were mainly dominated by herbaceous species (Strong and Leggat 1992), thus a similar shift away from woody species was not observed at lower elevations. It should also be noted that dominant woody species found in the foothills (i.e. *Populus tremuloides*) are also able to re-sprout quickly after fires via root crowns and underground structures (Lyon and Stickney 1974; Kulakowski et al. 2004; Brewen et al. 2021), further preventing a large shift in composition as observed in conifer-dominated ecoregions. As I had only four plots in the alpine ecoregion, I attribute the lack of any significant shift in composition in this ecoregion to low explanatory power.

The model of local change in community composition showed that severely burned plots were most dissimilar in composition when compared to their composition in 1994. This is expected because post-fire conditions (i.e. soil, light availability) would be most different from pre-fire conditions in the most severely burned plots. After a wildfire in Colorado, Stevens et al. (2019) found that greater burn severity caused plant communities to experience more drastic shifts in composition towards species with warm-xeric biogeographic affinities (i.e. *Chenopodium sp*. and *Phacelia heterophylla*). In this study, I similarly found *Chenopodium album*, *Phacelia hastata*, and *Phacelia sericea* as frequent colonizers in burned plots, suggesting that a similar shift towards warm-xeric species may be happening at burned plots in WLNP. In addition, more species from the original surveys have been lost at the most severely burned plots. On average, in severely burned 37% of the species present in 1994 were still present by 2019. This compares to 50% in moderately burned plots and 58% in unburned plots. This greater loss of legacy species in severely burned plots contributes to greater shifts in community composition compared to moderately burned or unburned plots.

2.5.2 Natural pressures as drivers of community change: the role of succession and forest encroachment

I predicted that unburned plots would see a decrease in species richness due to the encroachment of trees into more open areas creating unfavourable conditions for shade intolerant herbaceous species. In contrast, the results showed that unburned plots experienced an average gain of 22% in species richness since 1994. It is possible that this increase in species richness is due to the establishment of more shade tolerant species and the persistence of shade intolerant species, as forests continue to encroach onto grasslands. As these shade intolerant species begin to disappear over time due to a lack of resources (i.e. light; Lydersen et al. 2013), species richness in unburned communities could decrease. This delayed extirpation of certain species after a forcing event is known as an “extinction debt” and can take many generations before extinction occurs (Kuussaari et al. 2009; Jackson and Sax 2010). This finding is also consistent with previous studies that show plant species richness can increase with succession (e.g. Nicholson and Monk 1974; Jacquemyn et al. 2001). In the study by Jacquemyn et al. (2001), the authors suggest that the increasing structural complexity of plant communities over time can lead to greater species richness. Stand conditions at WLNP range from immature to mature with occasional windfall (Coen and Holland 1976), thus as microenvironmental heterogeneity increases over time, suitable growing conditions for a wider range of species will develop, resulting in greater species richness. Species richness could also increase over time as new species gradually disperse into these unburned plant communities; however, Nicholson and Monk (1974) note that the rate with which plots gain new species will decrease over time.

It is possible that warming temperatures have contributed to the overall increase in plant species richness at unburned plots, as warmer temperatures allow species to colonize areas that were formerly too cold (e.g. Wipf et al. 2013; Boutin et al. 2017; Steinbauer et al. 2018). Summer temperatures at the WLNP ELC plots have warmed by an average of 1.8^{o}C since the original surveys (*S. Kienzle unpub. data)*. However, if this was a major driver then higher elevations would see greater increases in species richness as species shift upwards in elevation as temperatures warm (e.g. Becker-Scarpitta et al. 2019), and I did not find this. Nevertheless, evidence of the effects of climate change on plant communities are plentiful (e.g. Pauli et al. 2012; Harrison et al. 2015) and may be contributing to changes at WLNP, warranting further investigation by future studies.

Increasing visitor numbers at WLNP may have also contributed to changes over the past 20 to 25 years. Species richness at unburned plots may have also increased because of an influx of exotic and/or disturbance associated species, which is commonly found after human disturbance (e.g. McCune and Vellend 2013; see section *2.5.3* for further discussion on this topic).

There was a decline in beta diversity in unburned areas over 25 years, but not enough to indicate significant biotic homogenization. This contrasts with previous Canadian legacy studies that found pronounced biotic homogenization over the past few decades (e.g. Beauvais et al. 2016; Becker-Scarpitta et al. 2019). Those previous studies found that the decrease in beta diversity was driven by the spread of common disturbance adapted species on landscapes dominated by human land-use (McCune and Vellend 2013), an increase of shade tolerant species during stand maturation after a canopy clearing disturbance (Beauvais et al. 2016), and a convergence in composition of higher elevation communities with communities at lower elevations due to increased temperatures promoting upward shifts of species' ranges (Savage and Vellend 2015). Although there is evidence that fire suppression has led to forest encroachment in WLNP over the past century (Levesque 2005), it is possible that losses of unique shade intolerant species and/or gains of common shade tolerant species across many plots has not yet occurred to a great enough extent to cause biotic homogenization over the 25-year timeframe of this study (Lydersen et al. 2013). In addition, the wide range of habitats present at WLNP due to the large elevation gradient may result in the establishment of different shade tolerant species in different areas of the Park. In that case, biotic homogenization is not expected to occur because plots will remain sufficiently unique in their composition. This contrasts to the previous Canadian legacy studies mentioned previously which were conducted in areas which feature more similar environmental characteristics throughout the study area (i.e. smaller elevation gradients).

The model of plot-level shifts in community composition showed that greater shifts have occurred at north-facing plots, which is consistent with the idea of encroachment by woody species on sites with relatively high soil moisture. Greater soil moisture has previously been shown to aid in tree seedling establishment and growth (Gatherum et al. 1963), and in Alberta, soils on north-facing slopes tend to have higher levels of soil moisture (Lieffers and Larkin-Lieffers 1987). This would enable tree species to expand more easily on north-facing slopes, driving plot-level composition away from more open communities seen in the original surveys.

2.5.3 Human disturbance as a driver of community change

Average species richness was 12% greater in 2019 compared to the original surveys. This is consistent with my prediction that increased human disturbance could lead to an increase in local species richness at WLNP because of unintentional seed dispersal, facilitating the spread of species to new areas around the Park. It should be noted that while exotic species have remained in relatively low abundance at WLNP, there was a significant increase in exotic species richness from 1994 to 2019. In this study, 18 exotic species were not previously found in the ELC plots but were known to be present elsewhere within WLNP in the 1990s. An additional three exotic species (*Artemisia absinthium*, *Carum carvi*, and *Lepidium latifolium*) found in this study had not been recorded in WLNP at the time of the original surveys. Similar to the increase in species richness, increases in exotic species have been shown to be driven by human activity (e.g. Ngugi et al. 2014; Li et al. 2018; Liedtke et al. 2020). As humans increase their use of roads and trails at WLNP, it is likely that further increases in native and exotic species will occur, as seeds carried on boots or tires are inadvertently deposited during use (Rew et al. 2018; Daniels et al. 2019).

The model for net changes in species richness showed that plots at lower elevations tended to gain more species than plots at higher elevations, providing more support to the idea of human activity driving changes in species richness at WLNP, because the density of roads and trails is highest in the lower elevation areas of the park. Roads and trails facilitate the unintentional dispersal of plant seeds by humans (Benninger-Traux et al. 1992). However, contrary to my prediction, plots farther away from trails and roads tended to gain more species at WLNP, although this trend was not significant once all other predictors were accounted for. It is possible that plant communities near trails already included most of the common human-dispersed species (including exotic species) in 1994. In contrast, plots further away from trails and roads may have recently gained these species as they spread outwards from trails, causing a larger increase in species richness in plots deeper within the forest matrix (Hofmeister et al. 2013; Pellissier et al. 2013).

I predicted that biotic homogenization would occur across all plots if human disturbance was the main driver of change at WLNP. I found a significant decrease in beta diversity only in burned plots, which indicates that the increase in exotic species and average species richness is not yet driving significant biotic homogenization in unburned plots. These changes in plant community structure caused by human disturbance may not have resulted in biotic homogenization because not all plots have been subjected to the same amounts of pressure from recreational use (Liedtke et al. 2020). For example, plant communities near roads and horse trails have been shown to host greater amounts of exotic species richness compared to those along hiking trails, which are used less intensively (Yang et al. 2018). In addition, human disturbance is more prevalent at lower elevations, thus plots at higher elevations may not been exposed to the same colonization pressure from species common in the foothills. Exotic species at WLNP are more prevalent at lower elevations. For example, there were three plots in the foothills where exotics accounted for more than 20% of the total abundance of species present. At higher elevations, plots either had no exotic species or a very low abundance of exotics (i.e. less than 10% of the total cover represented by exotic species). Therefore, although exotic species have increased in frequency and abundance, this has not resulted in significant biotic homogenization over the past 25 years.

Although plots at lower elevations had greater net gains in species over time than those at higher elevations, plots at higher elevation experienced greater changes in species composition. This does not support my prediction that human disturbance would drive greater shifts in community composition at lower elevations. In this study, the areas that saw the greatest changes in composition are found in the montane and subalpine ecoregions. In burned plots at higher elevations, communities shifted from forest and woodland communities in 1994 to communities dominated by (1) herbaceous and (2) short, fire following species. Fire followers are plant species with morphological and/or ecophysiological characteristics that allow for adaptation to post-fire environments such as short height at maturity, the ability to increase seed production after a fire, or having ground stored, fire-activated seeds (Lyon and Stickney 1974; Willson and Stubbendieck 1997; Shyrock et al. 214). The loss of species like *Abies lasiocarpa* coupled with the gains of species such as *Chamerion angustifolium* and *Vaccinium myrtillus* were common in these plots (see section *2.5.1* for more detailed discussion on the effects of the Kenow Fire on plot-level changes in composition). Meanwhile, in unburned plots this shift in composition is likely due to an increase in the abundance of (1) shade tolerant and (2) woody species as forests continue to densify (Lydersen et al. 2013), causing a shift in composition. Since the original surveys, species like *Veratrum viride, Alnus viridis,* and *Abies lasiocarpa* have been found in greater abundance at these high elevation unburned plots. In addition, certain species which were previously dominant have greatly decreased in frequency and abundance. For instance, *Pinus albicaulis* was found in much greater frequency and abundance during the 1990s. However, due to increasing rates of infection and mortality due to blister rust (Smith et al. 2008; Smith et al. 2013), this species is now very infrequent at WLNP. At lower elevations, unintentional seed dispersal by humans drives changes in plant communities at WLNP. However, if plots already contain many common plant species, then it would be unlikely that new seeds would cause drastic shifts in composition over time. My data also does not suggest a large decrease in abundance of any dominant species as seen with *Pinus albicaulis* in the unburned plots at higher elevations.

I also predicted that plots found near trails would see greater changes in composition, due to the influence of recreational activity on these communities. However, this was only true for moderately burned plots. My results show that plot-level compositional change is also driven by an interaction between burn severity and the distance to the nearest road or trail (see section *2.5.4* for an explanation of this interaction).

2.5.4 Interactions between natural pressures and human disturbance

This study shows that changes in plant communities at WLNP can be linked to the effects of natural drivers (i.e. the Kenow Fire) and human disturbance. More importantly, I found that these drivers of change can interact, such that the effect of anthropogenic disturbance can modify response to natural disturbance and vice versa. Plots at higher elevations, farther from human influence, were less likely to show a net gain in species richness over time. However, they were even less likely if they were severely burned in the Kenow fire.

Unburned plots, tended to have greater shifts in species composition as distance from roads and trails increased, possibly driven by the continuing spread of disturbance adapted and exotic species away from sources near roads and trails, which already hosted common herbaceous species in 1994 (Liebhold et al. 2017). In contrast, moderately burned plots tended to see greater shifts in species composition the closer they were to roads and trails. This shift in composition is likely due to greater changes in abundance at moderately burned plots closer to trails. Because these plots are found closer to edges, they were able to host a higher proportion of species with high relative abundance before the fire compared to plots found within the forest matrix (Suárez-Esteban et al. 2016). While many species were able to return, relative to severely burned areas, many of these species still saw a large drop in abundance after the fire, causing a shift in plot-level pairwise dissimilarity compared to 1994. In addition, it is easier for seeds to colonize plots found closer to roads and trails, since they can act as a vector for seed dispersal (Benninger-Traux et al. 1992). If the seeds that were able to colonize these moderately burned plots were (1) new species or (2) allowed different returning species to become much more abundant than in pre-fire conditions due to lesser competition or more ideal growing conditions, then plot-level dissimilarity will be even greater.

It is clear that these interactions between the effects of wildfire and human disturbance can play a large role in determining plant community trajectories. As the number of forest edges present in these communities increases in the future, it is likely that we will see more of these large shifts in composition after a wildfire, due to great declines in species abundance and an increase in fire following species which tend to be exotic. In unburned areas, increasing amounts of recreational use and forest edges can also lead to a greater abundance of undesired exotic species (McCune and Vellend 2013), which eventually disperse into the intact forest matrix (Liebhold et al. 2017). Therefore, it is imperative that human disturbance in protected areas is moderated through the responsible use of roads and trails and minimal disruption of intact habitats when making way for new recreational areas.

2.6 Conclusion

This study shows that a recent severe wildfire, successional processes, and increased levels of human disturbance have all contributed to changes in species richness and shifts in the species composition of plant communities at WLNP over the past 20 to 25 years. More importantly, I have shown that these drivers of change can interact, modulating the expected responses in species richness and compositional change. This study demonstrates the need to consider the effects of predictors of change in unison when assessing the responses of plant communities over time (Chazdon 2003; Hermy and Verheyen 2007; Lloren et al. 2020). As the number of recreational visitors to WLNP continues to increase, plant communities will likely continue to shift towards greater proportions of exotic species, especially in areas where wildfire opened space for colonization. Therefore, efforts to control populations of exotic species should focus on burned plots found at lower elevations. Although local species richness has increased on average since the 1990s, beta diversity has declined, especially in burned plots. In a protected area of great ecological and cultural value like WLNP, further research tracking community change is imperative to determine whether these drivers of change, independently or in conjunction, have the ability to set plant communities on new trajectories or whether a shift towards historical compositions will be observed in the future.

CHAPTER 3: USING SPECIES TRAITS AS PREDICTORS OF PLANT COMMUNITY TRAJECTORIES IN BURNED AND UNBURNED VEGETATION

3.1 Abstract

Legacy studies have been used to determine long-term plant community responses to natural and anthropogenic drivers of change. By examining the traits of plant species that have increased (“winners”) or decreased (“losers”) over time, we can better predict which species will be more likely to persist under changing conditions. Using data from re-surveys of vegetation plots established in the 1990s, I associated traits with winner and loser species at Waterton Lakes National Park (WLNP) in burned and unburned plots. Winners across all plots tended to be exotic, annuals, disturbance associated, and shade intolerant. I also found that communities in burned plots have shifted towards shorter, annual, disturbance associated, herbaceous species with lighter seed masses, as expected in post-fire communities. In unburned plots, winners were also more likely to be disturbance associated, suggesting that human disturbance is driving plant community change, even in this protected area. However, communities in unburned plots have shifted towards taller and woody species with heavier seed masses, which provides evidence of forest encroachment in these areas. These results show that while disturbance associated species colonizing all plots is indicative of the effects of human influence at WLNP, unburned communities have shown resistance to those species. In addition, the fire has resulted in two vastly different trajectories. In the unburned areas, forest encroachment is ongoing which can reduce the diversity of shade intolerant herbaceous species. However,

in the burned areas, the fire has created habitat for more of these species to succeed. So, while the Kenow Fire was devastating in nature, its role in setting back succession is crucial and can help maintain plant biodiversity.

3.2 Introduction

Ecologists have tracked changes in plant communities using long-term studies known as legacy studies – re-surveys of previously established and geo-referenced plots – to assess changes over time (de Ballo et al. 2020). Legacy studies have found that at the local scale, species richness can show a wide range of responses, such as increases, decreases, or no net change (Vellend et al. 2013a). In addition to changes in species richness, many legacy studies have found shifts in plant community composition over time (e.g. Savage and Vellend 2015; Beauvais et al. 2016; Becker-Scarpitta et al. 2019; Lloren et al. 2020), indicating that certain species have been benefiting from changing environmental conditions, while others have suffered.

To better understand why some species outperform others under certain conditions, we can determine the characteristics of these successful and struggling species. Legacy studies can do this by determining the identities of species that have increased (winners) or decreased (losers) in frequency or abundance since the original study and investigating whether these outcomes are associated with plant traits (e.g. McCune and Vellend 2013; Shyrock et al. 2014). Doing so will help ecologists make more general predictions about the responses of plant communities to particular drivers of change (Olden and Poff 2003; Tilman and Lehman 2001). For example, this information can improve monitoring and management efforts by answering questions such as "*which species are likely to invade affected areas after a wildfire*" or "*which species are likely to succeed with increasing human disturbance in natural areas?*".

Plant traits are linked to drivers of plant community change. For example, in the human-dominated landscapes of southern Vancouver Island, McCune and Vellend (2015) found that species which are exotic, annual, and/or shade intolerant were more likely to colonize in areas with greater road density in the surrounding landscape. In areas exposed to human disturbance, dominant plant species also tend to have lighter seeds, often dispersed by wind (Lososová et al. 2006; Mabry and Fraterrigo 2009). Lighter seeds are characteristic of herbaceous species (Houghton et al. 2013), which are found in greater proportions in human-dominated landscapes, as woody species are often targeted for removal to make way for human developments (Xu et al. 2019).

Natural disturbances like wildfires can favour plant species with some of the same traits promoted in human-disturbed areas. For example, previous studies have found increases in exotic species after wildfires (e.g. Turner et al. 1997; Coop et al. 2010; Abella and Fornwalt 2015), although often the increase did not result in long-term dominance within the community. A combination of factors determines whether exotic species will be able to dominate in post-fire communities. These include burn severity, the availability of light and bare soil, the presence of exotic species in pre-fire communities, regeneration ability and competitiveness of native species in post-fire communities, and proximity to seed sources (Fornwalt et al. 2010). In addition, plant species with greater colonization ability and lighter seed masses often dominate post-fire areas (Levine and Rees 2002). After fires and other canopy-removing disturbances, more light can reach the understory (Coop et al. 2010; Bolton and D’Amato 2019). As a result, dominant species are likely to be shade intolerant (Canham 1989). Species that succeed in post-fire communities also tend to be shorter, herbaceous species in contrast to the taller, woody species that dominate unburned communities (Shyrock et al. 2014, Abella and Fornwalt 2015).

In undisturbed areas, successful plant species tend to be those that have greater resource competitive ability (Zhang et al. 2018). Plant species in undisturbed forest areas are more likely to be shade tolerant (Mori and Takeda 2004; Lydersen et al. 2013). This allows plants to establish and maintain populations when light resources are scarce, outcompeting species that are unable to succeed in low-light conditions. Another trait that may signal greater resource competitive ability is taller maximum plant height. Previous studies have found that taller plant species are able to deplete resources from competitors, thereby limiting their growth (reviewed in Aarssen and Keogh 2002). In the absence of canopy-clearing disturbances such fires and logging, and when enough moisture is available, closed-canopy forests can invade more open vegetation types. As a result, areas once recorded as shrublands and native grasslands have shifted to forest communities (e.g. Arno and Gruell 1986; Levesque 2005; Coop and Givnish 2007; Stockdale et al. 2019). As grasslands shift to forest communities, average seed mass increases as tree species with typically heavier seeds replace light-seeded annual grasses and forbs (Houghton et al. 2013). This is a common trade-off observed in plants where woody species will produce few, larger seeds which are more capable of establishing in low-light conditions under forest canopies than smaller-seeded species (Turnbull et al. 2008).

Waterton Lakes National Park (WLNP), located in the southern Canadian Rocky Mountains, is experiencing increasing human disturbance yearly due to its popularity for recreational use. The number of visitors at the Park per year has doubled from approximately 300,000 in the 1990s to nearly 600,000 by 2016 (Parks Canada 2008; Parks Canada 2019a). The landscape has also been affected by changing wildfire regimes. Previous studies have found that over the past 100 years, forests have been encroaching on grasslands within the Park (Levesque 2005; Stockdale et al. 2019). The authors linked this finding to lengthening fire return intervals over the past century. In August 2017, a lightning-induced wildfire burned 50% of the vegetation at WLNP (Greenaway 2018). Re-surveys of previously established vegetation plots at WLNP revealed significant biotic homogenization in post-fire communities but not in unburned areas over the past 25 years, and an increase in local species richness (see Chapter 2). These changes in species richness and composition in local plant communities have been linked to the effects of wildfire, environmental factors, human disturbance, and their interactions. However, it is still unclear which plant traits, if any, are associated with species that have increased or declined significantly over the past two decades, and how these traits differ in burned and unburned communities.

In this chapter, I test for significant differences in the plant traits of winners and losers in burned and unburned communities, and measure shifts in mean trait values within local communities over time, to determine the relative influence of human and natural disturbances and succession. If human disturbance and wildfire are the major drivers of change, then I expect winners will tend to be exotic, disturbance associated, annual, shade intolerant, herbaceous, and have lighter seeds and shorter maximum heights (Turner et al. 1997; Crawford et al. 2001; Lososová et al. 2006; Mabry and Fraterrigo 2009; Houghton et al. 2013; McCune and Vellend 2013; Coop et al. 2010; Shyrock et al. 2014; Abella and Fornwalt 2015). If communities are mainly driven by succession, then I expect that winners will be significantly more likely to be shade tolerant, woody, have taller maximum height, and heavier seed mass (Levesque 2005; Turnbull et al. 2008; Houghton et al. 2013; Lydersen et al. 2013; Stockdale et al. 2019). I also hypothesize that the relative abundance of species with these traits will have increased significantly over time as conditions will have favoured their establishment (Smart et al. 2003; Becker-Scarpitta et al. 2019).

3.3 Methods

3.3.1 Study area

Waterton Lakes National Park (WLNP; 49°08’N 113°92’W; Figure 1) was established in 1895 and designated a National Park in 1930 (Parks Canada 2020a). Known for its diverse landscapes, WLNP hosts four ecoregions (foothills parkland, montane, subalpine, and alpine) which support a diverse range of plant communities. There are more than 1000 known vascular plant species at WLNP (Parks Canada 2018b), most of which are native to North America. I surveyed 98 vegetation plots during the 2019 and 2020 field seasons and recorded 426 vascular plant species, only 7% of which were exotic. Herbaceous exotic species (i.e. *Bromus inermis*, *Phleum pratense*, *Taraxacum officinale*) occur in low abundance throughout the Park, and are more commonly present at lower elevations. On average, the relative abundance of exotic species was 3% in plots surveyed in 2019-2020 (Chapter 2). However, this ranged from 0.5% to 43.9%, with plots in the foothills, where human activities are greatest, having the highest cover of exotics.

3.3.2 Data collection

From June to August in 1994, 1995, and 1999, Achuff et al. (2002) established 330 vegetation plots for the purpose of providing vegetation classification of areas within WLNP for integration into the Ecological Land Classification (ELC) project. They delineated 20m x 20m plots in forested areas, 15m x 15m plots in shrublands, and 10m x 10m plots in meadows, and visually estimated the abundance of all vascular plant species within the plot. They recorded the coordinates of the plots using a handheld GPS. Parks researchers later corrected these coordinates using differential correction – a postprocessing method of correcting GPS coordinates that had been scrambled by the United States prior to the year 2000 (*P. Achuff pers. comm.*; Trimble Navigation 2004).

In 2019 and 2020, I used a GPS and field notes to re-locate and re-survey a subset of the ELC plots (3 to 5m accuracy). Despite potential imperfect re-location, re-surveys of semipermanent plots allow for reliable comparisons of plant communities (Kopecký and Macek 2015). I conducted the surveys from June to August, with an attempt to survey plots around the same time in the season as the original surveys. In total, I re-surveyed

104 plots. Six of the plots I surveyed contained plant communities that did not match those given in the original surveys (i.e. a meadow instead of a forest in an unburned area), therefore I excluded these plots from the study due to likely errors in the original coordinates. Of the remaining 98 plots, 53 burned in the Kenow Wildfire and 45 were unburned (Figure 1). I followed the same protocol as the original surveys, except I delineated each plot using tape measures instead of pacing. I also placed rebar at the centre of each plot as a permanent marker, allowing future surveys to be conducted at the same locations.

Both surveys classified the vegetation into four layers by height and estimated the abundance of each species to the nearest percent cover in each layer. Prior to the analysis, I summed the abundance across all layers for each species. I used the Integrated Taxonomic Information System (https://www.itis.gov/) to standardize plant species names across all surveys. To avoid inaccuracies relating to misidentification, I lumped some species to the genus level (e.g. *Danthonia sp*. includes *D. californica*, *D. intermedia,* and *D. parryi;* Supplementary Table 1).

I compiled a list of seven plant traits – defined as qualitative and quantitative characteristics of plant species that may be linked to drivers of change – for all the species found in the original and recent vegetation surveys. These traits included origin, shade tolerance, lifeform, lifespan, disturbance association, maximum height, and seed mass. I included origin because it has been previously shown that disturbances like wildfires and roads cause an increase in the abundance and frequency of exotic species (e.g. Crawford et al. 2001; Coop et al. 2010; McCune and Vellend 2013). I define exotic species as those which are present in Alberta due to direct or indirect human intervention (NatureServe 2013). Previous research has shown that exotic species tend to be associated with disturbance (Pyle 1995; Stapanian et al. 1998; Jesson et al. 2000). Shade tolerance has been found to affect plant species growth, where shade tolerant species tend to succeed under closed canopies and shade intolerant species preferring gaps and more open habitats (Canham 1989; Lydersen et al. 2013). Natural and anthropogenic disturbances have been shown to cause shifts towards short-lived and herbaceous species (Hobbs 1997; Shyrock et al. 2014), therefore I included lifespan and lifeform traits. I included maximum height due to the association of taller species with forest encroachment in contrast to a shift to shorter, herbaceous species after a wildfire (Levesque 2005; Shyrock et al. 2014; Stockdale et al. 2019). I included seed mass to test whether the prevalence of species with different reproduction strategies has changed over time (Lososová et al. 2006; Houghton et al. 2013; Mabry and Fraterrigo 2009). For example, smaller seeds are commonly found among long-distance colonizers after a fire (Lyon and Stickney 1974), whereas late successional communities tend to feature larger seeds that are indicative of stronger competitive ability (Turnbull et al. 2008). Finally, I considered changes in disturbance association because previous studies have found that both exotic and native species can be associated with disturbance (e.g. McCune and Vellend 2013). This metric allows me to compare changes in disturbance association irrespective of origin. I also gathered fire association and specific leaf area data for inclusion in this analysis because these traits have been associated with species persistence in both post-fire and unburned communities (Zhang et al. 2018; Pausas 2019). However, because reliable data for these two traits only covered 37% and 28% of species present at WLNP respectively, I was not able to include these traits in this study.

To determine species origin, I used the Alberta Conservation Information Management System (ACIMS) plant species ranking database (Kershaw 2015), which designates each species as either native or exotic to Alberta based on whether it is present in the province due to direct or indirect human intervention (NatureServe 2013). I compiled shade tolerance data from the USDA PLANTS Database (USDA, NRCS 2021), the Electronic Atlas of the Flora of British Columbia (Klinkenberg 2021), and the Flora of North America (Flora of North America Editorial Committee, eds 1993). Shade tolerance describes the relative ability of a certain species to persist under shade conditions. I included three categories: shade intolerant, shade intermediate, and shade tolerant. To determine the lifespan, lifeform, and disturbance tolerance of species present at WLNP, I used the Flora of Alberta (Moss and Packer 1994) and A Flora of Waterton Lakes National Park (Kuijt 1982). Lifespan describes the longevity of a species where annuals complete their lifecycle in one growing season, biennials persist for two growing seasons, and perennials persist for more than two growing seasons. I lumped annual and biennial species in this analysis as they both describe short-lived species relative to perennials and very few species were biennials. Lifeform is used to describe the growth habit of each species, where woody species include all trees, shrubs and vines, and herbaceous species include forbs, ferns, and graminoids. I categorized a species as disturbance associated if its habitat description included examples of typical disturbed habitats such as: disturbed areas, clearings, roadsides, waste grounds, gardens, and lawns.

I compiled maximum species height in centimetres as noted in the Flora of Alberta, A Flora of Waterton Lakes National Park, or the Flora of North America (Flora of North America Editorial Committee, eds 1993). I used the Royal Botanic Gardens Kew Seed Information Database (SID; Royal Botanic Gardens Kew 2021) to retrieve seed mass data. The Kew SID is an amalgamation of data gathered by the Kew Seed Conservation Department. The seed masses provided represent the mass of 1000 seeds as reported in collections and published literature.

3.3.3 Statistical analysis

1. Indicator species analysis

For simplicity, I will be referring to the original survey years as "1994" and the recent re-survey years as "2019". To determine which species have been winners or losers over the past 25 years, I conducted three indicator species analyses. This analysis uses the relative abundance and frequency of each species in each year to compute an indicator value for each species within different test groups. The method uses permutation to test the significance of these indicator values by assigning sample units (i.e. plots) randomly to different groups (i.e. 1994 versus 2019) to see whether it produces a greater indicator value than the real data (Dufrêne and Legendre 1997). I define "winners" as species that are significant indicators of 2019 and "losers" as species that are significant indicators of 1994. I used an alpha of 0.1 because it produced the same qualitative results as an alpha of 0.05, however it provides larger sample sizes for testing the association of particular traits with winner versus loser status. First, I conducted an indicator species analysis comparing 2019 to 1994 across all plots. I also wanted to know which species were indicators of the Kenow Fire, since this event has been shown to have a major role in driving plant community change (see Chapter 2). Therefore, I conducted a separate indicator species analysis on burned plots only, comparing species frequencies and abundances in 1994 and 2019. Finally, I conducted a third indicator species analysis to determine which species have become more abundant and/or frequent in unburned plots only between 1994 and 2019. This allows me to determine whether succession or human disturbances are driving changes in these communities.

2. Winner and loser trait differences

I then tested for significant associations between winners or losers and each trait. For categorical traits, I tested for significant differences in the proportions of winners and losers having different traits using Fisher's exact tests (Fisher 1922). I tested for differences in mean trait values between winners and losers in continuous traits using Wilcoxon rank sum tests (Mann and Whitney 1947). I performed these tests across three different groups of winners and losers separately: (1) indicators across all plots, (2) indicators within burned plots only, and (3) indicators within unburned plots only. I do not report the results for indicators in burned plots only, as those results were very similar to the results for all plots (Supplementary Figure 1, 2; Supplementary Table 5).

3. Changes in community-weighted mean traits

I also ran tests to consider whether changes in the relative abundances of plant species in burned and unburned communities over time indicate a shift towards certain traits. This is a useful analysis to conduct because it can reveal patterns occurring at the community-level, whereas the indicator species analysis focuses on changes in each species individually, from one year to another. By conducting this test, I am also able to consider the traits of species that may have increased or declined in abundance but were not frequent enough to register in the indicator species analysis. To determine whether the relative abundance of species with particular traits in burned and unburned plots has changed since the original surveys, I analysed the community-weighted mean (CWM) for each trait in each plot 1994 and 2019. For categorical variables, I determined the CWM by first assigning a value to each trait category. For example, for species origin, I assigned native species a value of 0 and exotics a value of 1. Then I multiplied this value by the relative abundance of each species present at each plot, giving me the abundance-weighted trait value for each species. To obtain the final community-weighted mean trait value, I then summed all abundance-weighted trait values of each species present at each plot. A plot with 100% cover made up of native species would have a CWM origin value of 0. A significant increase in CWM origin from 1994 to 2019 indicates that exotic species made up a greater proportion of total abundance over time. For continuous variables, I calculated the CWM by multiplying the maximum height and seed mass of each species present at a plot by its relative abundance and summing these abundance-weighted values for all species present at each plot. I then conducted Wilcoxon signed rank tests comparing the CWM for each trait in 1994 to the CWM in 2019 in burned and unburned plots separately (Wilcoxon 1945). I included only those plots where at least 80% of the total abundance of species in both years was represented by species for which trait data was available. Origin, lifeform, lifespan, disturbance association, and height all had data available for all species in each plot in 1994 and 2019. For seed mass, 70 plots had at least 80% of their total cover made up by species with seed mass values available. There were 74 plots for which less than 80% of the total abundance in 1994, 2019, or both years was made up of species with shade tolerance values available. Therefore, I omitted shade tolerance from this analysis.

I conducted all tests in R version 3.5.0 (R Core Team 2018). I used the “labdsv” package to conduct the indicator species analysis with 10,000 permutations (Roberts 2019). I used base R to conduct the Fisher’s exact, Wilcoxon rank sum, and Wilcoxon signed rank tests.

3.4 Results

3.4.1 Indicator species analysis

I found 56 significant indicator species across all plots (26 winners and 30 losers; Table 4). Of these, all but one winner (*Sambucus racemosa*) and five losers (*Abies lasiocarpa*, *Juniperus communis*, *Menziesia ferruginea*, *Pinus albicaulis*, and *Vaccinium membranaceum*) were herbaceous. In addition, seven winners (*Bromus inermis*, *Chenopodium album*, *Descurainia sophia*, *Medicago lupulina*, *Phleum pratense*, *Poa compressa*, and *Taraxacum officinale*) and one loser (*Hypericum perforatum*) are exotic.

When analyzing burned plots only, 18 species were indicators of 2019 and 29 were indicators of 1994. The groups containing all plots and only burned plots shared 16 of the same winners and 19 losers. The indicator species analysis conducted on only unburned plots revealed 10 winners and four losers. Of these, only one winner (*Sorbus scopulina*) and one loser (*Spiraea betulifolia*) were woody. Two species were winners in all three groups: *Symphyotrichum laeve* and *Taraxacum officinale*. There were no losers in common with all three groups. *Goodyera oblongifolia* is the only species to appear as a loser in one group (burned plots only) and a winner in another (unburned plots only).

Table 4 Significant indicator species across all plots, burned plots only, and unburned plots only. These results are based on an indicator species analysis with 10,000 permutations to determine significance at $p < 0.1$. Species in red are losers (significant indicators of 1994), species in blue are winners (significant indicators of 2019), and species with an asterisk are exotic.

All plots (n=56)	Burned plots only (n=47)	Unburned plots only (n=14)
Abies lasiocarpa	*Abies lasiocarpa*	
	Actaea rubra	
Agoseris glauca		*Agoseris glauca*
Androsace septentrionalis	*Androsace septentrionalis*	
	Anemone multifida	
Angelica arguta		*Angelica arguta*
Angelica dawsonii	*Angelica dawsonii*	
Antennaria parvifolia	*Antennaria parvifolia*	
Antennaria racemosa		
	Antennaria spp.	
	Anthoxanthum nitens	
Anticlea elegans		*Anticlea elegans*
Anticlea occidentalis	*Anticlea occidentalis*	
Arnica cordifolia	*Arnica cordifolia*	
	Arnica ovata	
Boechera holboellii	*Boechera holboellii*	
*Bromus inermis**	*Bromus inermis**	
		Bromus vulgaris
Calamagrostis montanensis		
Chamerion angustifolium	*Chamerion angustifolium*	
*Chenopodium album**	*Chenopodium album**	
Chimaphila umbellata	*Chimaphila umbellata*	
Clematis occidentalis	*Clematis occidentalis*	
*Descurainia sophia**	*Descurainia sophia**	
Dracocephalum parviflorum	*Dracocephalum parviflorum*	
Erigeron peregrinus		
Erysimum inconspicuum	*Erysimum inconspicuum*	
Eucephalus engelmannii	*Eucephalus engelmannii*	
Festuca altaica		
Geranium bicknellii	*Geranium bicknellii*	
	Goodyera oblongifolia	*Goodyera oblongifolia*
Hedysarum sulphurescens		*Hedysarum sulphurescens*
Heracleum sphondylium		

All plots (n=56)	Burned plots only (n=47)	Unburned plots only (n=14)
Heuchera glabra		
Hieracium triste		
Hieracium umbellatum		*Hieracium umbellatum*
*Hypericum perforatum**		
Juniperus communis	*Juniperus communis*	
	Lonicera utahensis	
Luzula hitchcockii		
Maianthemum racemosum	*Maianthemum racemosum*	
*Medicago lupulina**		
Menziesia ferruginea	*Menziesia ferruginea*	
Orthilia secunda	*Orthilia secunda*	
Osmorhiza depauperata	*Osmorhiza depauperata*	
Osmorhiza occidentalis	*Osmorhiza occidentalis*	
Pedicularis bracteosa	*Pedicularis bracteosa*	
Penstemon albertinus	*Penstemon albertinus*	
Penstemon lyallii	*Penstemon lyallii*	
Phacelia hastata	*Phacelia hastata*	
Phacelia sericea	*Phacelia sericea*	
*Phleum pratense**		*Phleum pratense**
	Picea engelmannii	
Pinus albicaulis	*Pinus albicaulis*	
Poa alpina		
*Poa compressa**	*Poa compressa**	
	Pseudotsuga menziesii	
	Pyrola asarifolia	
	Ribes viscosissimum	
Sambucus racemosa		
		Silene parryi
		Sorbus scopulina
		Spiraea betulifolia
Streptopus amplexifolius		*Streptopus amplexifolius*
Symphyotrichum foliaceum		
Symphyotrichum laeve	*Symphyotrichum laeve*	*Symphyotrichum laeve*
*Taraxacum officinale**	*Taraxacum officinale**	*Taraxacum officinale**
Thalictrum spp.	*Thalictrum spp.*	
Vaccinium membranaceum	*Vaccinium membranaceum*	
Valeriana sitchensis	*Valeriana sitchensis*	
	Veratrum viride	
Vicia americana		

3.4.2 Winner and loser trait differences

Across all plots, winners were more likely to be exotic (Fisher's exact test: $p = 0.019$; Figure 7a), annual (Fisher's exact test: $p < 0.01$; Figure 7b), disturbance associated (Fisher's exact test: $p < 0.01$; Figure 7c), and less likely to be shade tolerant (Fisher's exact test: $p = 0.024$; Figure 7d). There was no significant difference in proportion of lifeforms (Fisher exact test: $p = 0.200$; Figure 7e) or maximum height (Wilcoxon rank sums test: $p = 0.747$; Figure 8a) between winners and losers. Although winners tended to have a lower median seed mass, this difference was not significant (Wilcoxon rank sums test: $p = 0.362$; Figure 8b).

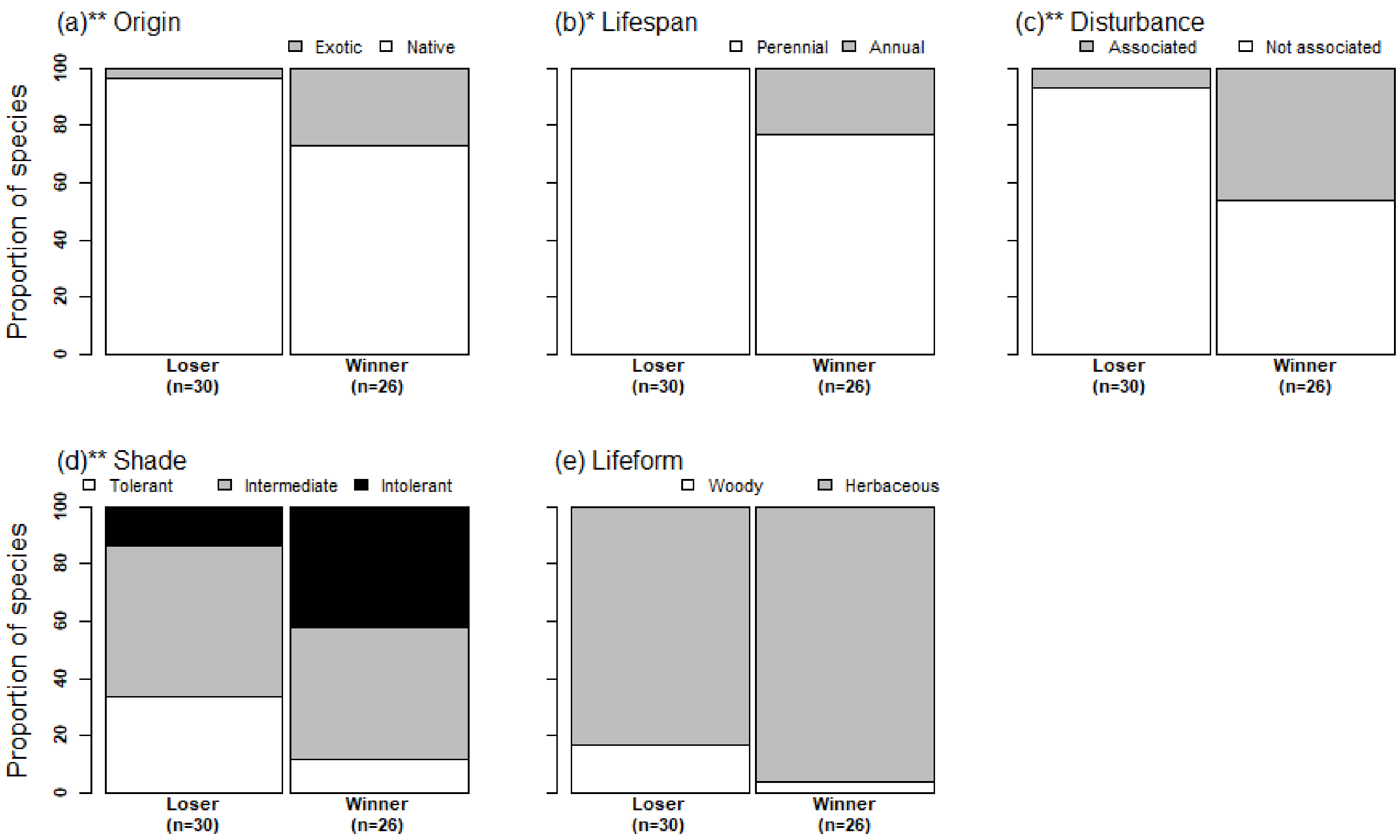

Figure 7 The proportion of species within winner and loser indicator groups in each trait category across all plots by (a) origin, (b) lifespan, (c) disturbance association, (d) shade tolerance, and (e) lifeform. * indicates $p < 0.05$, ** indicates $p < 0.01$ according to a Fisher's exact test.

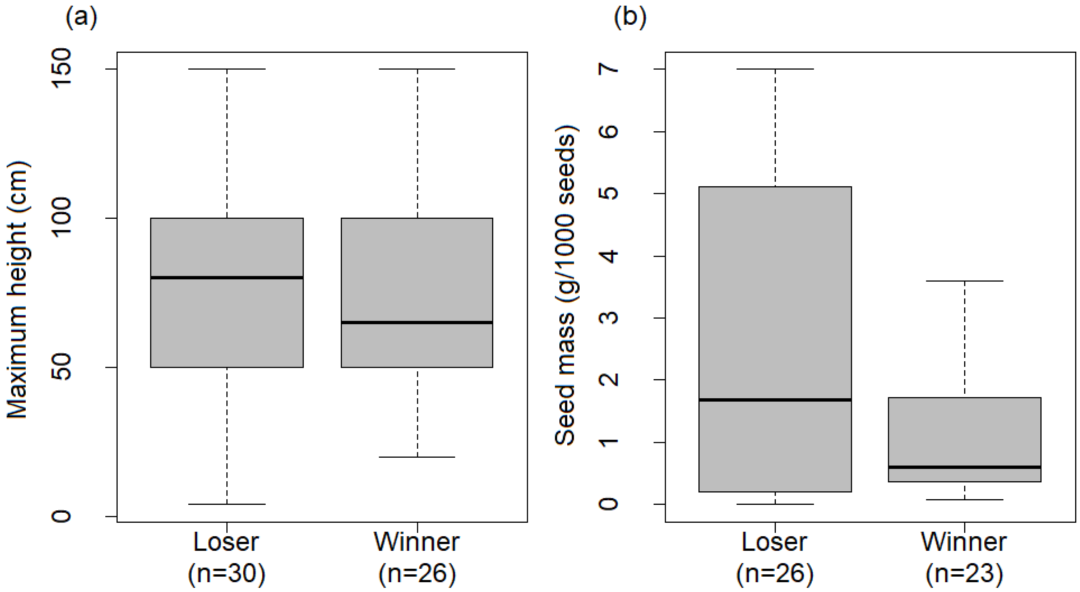

Figure 8 The distribution of (a) maximum height and (b) seed mass per 1000 seeds of winners and losers across all plots. The black line indicates the median height and seed mass for that survey group. Whiskers are 1.5 times the interquartile range. No significant differences according to Wilcoxon rank sums tests.

In unburned plots, winners were more likely to be associated with disturbance (Fisher's exact test: $p < 0.05$; Figure 9c). Winners and losers were not significantly more or less likely to be exotic (Fisher's exact test: $p = 0.274$; Figure 9a), annual (Fisher's exact test: $p = 1$; Figure 9b), shade intolerant (Fisher's exact test: $p = 0.245$; Figure 9d) or woody (Fisher exact test: $p = 0.502$; Figure 9e). Winners in unburned plots appeared to be taller than losers, although this difference was not significant (Wilcoxon rank sums test: $p = 0.431$; Figure 10a). Like the pattern observed across all plots, winners tended to have lighter seed mass but again this difference was not significant (Wilcoxon rank sums test:

p = 0.539; Figure 10b). Explanatory power was low for this analysis, because I had only 14 significant indicator species.

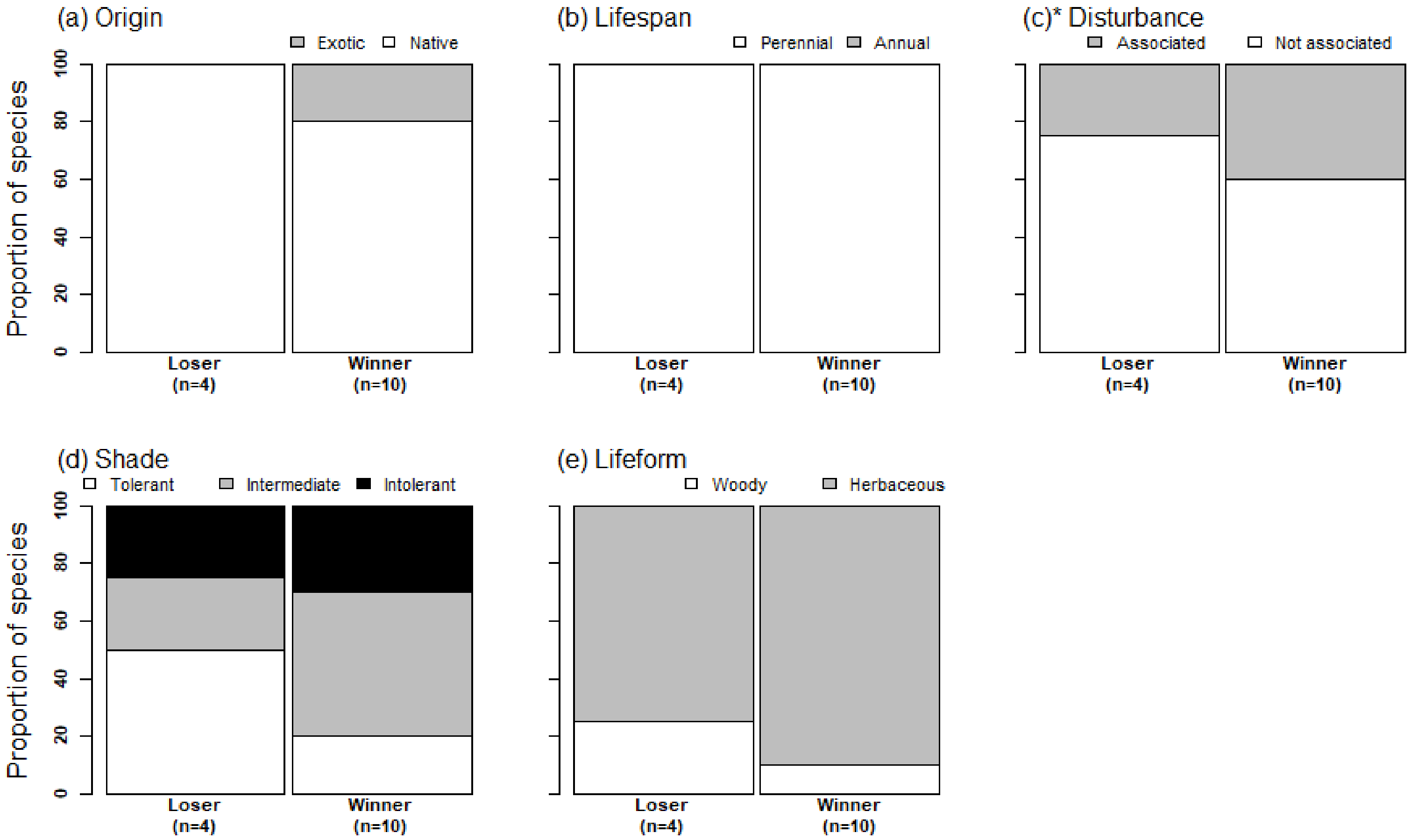

Figure 9 The proportion of species within winner and loser indicator groups in each trait category across unburned plots only by (a) origin, (b) lifespan, (c) disturbance association, (d) shade tolerance, and (e) lifeform. * indicates $p < 0.05$ according to a Fisher's exact test.

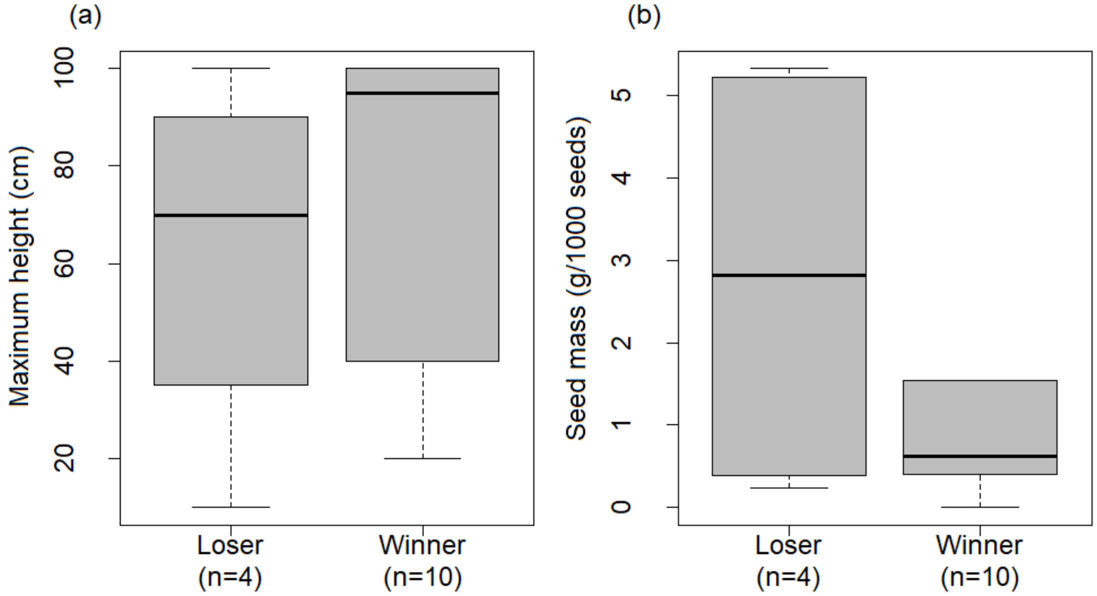

Figure 10 The distribution of (a) maximum heights and (b) seed mass per 1000 seeds of the species within loser and winner indicator groups across unburned plots only. The black line indicates the median height and seed mass for that survey group. Whiskers are 1.5 times the interquartile range. No significant differences according to Wilcoxon rank sums tests.

3.4.3 Changes in community weighted means

In burned plots, there was a significant shift in the relative abundance of exotic species (Wilcoxon signed rank test: $p < 0.01$; Figure 11a) from 1994 to 2019 (2-3 years post-fire). Burned plots at WLNP also shifted towards greater relative abundance of shorter (Wilcoxon signed rank test: $p < 0.001$; Figure 11b), herbaceous (Wilcoxon signed rank test: $p < 0.01$; Figure 11c), annual (Wilcoxon signed rank test: $p < 0.01$; Figure 11d), disturbance associated species (Wilcoxon signed rank test: $p < 0.01$; Figure 11e) with lighter seed mass (Wilcoxon signed rank test: $p < 0.01$; Figure 11f).

From 1994 to 2019, communities in unburned plots also experienced a shift towards exotic species (Wilcoxon signed rank test: $p < 0.05$; Figure 11a). There was also an increase in the relative abundance of taller (Wilcoxon signed rank test: $p < 0.001$; Figure 11b) and woody plant species (Wilcoxon signed rank test: $p < 0.001$; Figure 11c), with heavier seed mass (Wilcoxon signed rank test: $p < 0.01$; Figure 11f). There was no evidence of a significant shift towards annual (Wilcoxon signed rank test: $p = 0.975$; Figure 11d), or disturbance associated species (Wilcoxon signed rank test: $p = 0.398$; Figure 11e) in unburned plots.

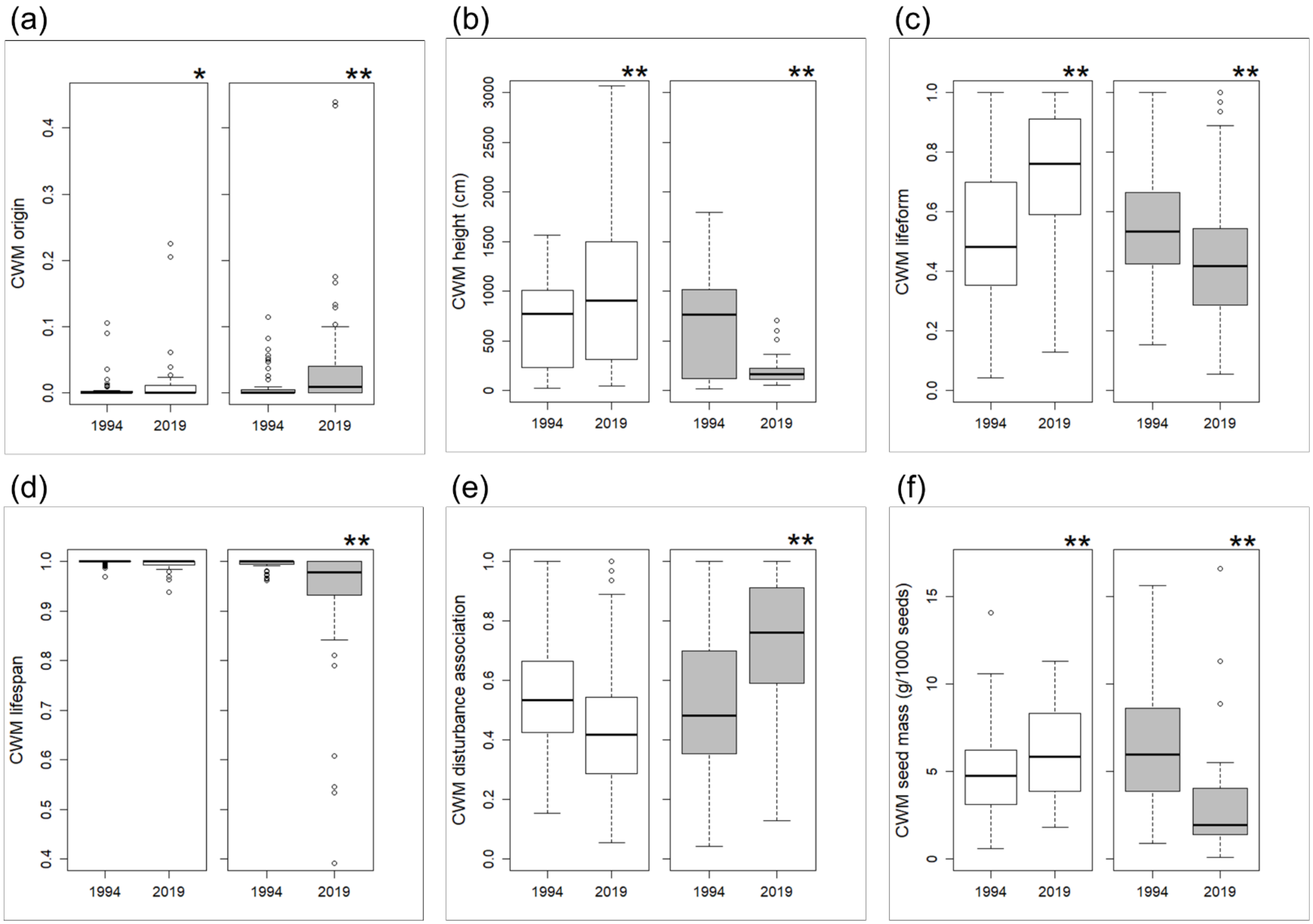
(a)
CWM origin
0.0
0.1
0.2
0.3
0.4
*
**
1994
2019
1994
2019
(b)
CWM height (cm)
0
500
1000
1500
2000
2500
3000
**
**
1994
2019
1994
2019
(c)
CWM lifeform
0.0
0.2
0.4
0.6
0.8
1.0
**
**
1994
2019
1994
2019
(d)
CWM lifespan
0.4
0.5
0.6
0.7
0.8
0.9
1.0
**
1994
2019
1994
2019
(e)
CWM disturbance association
0.0
0.2
0.4
0.6
0.8
1.0
**
1994
2019
1994
2019
(f)
CWM seed mass (g/1000 seeds)
0
5
10
15
**
**
1994
2019
1994
2019

Figure 11 (previous page) The community-weighted mean (CWM) for (a) origin (native species = 0, exotic species = 1), (b) height, (c) lifeform (herbaceous plants = 0, woody plants = 1), (d) lifespan (annual/biennial species = 0, perennial species = 1), (e) disturbance association (not disturbance associated = 0, disturbance associated =1), and (f) seed mass in 1994 compared to 2019. White boxes = unburned plots only, gray boxes = burned plots only. The black line indicates the median community-weighted value for that survey group. Whiskers are 1.5 times the interquartile range. * indicates $p < 0.05$, ** indicates $p < 0.01$ according to a Wilcoxon signed rank test.

3.5 Discussion

3.5.1 Influence of disturbances on species traits

It is clear that the Kenow Fire has been a major driver of recent changes at WLNP. Like many previous post-fire studies (e.g. Turner et al. 1997; Crawford et al. 2001; Coop et al. 2010), I found that exotic species were significantly more likely to increase in frequency and/or abundance in the years immediately following the Kenow Fire, at least compared to baseline surveys from the mid-1990s. Exotics tend to be rapid colonizers which allows them to dominate vegetation even with low propagule pressure (Louback-Franco et al. 2020). In this study, *Chenopodium album* and *Descurainia sophia* were two exotic species that were not previously found at these plots in the 1990s (although present elsewhere in WLNP). It is likely that the few individuals of these species that managed to establish over the past two decades were able to take advantage of less intense competition from neighbouring species and become more dominant in post-fire communities. My measurement of the community-weighted mean (CWM) origin also showed a significant shift towards exotics in burned plots by 2019. This means that exotic species have not only increased among winners, but also across the broader community as a whole.

Another expected finding is that winners in the burned plots are more likely to be short-lived species. Lyon and Stickney (1974) suggest that fire-adapted species are often short-lived, with ground-stored and fire-activated seeds, as exhibited by *Geranium bicknellii* and *Dracocephalum parviflorum*, both of which were winners among burned plots in this study. The authors also note that certain native species (i.e. *Chamerion angustifolium*) are known to dramatically increase in cover after fires due to their ability to re-establish via rhizomes *and* the spread of airborne seeds from sites well-removed from the burn. Some grass species have also been known to re-sprout from surviving underground parts (e.g. *Bromus inermis*; Blaisdell 1953) or increase seed production (e.g. *Calamagrostis montanensis*; Willson and Stubbendieck 1997) after fires, which could explain why these species have been able to increase significantly. The measurement of CWM lifespan also indicates that short-lived species are now dominating post-fire communities. Turner et al. (1997) found that annual species in Yellowstone National Park followed a “boom and bust” cycle following the wildfires there in 1988. This describes the phenomena where certain species – in this case annuals – will see a very rapid increase in cover in the years immediately following the disturbance, but eventually return to previously recorded abundances.

Although winners were no more likely to be herbaceous, I found that post-fire communities were more heavily weighted towards herbaceous species. This is expected as previously dominant woody species (i.e. *Abies lasiocarpa*, *Juniperis communis*, *Menziesia ferruginea*, and *Pinus albicaulis*) were lost in the fire. In addition, herbaceous species have been found to increase in post-fire communities due to quicker growth rates and shorter generation lengths (Shyrock et al. 2014), which allows for rapid reproduction rates. This shift towards herbaceous species also explains why post-fire communities tended to have a shorter CWM height. In the future, communities may revert to taller and woody species as species like *Ceanothus velutinus* and *Pinus contorta* re-establish in burned areas via fire-adapted seeds (Lyon and Stickney 1974). Finally, communities in burned plots demonstrated a shift towards lighter seed masses. This can be correlated to the shift towards herbaceous species in these communities as woody species have been shown to have heavier seeds (Houghton et al. 2013).

In unburned plots, I found support for the hypothesis that human disturbance is driving change at WLNP. Winners in unburned plots were significantly more likely to be disturbance associated. In a study of upland forest communities in Wisconsin and Michigan, Wiegmann and Waller (2006) similarly found that human disturbance has led to the increase of disturbance tolerant winners and a decrease of disturbance intolerant losers. In forests in Germany, Naaf and Wulf (2011) found that traits that predicted disturbance-tolerant winners over a two-decade study period included having long-lived seeds and long-distance dispersal ability. The authors state that these traits allow species to re-establish from (1) persistent seed banks after damage to the soil surface and (2) sources far from where the disturbance occurred, allowing these species to replace lost individuals. These are characteristics possessed by *Agoseris glauca*, *Hieracium umbellatum*, *Phleum pratense* and *Taraxacum officinale* which are responsible for the increase in disturbance association among winners in unburned plots. Interestingly, the CWM disturbance association in unburned plots has not shifted significantly towards greater abundance of disturbance-associated species even though winners tend to possess that trait. In fact, the trend – though not significant – is in the opposite direction. This indicates that while four disturbance associated species have increased significantly in frequency and abundance since the 1990s, they still only account for a small proportion of the overall community among unburned plots. For example, of the 100 most abundant species found in unburned plots, only two (*Hieracium umbellatum* and *Phleum pratense*) were disturbance associated winners.

I did not find that winners were significantly more likely to be exotic than losers in unburned plots. However, I did find that those communities have experienced a significant increase in the relative abundance of exotic species. This finding is supported by previous studies which have similarly found that human disturbance can result in a greater abundance of exotic plant species (i.e. Benninger-Truax et al. 1992; McCune and Vellend 2015; Rew et al. 2018). This is likely to have occurred through the accumulation of exotic species new to unburned plots since the original surveys. However, most of those new species have each remained in low abundance, thus not appearing as winners in the indicator species analysis (see Chapter 2).

3.5.2 Successional processes as drivers forest encroachment

Historical ecological research has documented the encroachment of forests onto grasslands in WLNP over the past 100 years using historical photographs and land survey data (Levesque 2005; Stockdale et al. 2019). However, it has been unclear whether these trends have been continuing over the past couple of decades, or whether these communities have reached a stable state. My results show that succession in the form of forest encroachment of more open vegetation is ongoing and has been a driver of plant community change at WLNP over the past 25 years. Although my analysis of indicator species did not suggest winners were more likely to be shade tolerant, woody, have taller maximum height, or heavier seed mass in unburned areas, this may have been due to the small sample size of indicators for the 45 unburned plots alone. The significant changes in CWM trait values in unburned plots clearly show shifts towards greater abundance of taller, woody species with heavier seeds – the trend predicted for communities undergoing succession towards dense, closed-canopy vegetation. Arno and Gruell (1986) found that lengthening fire return intervals resulted in forest encroachment of grasslands in southwestern Montana. Fire return intervals are estimated to be about 100 years at WLNP (Shaw 2009; Stockdale et al. 2019). Although, a study by Rogeau (2016) claims fire return intervals of about 30-60 years at WLNP, depending on the ecoregion. Nevertheless, the unburned plots included in this study have not burned for more than 100 years. The most recent fire in this area was the southern Alberta wildfires of 1910 and this event did not affect any of the ELC plots according to historical fire maps (Arthur 2014). This suggests that the trends seen over the past 100 years, with respect to forest encroachment (e.g. Levesque 2005; Stockdale et al. 2019), have continued over the past two decades.

3.6 Conclusion

Wildfires like the one experienced at WLNP result in the opening of canopies. This allows shade intolerant species, which may have been suppressed in pre-fire communities, to avoid further declines in populations (Pausas and Keeley 2019). However, maintaining intact and unburned forests allow shade tolerant species, like *Goodyera oblongifolia*, to persist. Previous studies have suggested that fire events that result in remnant unburned patches allow for greater plant diversity by the creation of a heterogeneous mix of areas which burned at varying levels of severity or were not burned at all (Turner et al. 1997; DeSiervo et al. 2015; Pinno and Errington 2016; Richter et al. 2019). Although wildfires have been shown to increase the presence and abundance of exotic species (e.g. Crawford et al. 2001; Coop et al. 2010), studies like the one conducted by Fornwalt et al. (2010) show that exotics can eventually return to pre-fire abundances over the long-term. Exotic species remain in low abundance and frequency at WLNP, but continued monitoring can inform ecologists whether the establishment of these species, which has been facilitated by the fire, will result in their continued dominance of post-fire communities in the future.

This study has also shown that while winners in unburned areas are more likely to be disturbance-associated, communities overall are trending towards traits indicative of forest encroachment. With increasing human recreational activity, disturbance associated species are predicted to increase in frequency and abundance, potentially resulting in biotic homogenization (McKinney and Lockwood 1999). Yet, in plots far from human influence, where succession towards closed canopy forests continues, these species may not be able to take hold. Continued monitoring of these plots will help determine whether disturbance-associated species will be able to increase in abundance in the future, or if late-successional communities will remain resistant to colonization by these species.

CHAPTER 4: CONCLUSION

While plant communities may appear to be static, they are in fact continuously changing over time. However, we often notice changes only after major disturbances like wildfires occur, meaning many of the more subtle changes that occur over time can go unnoticed. Legacy studies are an excellent method that ecologists can use to reveal these gradual changes in plant communities (de Ballo et al. 2020). From this, we can determine whether local plant diversity has increased, decreased, or remained stable over time (Vellend et al. 2013a). In addition, it allows us to determine whether there have been any shifts in composition. There have been a few legacy studies conducted in Canada (e.g. McCune and Vellend 2013, Beauvais et al. 2016; Becker-Scarpitta et al. 2019; Lloren et al. 2020; Pinceloup et al. 2020), which cover a small sample of the different environments present in the country. In areas like the southern Rocky Mountains, we have not yet quantified how local plant communities have changed over the past few decades.

The goal of this research was to quantify plant community change at Waterton Lakes National Park (WLNP) over the past 25 years. WLNP is an intriguing study site because of the large elevation gradient and correspondingly diverse vegetation present in this area. In addition, natural and human disturbances have been increasing in the Park over recent years through wildfires and recreational use, respectively. I set out to (1) quantify magnitudes of change in the diversity and composition of plant communities over the past 25 years, (2) determine whether these changes are predictable based on the effects of a wildfire, environmental factors or human natural disturbances, (3) identify interactions between natural and human drivers of change, and (4) determine “winners” and “losers” within plant communities and link species persistence and establishment to plant traits. By conducting this study, I have been able to create a baseline which future studies can use to assess changes in plant communities, further develop our understanding of theoretical plant community change, and help applied ecologists and resource managers (i.e. Parks Canada) answer important questions on the impacts of human activity and the 2017 Kenow Fire on plant communities at WLNP.

There are two broad takeaways revealed in this thesis. First, is the importance of conducting studies of plant communities at different scales. In Chapter 2, I found no significant change in species richness on average from 1994 to 2019 across burned plots at WLNP. However, a wide range of responses were observed at the plot-level including increases, decreases, and no net change. Similarly, I found little change in community composition across all unburned plots, but the plot-level analysis showed that many of these communities have changed in composition since the original surveys, especially plots that burned severely. In Chapter 3, I found differing drivers of change with respect to dominant plant traits in unburned communities. At the species-level, human disturbance was the main driver as shown in my finding that winners were more likely to be associated with disturbance. At the community-level, succession and forest encroachment are driving changes in unburned plots at WLNP.

Secondly, this thesis provides further support to the notion that different drivers of change should be considered in unison. In Chapter 2, I found that the effects of the wildfire and human disturbance can interact to modify how each influences plant communities. For example, increases in species richness were greater at lower elevations, where human disturbance is most prevalent, and this effect was magnified the more severe the fire. In Chapter 3, I showed the striking contrast in the trajectories of change in communities of burned versus unburned vegetation. For example, in burned plots, species that have lighter seeds and are smaller, short-lived, exotic, and disturbance associated are more likely to increase in abundance and/or frequency. In contrast, taller and woody species with heavier seeds have increased in unburned plots. By considering the effects of different drivers of change in unison, ecologists will be able to more easily determine where problem areas are more likely to be. For example, if the removal of harmful exotic species is a priority, then resource managers should focus efforts in burned areas that are subjected to more frequent recreational use by humans.

4.1 Limitations and future directions

In Chapter 2, I hypothesized that species richness would increase at higher elevations due to warming temperatures. I did not find any evidence to support this hypothesis, however this does not mean that warming temperatures have not influenced plant communities at WLNP. Future studies could test for direct influences of temperature change at WLNP by investigating whether changes in temperature have caused species to move upward in terms of elevation or determining whether warmer temperatures have favoured species with more southerly distributions. For example, legacy studies conducted in Canada (e.g. Becker-Scarpitta et al. 2019; Boisvert-Marsh et al. 2019) have incorporated community indices to assess community responses to changes in temperature over time. Doing so would provide another perspective to the results I present in this thesis and could reveal the magnitude with which climate warming has influenced plant communities over the past 25 years.

My results also risk being affected by the improper re-location of the original vegetation plots. When these plots were originally established for the Ecological Land Classification project, the plots were not permanently marked. However, the relocation accuracy of this study is likely higher than many legacy studies because the original surveyors did take GPS locations. I also had the opportunity to conduct multiple surveys with Dr. Peter Achuff, during which I was able to obtain advice regarding site selection and establishment for the original surveys. Doing so allowed me to further reduce potential errors regarding plot re-location. In addition, Dr. Achuff was able to provide insightful information regarding taxonomic changes and errors in the previously identified plant species present at WLNP. While re-location errors remain possible, it is important to note that the goal of this research was to examine trends across all plots. Therefore, I do not expect small spatial errors to bias my results. The plots surveyed for this study have now been permanently marked which will allow future re-location and surveys of these same plots to be more easily conducted in the future.

Another limitation of this study is the lack of survey points in between 1994 and today. While legacy studies are important to conduct, the gap in time between the original and re-surveys limits our understanding of how quickly these changes occurred, and precisely when. It would also have been beneficial if surveys were conducted immediately before the Kenow Fire. This would have allowed me to conduct more accurate before-after comparisons. However, the inclusion of unburned plots with similar environmental characteristics as nearby burned plots allows me to infer the likely changes that occurred in the burned plots prior to the fire event.

4.2 Concluding statement

Legacy studies across Canada cover a very small sample of the vegetation present within the country. The work presented in this thesis demonstrates how the dominant drivers of change in plant communities can vary in different regions of the country. Using re-surveys of semi-permanent (now permanent) vegetation plots and an analysis of changes in (1) species richness, (2) community composition, and (3) species traits, I present evidence that the effects of anthropogenic drivers of change in plant communities can be modified by natural drivers, and vice versa. Ecologists should continue to conduct long-term studies of plant communities in regions little studied in Canada, where legacy data can be unearthed.

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Appendix A – Chapter 2 Supplementary Material

Supplementary Table 1 Species identified to genus level due to difficulties in differentiating between them.

Genus	Entries included in dataset prior to lumping	Reason for lumping
Antennaria	*alpina* *anaphaloides* *lanata* *media* *neglecta* *umbrinella*	*Prior to the flowering stage, these species are very similar in morphology, making field identification difficult.*
Botrychium	*spp.* *virginianum*	*A tricky genus, these plants are difficult to ID when vegetative.*
Danthonia	*californica* *intermedia* *parryi*	*This genus requires a dissecting scope for proper identification. Previous records of Danthonia in WLNP differ from what is provided in A Flora of Waterton Lakes National Park.*
Draba	*lonchocarpa* *nemorosa* *porsildii* *praealta* *verna*	*These species are difficult to ID given their similar morphology prior to flowering.*
Equisetum	*arvense* *fluviatile* *hyemale* *pratense* *scirpoides*	*These species are very similar in morphology and can exhibit a wide range of variations.*
Rosa sp.	*acicularis* *woodsii*	*These two species are very similar in morphology and can be found in the same habitat, making identification of these species difficult.*
Primula	*conjugens* *pauciflora*	*These two species are very similar in appearance and difficult to ID in the field. Because few individuals were only ever found, in a given plot, no samples were taken.*
Thalictrum	*occidentale* *venulosum*	*These two species are very similar in morphology, especially when not fruiting.*

Supplementary Table 2 Absolute values of the Pearson correlation coefficients between all potential predictors and response variables (Chapter 2). Ecoregion was not included as a predictor in the models due to high correlation with elevation.

Variable	Dissimilarity (1994-2019)	Northness	Difference in survey date	Species richness in 1994	Elevation	Slope	Soil drainage	Ecoregion	Burn severity	Distance to nearest trail or road
Change in species richness (1994-2019)	0.15	0.12	0.15	0.20	0.24	0.17	0.011	0.24	0.20	0.061
Dissimilarity (1994-2019)		0.15	0.056	0.0044	0.18	0.18	0.15	0.20	0.52	0.15
Northness			0.30	0.25	0.19	0.053	0.17	0.088	0.20	0.18
Difference in survey date				0.30	0.056	0.04	0.19	0.12	0.079	0.33
Species richness in 1994					0.42	0.0044	0.064	0.39	0.11	0.23
Elevation						0.45	0.24	**0.92**	0.069	0.11
Slope							0.37	0.42	0.11	0.017
Soil drainage								0.22	0.18	0.046
Ecoregion									0.068	0.13
Burn severity										0.068

Supplementary Table 3 The following species were only recorded in the original ELC surveys (1994, 1995, 1999). Species ranks as noted in the Alberta Conservation Management Information System 2015. Alberta species rank list are noted for provincially rare species (S1 = critically imperiled, S2 = imperiled, S3 = vulnerable).

Species name	Present in # of plots	Mean abundance (% coverage)	Notes
Adenocaulon bicolor	1	1	S2
Alopecurus magellanicus	1	0.5	S3
Anemone occidentalis	1	0.5	
Anemone parviflora	1	1	
Anthoxanthum nitens	1	0.5	
Aquilegia jonesii	1	0.5	S1
Arabis hirsuta	1	0.5	
Arnica fulgens	1	0.5	
Astragalus gilviflorus	1	0.5	S3
Astragalus laxmannii	2	0.5	
Astragalus miser	1	0.5	
Braya humilis	1	0.5	S3
Carex atrosquama	1	8	
Carex filifolia	1	5	
Carex leptalea	1	0.5	
Carex phaeocephala	1	0.5	
Carex siccata	1	0.5	
Carex simulata	1	0.5	S3
Ceanothus velutinus	1	15	
Claytonia lanceolata	1	15	Burned plot
Corallorhiza maculata	1	0.5	
Corallorhiza trifida	3	0.5	
Crepis intermedia	1	1	S3
Crepis runcinata	1	0.5	
Dryas drummondii	1	45	Burned plot
Elymus trachycaulus	2	0.5	
Epilobium hornemannii	1	0.5	S3
Festuca ovina	2	3	Possible misidentification
Festuca subulata	1	3	Burned plot, S1
Fragaria vesca	1	0.5	
Galium trifidum	1	0.5	
Geocaulon lividum	1	0.5	
Geum aleppicum	2	0.5	
Hackelia floribunda	2	3	S3
Heuchera glabra	7	0.5	
Hypericum perforatum	7	0.5	
Hypopitys monotropa	1	0.5	S3
Juncus longistylis	1	0.5	
Kobresia myosuroides	1	1	
Lilium philadelphicum	1	0.5	
Melica smithii	1	1	S2
Mertensia lanceolata	1	0.5	S2
Mertensia longiflora	1	0.5	S2
Minuartia austromontana	2	0.5	S3
Musineon divaricatum	1	5	S3
Orobanche fasciculata	1	0.5	S3
Packera paupercula	1	0.5	
Penstemon eriantherus	1	2	Burned plot, S2
Phacelia lyallii	1	0.5	S2
Phyllodoce empetriformis	1	2	Burned plot
Platanthera hyperborea	1	0.5	

Species name	Present in # of plots	Mean abundance (% coverage)	Notes
Platanthera obtusata	1	0.5	
Platanthera unalascensis	3	0.5	S2
Podagrostis thurberiana	1	0.5	S3
Potentilla concinna	1	0.5	
Potentilla ovina	2	0.5	S3
Potentilla pensylvanica	2	1	
Potentilla rivalis	1	0.5	
Potentilla uniflora	2	2	
Potentilla villosa	1	5	Burned plot
Pterospora andromedea	1	0.5	
Ranunculus eschscholtzii	1	1	
Ranunculus pedatifidus	1	0.5	
Rhododendron columbianum	1	0.5	
Rhodiola rosea	3	0.5	
Rubus pubescens	2	5	
Salix nivalis	1	0.5	
Saxifraga cespitosa	1	0.5	
Silene menziesii	1	0.5	S3
Streptopus streptopoides	1	0.5	S1
Symphyotrichum subspicatum	2	0.5	S3
Townsendia parryi	1	3	Burned plot, S3
Triglochin palustris	1	0.5	
Vahlodea atropurpurea	2	1	
Valeriana dioica	3	0.5	
Veronica americana	1	0.5	
Zizia aptera	1	5	Burned plot

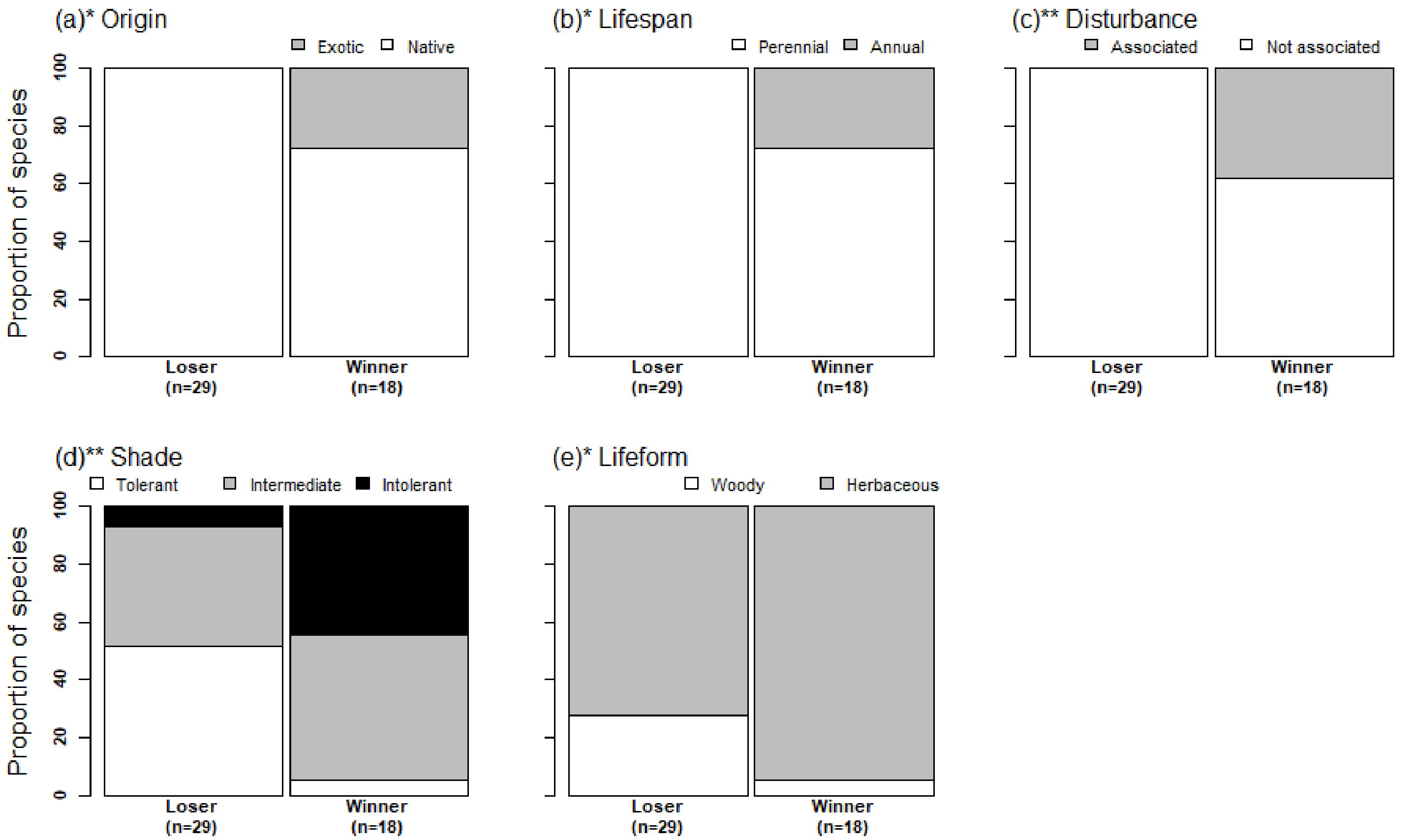
Supplementary Table 4 The following species were only recorded in the re-surveys of the ELC plots (2019 – 2020). *indicates exotic species.

Species name	Present in # of plots	Mean abundance (% coverage)	Notes
Achnatherum occidentale	4	1.5	Not known to be in WLNP in the 1990s
Agrostis exarata	1	0.5	
Agrostis scabra	1	1.5	
*Agrostis stolonifera**	1	2	
Anaphalis margaritacea	3	0.5	
*Arenaria serpyllifolia**	1	0.5	
Arnica diversifolia	1	0.5	
*Artemisia absinthium**	1	0.5	Not known to be in WLNP in the 1990s
Artemisia borealis	1	0.5	
Artemisia frigida	6	1	
Astragalus aboriginum	1	0.5	
Astragalus americanus	1	0.5	
Beckmannia syzigachne	1	1	
Boechera collinsii	1	0.5	Not known to be in WLNP in the 1990s
Boechera lemmonii	1	0.5	
Calamagrostis purpurascens	3	1	
Carex albonigra	1	0.5	
Carex aquatilis	1	0.5	
Carex concinna	1	0.5	
Carex houghtoniana	1	0.5	Not known to be in WLNP in the 1990s
Carex inops	2	1	Not known to be in WLNP in the 1990s
Carex leporinella	1	0.5	
Carex magellanica	1	0.5	Not known to be in WLNP in the 1990s
Carex nigricans	1	0.5	
Carex obtusata	1	0.5	
Carex simulata	1	0.5	
Carex tahoensis	4	0.5	Not known to be in WLNP in the 1990s
*Carum carvi**	1	0.5	Not known to be in WLNP in the 1990s
Castilleja hispida	2	0.5	
*Centaurea stoebe**	3	2	
Cerastium nutans	3	0.5	
*Chenopodium album**	6	0.5	
Cirsium scariosum	2	0.5	
Corallorhiza striata	1	0.5	
Corydalis aurea	1	0.5	
Cryptogramma acrostichoides	1	0.5	
Cryptantha celosioides	2	0.5	
Dalea purpurea	1	0.5	Not known to be in WLNP in the 1990s
*Descurainia sophia**	5	1.5	
*Dianthus armeria**	1	0.5	
Dracocephalum parviflorum	13	3	Common post-fire species
*Dryopteris dilatata**	1	2	Not known to be in WLNP in the 1990s
Dryopteris filix-mas	2	0.5	
Epilobium glaberrimum	1	0.5	

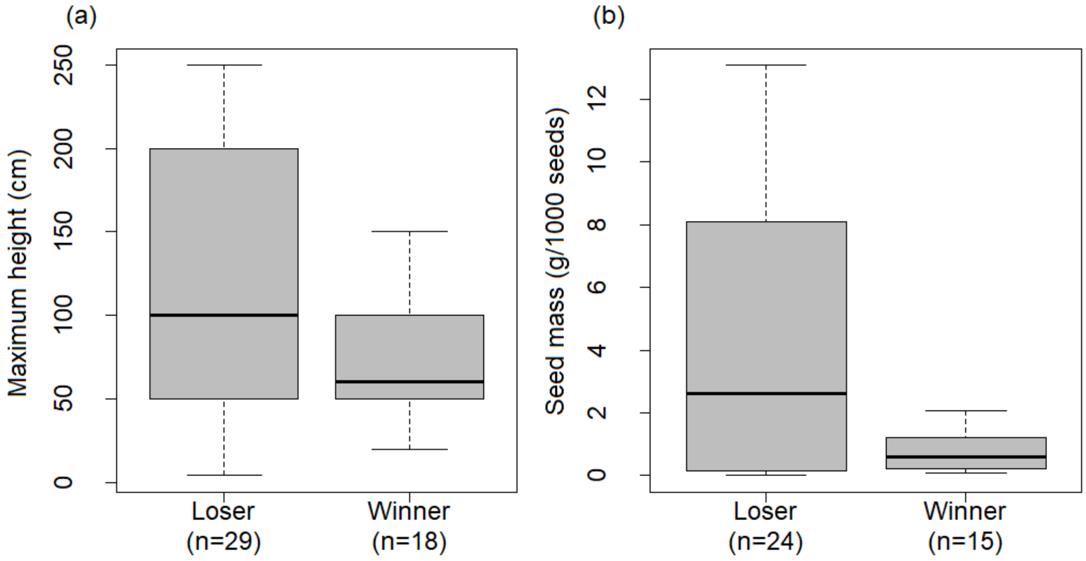
Species name	Present in # of plots	Mean abundance (% coverage)	Notes
Erigeron ochroleucus	1	0.5	
Erigeron strigosus	1	0.5	Not known to be in WLNP in the 1990s
Erysimum inconspicuum	11	1.5	
Euthamia graminifolia	1	0.5	
Festuca campestris	2	1	
Festuca rubra	1	0.5	
Galium bifolium	1	0.5	Not known to be in WLNP in the 1990s
Geranium bicknellii	11	10	Common post-fire species
Gymnocarpium dryopteris	1	5	
Hieracium umbellatum	6	0.5	
Hydrophyllum capitatum	1	0.5	
Hypericum scouleri	1	1	Not known to be in WLNP in the 1990s
Iliamna rivularis	1	0.5	
Juncus mertensianus	2	2	
Juncus parryi	2	0.5	
Lepidium densiflorum	1	0.5	
*Lepidium latifolium**	2	0.5	Not known to be in WLNP in the 1990s
*Leucanthemum vulgare**	3	0.5	
Liatris punctata	1	0.5	
Lonicera dioica	1	0.5	
Luzula parviflora	1	0.5	
Lychnis drummondii	2	0.5	
*Medicago lupulina**	5	0.5	
*Melilotus officinalis**	1	8	
Melica subulata	1	0.5	
Micranthes lyallii	2	0.5	
Micranthes occidentalis	2	0.5	
Mitella pentandra	1	0.5	
Muhlenbergia cuspidata	1	0.5	Not known to be in WLNP in the 1990s
Myosotis asiatica	2	0.5	
*Myosotis stricta**	2	0.5	
Oenothera biennis	1	0.5	
Oenothera villosa	1	0.5	Not known to be in WLNP in the 1990s
Oxyria digyna	1	0.5	
Oxytropis deflexa	2	0.5	
Packera contermina	1	0.5	
Packera cymbalaria	1	0.5	
Pascopyrum smithii	1	0.5	
Penstemon lyallii	8	1	
Penstemon procerus	1	0.5	
Perideridia gairdneri	2	0.5	
Phlox hoodii	2	0.5	
*Plantago major**	1	0.5	
Platanthera aquilonis	1	0.5	Not known to be in WLNP in the 1990s
*Poa compressa**	5	0.5	
Polygonum douglasii	3	0.5	
*Potentilla argentea**	1	0.5	
Potentilla nivea	1	0.5	
Prunella vulgaris	1	0.5	
*Ranunculus acris**	3	0.5	

Species name	Present in # of plots	Mean abundance (% coverage)	Notes
Ranunculus aquatilis	1	0.5	
Ranunculus macounii	1	0.5	
Rumex acetosa	1	0.5	
Salix exigua	1	3	
Senecio integerrimus	1	0.5	
*Sisymbrium altissimum**	1	1	
Stachys palustris	1	0.5	
Symphyotrichum foliaceum	6	3.5	
*Thlaspi arvense**	1	0.5	
*Trifolium pratense**	1	0.5	
*Trifolium repens**	2	0.5	
Typha latifolia	2	0.5	Not known to be in WLNP in the 1990s
*Verbascum Thapsus**	1	2	
Viburnum edule	2	0.5	

Appendix B – Chapter 3 Supplementary Materials



Supplementary Figure 1 The proportion of species within winner and loser indicator groups in each trait category across burned plots only by (a) origin, (b) lifespan, (c) disturbance association, (d) shade tolerance, and (e) lifeform. * indicates $p < 0.05$, ** indicates $p < 0.01$ according to a Fisher's exact test.



Supplementary Figure 2 The distribution of (a) maximum heights and (b) seed mass per 1000 seeds of the species within loser and winner indicator groups across burned plots only. The black line indicates the median height and seed mass for that survey group. Whiskers are 1.5 times the interquartile range. No significant differences according to Wilcoxon rank sums tests.

Supplementary Table 5 Results of the tests for significant associations between winners and losers and each trait in burned plots. Categorical variables are tested using a Fisher's exact test and continuous variables are tested using Wilcoxon rank sums tests.

Trait	P-value
Origin	0.012
Lifespan	0.012
Disturbance association	<0.001
Shade tolerance	<0.001
Lifeform	0.017
Maximum height	0.221
Seed mass	0.061