INVESTIGATING THE MAGNITUDE AND EXTENT OF RECREATIONAL TRAIL EFFECTS ON PLANT COMMUNITIES IN WATERTON LAKES NATIONAL PARK

HEATHER JENELLE DAVIS
Bachelor of Science, University of Alberta, 2011

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Department of Biological Sciences
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

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Dr. J. L. McCune	Associate Professor	Ph.D.
Thesis Supervisor		
Dr. M. Bogard	Associate Professor	Ph.D.
Thesis Examination Committee Member		
Dr. L. Chasmer	Associate Professor	Ph.D.
Thesis Examination Committee Member		
University of Western Ontario		
London, Ontario		
Dr. Dmytro Yevtushenko	Associate Professor	Ph.D.
Chair, Thesis Examination Committee		

ABSTRACT

Protected area managers are faced with the challenge of balancing environmental protection and recreation in a context of increasing wildfire frequency and severity. However, few studies have assessed how trail use levels, vegetation type, wildfire, and the interactions between them impact nearby plant communities. I assessed 70 trailside transects adjacent to low, medium, and high use trails and 14 off-trail transects in Waterton Lakes National Park, Alberta, Canada. I measured plant species richness and community composition at 0m, 2m, 5m, 10m and 15m from the trail edge, and tested for differences in these metrics based on distance from the trail, trail use level, vegetation type, burn status, and interactions between these factors. To calculate the total area of influence, I multiplied the extent of significant trail effects by the total trail length with the associated characteristics. As expected, species richness was elevated near trail edges compared to the 15m quadrat. However, species richness was highest along low and medium use trails relative to high use trails and off-trail. The occurrence of exotic species near trails was elevated post-fire, but only in coniferous forests. Additionally, the abundance of exotic species was higher 15m from trail edges in burned sites than unburned sites. Trails affect up to 3.1km^2 (0.61%) of vegetation in Waterton, and up to 4.5km^2 (0.89%) if informal routes have similar effects. The magnitude and extent of trail effects on plant communities depend on the complex interactions between trail use levels, vegetation type, and recent wildfire. While the total area affected is relatively small, it may increase as visitation increases and recreationalists continue to explore informal routes; therefore, this study serves as a baseline for ongoing changes caused by trails.

CONTRIBUTIONS OF AUTHORS

Chapter 2 represents original and unsubmitted work by Heather Davis (primary author) that is co-authored by Dr. Jenny McCune. Heather Davis contributed to study design and led the field work, plant identifications, data analysis, and writing. Dr. Jenny McCune conceived the project and contributed supervisorship, project management, and editing.

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LIST OF ABBREVIATIONS

AIC	Akaike Information Criterion
ANOVA	Analysis of Variance
DF	Degrees of Freedom
ELC	Ecological Land Classification
GIS	Geographic Information System
GLMMs	Generalized Linear Mixed Models
GPS	Global Positioning System
LMMs	Linear Mixed Models
LRT	Likelihood Ratio Test
PVC	Polyvinyl Chloride
REML	Restricted Maximum Likelihood
SE	Standard Error
UNESCO	United Nations Educational, Scientific and Cultural Organization
USA	United States of America

Ecoregions

FP	Foothills Parkland
MO	Montane
SL	Lower subalpine
SU	Upper subalpine
AL	Alpine

CHAPTER 1: INTRODUCTION

Canada's earliest protected areas began as tourist attractions and later become known for their conservation values (Foster, 1978). Banff National Park was the first park protected in Canada, and the Canadian Pacific Railway would attract visitors from Europe by promoting an abundance of unnamed peaks to summit and hot springs to renew health (Foster, 1978; Interpretive Guide Association, 2019). Waterton Lakes National Park (Waterton) became protected only a few years after Banff, but instead of a railway to transport people, passage by boat from Glacier National Park, USA drew people to the area. The original advocacy for protecting Waterton came from letters asking the government to protect the area because there were few such spectacular places to enjoy and that a select few could ruin it for others (Getty, 1971). In 1895, a small area near Waterton Lakes was protected. Later on in 1932, Waterton and Glacier National Park became the first international peace park in the world, announcing their significance of peace across international borders (Government of Canada, 2023). What started off as peace between two countries then became a conservation icon with an official United Nations Educational, Scientific and Cultural Organization (UNESCO) designation in 1995 commemorating the peace park for its "distinctive climate, physiographic setting, mountain-prairie interface, and tri-ocean hydrographic divide" (UNESCO, 1995). Now, Parks Canada manages national parks, and their first priority is "to protect the natural and cultural heritage of our special places and ensure that they remain healthy and whole" (Government of Canada, 2026). Conservation becomes a challenge with increasing visitation, more demand for infrastructure, and balancing disturbance from recreation with threats from climate change and associated natural disturbances.

Waterton is located in the Canadian Rocky Mountains, and many people are attracted to its beautiful landscapes. Navigating wilderness areas has become easier for people, especially with the introduction of smart phone applications (hereafter apps) guiding travel on- and off-trail. Meanwhile, very little is known about how the increase in outdoor recreation will affect the plants and animals the national parks aim to protect. Personally, I work as a professional guide, am an avid recreationalist, and previously managed a recreational program for the provincial government. Recreation is an important industry, but I have also seen how the lack of management and resources can quickly cause damage to the natural

environment. Additionally, I witness more people travelling off-trail, causing vegetation trampling, water runoff, and soil erosion.

It is well-known that trails can impact wildlife such as birds and mammals, and alter biotic and abiotic conditions near trails. Trails can cause large mammal redistribution (Marion et al., 2024; Rogala et al., 2011), cause changes in bird community composition and abundance (Bötsch et al., 2018), increase bird nest predation (Miller et al., 1998), and enhance water runoff and soil erosion (Marion et al., 2016; Wilson & Seney, 1994). Thompson et al. (2025) estimated the zone of influence of trail effects on carnivorous mammals, finding a decrease in detection rates within 267m of trails for grizzly bears and within 576m for wolves. Additionally, trails can impact nesting birds - depending on the vegetation type and the height of the bird nest. For example, in a grassland, ground-nesting birds will often leave their nest when a trail user passes by (Miller et al., 1998; Thompson, 2015). However, in montane forests, bird nests are higher off the ground and trail influence is unlikely to be the cause of declines in local bird populations (Deluca & King, 2014).

Recreational trails also affect plant communities. Once a trail is built, canopy removal allows more sunlight and rainfall to reach the forest floor, shifting plant communities to shade-intolerant species and increasing species richness. Trail users also spread seeds, often seeds of disturbance-associated or exotic species, which leads to greater occurrence and abundance of these species near trails (Benninger-Truax et al., 1992). Furthermore, trail users may step off the trail causing vegetation trampling and soil compaction. In a beech stand, the impact from road disturbances on soil and vegetation extended up to 30m (Deljouei et al., 2018). In other recent studies, trail impacts extended to at least 5m (Jaksi et al., 2026) and 10m (Chisholm & McCune, 2024) from the trail edge, with the extent of trail influence often depending on the type of vegetation traversed. However, sometimes trails can benefit plants. For instance, Catling and Kostiuk (2011) found that trails enhanced the abundance of native populations of orchids, likely because trails enhance light variability along the trailside. In addition, Dale and Weaver (1974) found that native meadow species were most prevalent at trail edges. While it is known that trails can have an impact on plant communities, very few studies (e.g. Chisholm & McCune, 2024) have assessed trail impacts and their extent in the Canadian Rocky Mountains, a world-renowned destination.

It is clear that trails have an impact on plant communities but less is known about the interactions between trail use levels, vegetation types, and wildfire. For example, can trails – especially high use trails - increase species richness or exotic species presence and abundance after wildfires? Trails can act as a pathway for seed introduction, for both desirable and undesirable species, and the magnitude of this impact may differ based on the vegetation type the trail traverses, how much use the trail receives, and whether or not the area was recently burned.

In this study, I investigated the extent and magnitude of the effects of recreational trails on plant communities in Waterton Lakes National Park. Waterton is situated in the southwest corner of Alberta bordering Montana, USA and British Columbia. The park has high plant biodiversity partly due to the fact that it encompasses four natural subregions in a relatively small area (Government of Canada, 2025a). Over 50% of the vascular plant species found in Alberta grow within Waterton's 505km^2 area (Government of Canada, 2025b). Waterton boasts an extensive trail network with over 200km of trails (Government of Canada, 2025b) and is visited by outdoor enthusiasts from Canada and around the world. In September 2017, Waterton experienced a significant wildfire, the Kenow Wildfire, that burned 50% of the park's vegetation (Government of Canada, 2025b). Therefore, Waterton provides a unique opportunity to quantify the effect of trails on plant communities and how these effects vary with trail usage, vegetation type, wildfire, and the interactions between them. This knowledge will contribute to our fundamental understanding of how, why, and when trails cause changes in ecological communities. These results can also provide information to land managers to make decisions, apply changes, and prioritize their actions to better balance conservation with recreation.

CHAPTER 2: INVESTIGATING THE MAGNITUDE AND EXTENT OF RECREATIONAL TRAIL EFFECTS ON PLANT COMMUNITIES IN WATERTON LAKES NATIONAL PARK

2.1. Abstract

Outdoor recreation and natural disturbances such as wildfire are both increasing in frequency. This makes it crucial for managers of protected areas to understand the magnitude and extent of trail effects on biodiversity. Trail effects may be magnified near popular high use trails, some vegetation types may be more sensitive to trail impacts, and trail effects could be magnified by wildfire. I evaluated the impacts of recreational trails on plant communities in Waterton Lakes National Park, a popular destination in Canada's Rocky Mountains. I assessed 70 trailside transects adjacent to low, medium, and high use trails and 14 off-trail transects in Waterton Lakes National Park, Alberta, Canada. I measured plant species richness and community composition at 0m, 2m, 5m, 10m and 15m from the trail edge, and tested for differences in these metrics based on distance from the trail, trail use level, vegetation type, burn status, and interactions between these factors. To calculate the total area of influence, I multiplied the extent of significant trail effects by the total trail length with the associated characteristics. As expected, species richness was elevated near trail edges compared to the 15m quadrat. However, species richness was highest along low and medium use trails relative to high use trails and off-trail. The occurrence of exotic species was elevated post-fire, but only in coniferous forests. Additionally, the abundance of exotic species was higher 15m from trail edges in the burned sites compared to unburned sites. Trails affect up to 3.1km^2 of vegetation in Waterton, and up to 4.5km^2 if informal routes have similar effects. The magnitude and extent of trail effects on plant communities depend on the complex interactions between trail use levels, vegetation type, and recent wildfire. While the trail effect is relatively small, it may increase as visitation increases and recreationalists continue to explore informal routes; therefore, this study serves as a baseline for ongoing changes caused by trails.

2.2. Introduction

Outdoor recreation is increasing globally as the human population continues to grow and people seek outdoor connection and experiences (e.g. Custom Market Insights, 2024; Outdoor Foundation, 2024).

In Canada, national parks received approximately 22.5 million visits in 2023/24 and 23.2 million visits in 2024/25 (statista, 2026). At the same time as visitation is increasing, managers of national parks strive to conserve these areas in a condition that is characteristic of their natural state, including the composition and abundance of native species and biological communities (e.g. Government of Canada, 2025c). Recreational disturbance is facilitated by and tends to be concentrated along trails that allow access for multiple activities including hiking, bicycling, or motorized use. It is important to understand the effects of recreational trails on plant communities so that land managers can make evidence-based decisions about invasive species management plans, trail use capacity, trail density, appropriate locations for new and/or rerouted trails, where and when to implement seasonal trail closures, and potential permanent trail closures and/or reclamation. Remarkably, I am not aware of any published studies that quantified trail effects on plant communities in Canada's National Parks.

Recreational trails often cause a shift in the diversity and composition of the plant communities they traverse (e.g. Chisholm & McCune, 2024; Dale & Weaver, 1974; Pescott & Stewart, 2014). For example, the total number of plant species present is often elevated near trail edges (Chisholm & McCune, 2024; Wedegärtner et al., 2022) because the trail allows more light to penetrate the forest floor, especially when trees are removed to build a trail and provide gaps in the forest canopy (Beckage et al., 2008). Some herbaceous plant species can survive with less than 2% of full daylight, but most land plants that grow naturally in the open need at least 30% of full daylight to thrive and photosynthesize (Stern et al., 2008). Trails can also cause changes in plant community composition: that is, which species are present and in what relative abundances. Conditions near trail edges tend to favour exotic species and species adapted to disturbance (Bates, 1935; Liedtke et al., 2020; Mount & Pickering, 2009). For example, the frequent trampling along trail edges favours low-growing, herbaceous species that can tolerate or quickly recover from trampling damage (Bates, 1935; Pescott & Stewart, 2014). Furthermore, trail edges promote shade-intolerant species that cannot persist in closed-canopy environments (Bates, 1935; Dale & Weaver, 1974). It is often unknown how far from the trail these impacts extend and thus the total area of altered plant community diversity and composition is also unknown for most recreational areas.

The effects of trails on plant communities and their extent of influence into the surrounding vegetation might vary depending on trail use levels. The amount of trail use varies based on the popularity of the trail and how far people venture from the trailhead (Kariel, 1984). High use trails may have higher trailside species richness relative to infrequently used trails because seeds can attach to clothing, gear, or even animal fur and then be released beside the trail (Liedtke et al., 2020; Mount & Pickering, 2009; Will & Tackenberg, 2008), leading to greater seed dispersal rates with higher trail use levels. At the same time, plant communities adjacent to very highly used trails could see reduced species richness due to very high levels of trailside trampling, despite high seed dispersal rates. For example, Parikesit et al. (1995) found species richness to be highest along moderately used trails compared to low and high use trails. They suggested that moderate levels of trampling prevent dominance by the most competitive species, promoting higher species richness, but too much trampling reduces species richness because only a few species can tolerate such high levels of disturbance.

The magnitude of trail effects on plant communities could also vary depending on the vegetation type that the trail traverses. For instance, when a trail is built within a closed-canopy forest it allows more light to penetrate into the forest along the trail edge which shifts plant communities from shade-tolerant to light-tolerant species (Ballantyne & Pickering, 2015; Marion et al., 2016). Chisholm and McCune (2024) found that plant species richness was elevated near trails edges compared to 10m away in forests but not in grasslands. They suggest the light availability is consistently high in grasslands even when moving away from the trail edge; therefore, the trail does not change the light intensity beside the trail or far away from the trail. Additionally, van Vierssen Trip and Wiersma (2015) tested how all-terrain vehicles impacted habitat types (boreal forest, heaths, and bogs) and found that dry forested sites were more resilient to direct on-trail erosion than wet heaths or bogs but less resistant to indirect off-trail vegetation disturbance.

The increase in outdoor recreation is occurring at the same time as wildfire severity and frequency are increasing (Bowman et al., 2011; Wenrui et al., 2025). The effects of trails on plant communities could be magnified by natural disturbances like wildfire. Prior to a natural disturbance, the presence of established native species may prevent colonization by exotics or other disturbance-associated species outwards from trail edges. However, if a natural disturbance removes the existing vegetation to uncover bare soil and

additional nutrients (Crawford et al., 2001; Freeman et al., 2007; Rejmánek, 1989) this may enable exotic and/or disturbance-associated species to spread farther along a trail and away from the trail edge. Lloren and McCune (2024) found that increases in disturbance-associated plant species two to three years following a wildfire were magnified in sites closer to roads or recreational trails. However, some studies have shown that the increase in abundance of exotic species is short-lived after a wildfire. Romme et al. (2011) noted an increase in exotic species abundance initially post-fire in Yellowstone National Park, but within two decades the exotic species declined as succession advanced. While much is known about the relationship between fire and vegetation recovery, the influence of trails on the recovery of plant communities post-fire remains unclear. For example, a low use trail may not introduce many new species post-fire, but trails frequented often might enhance the seed bank and affect post-fire recovery through human-assisted seed dispersal. Some seeds may be beneficial to the burned area and help with re-establishment of vegetation post-fire; however, some seeds may be undesirable exotic species. Therefore, it is important to understand how trails interact with natural disasters to facilitate shifts in plant communities.

In this thesis, I quantify the effects of recreational trails on plant communities in Waterton Lakes National Park, in Canada's southern Rocky Mountains. There are 202km of formal recreational trails in the park (Government of Canada, 2025b) and visitation is increasing, with a 6.8% increase from 2024 to 2025 when Waterton welcomed nearly 585,000 visitors (statista, 2026). Both formal trails and informal routes transect four different ecoregions supporting diverse plant communities including coniferous and deciduous forests, shrublands, and grasslands. In September 2017, the Kenow Fire burned approximately 50% of the vegetation, which allows me to contrast trail effects in burned and unburned areas. My objectives were:

1. To measure the effect of recreational trails on species richness, community composition, and the presence and relative abundance of exotic species, and to quantify how far these effects extend away from trails.
2. To test how trail use levels, vegetation type, burn status or interactions between them influence the effect of trails on species richness, community composition, and the presence and relative abundance of exotic species.

3. To estimate the total area of influence from recreational trail use on plant communities in Waterton based on the total length of (a) formal trails, and (b) both formal and informal trails.

2.3. Methods

2.3.1. Study Area

Paahtómahksikimi (or Waterton Lakes National Park, hereafter Waterton) is situated in the southwest corner of Alberta bordering the state of Montana, USA and the province of British Columbia (**Figure 1**). Waterton was first protected as a Dominion Forest Park and Wildlife Reserve in 1895 and

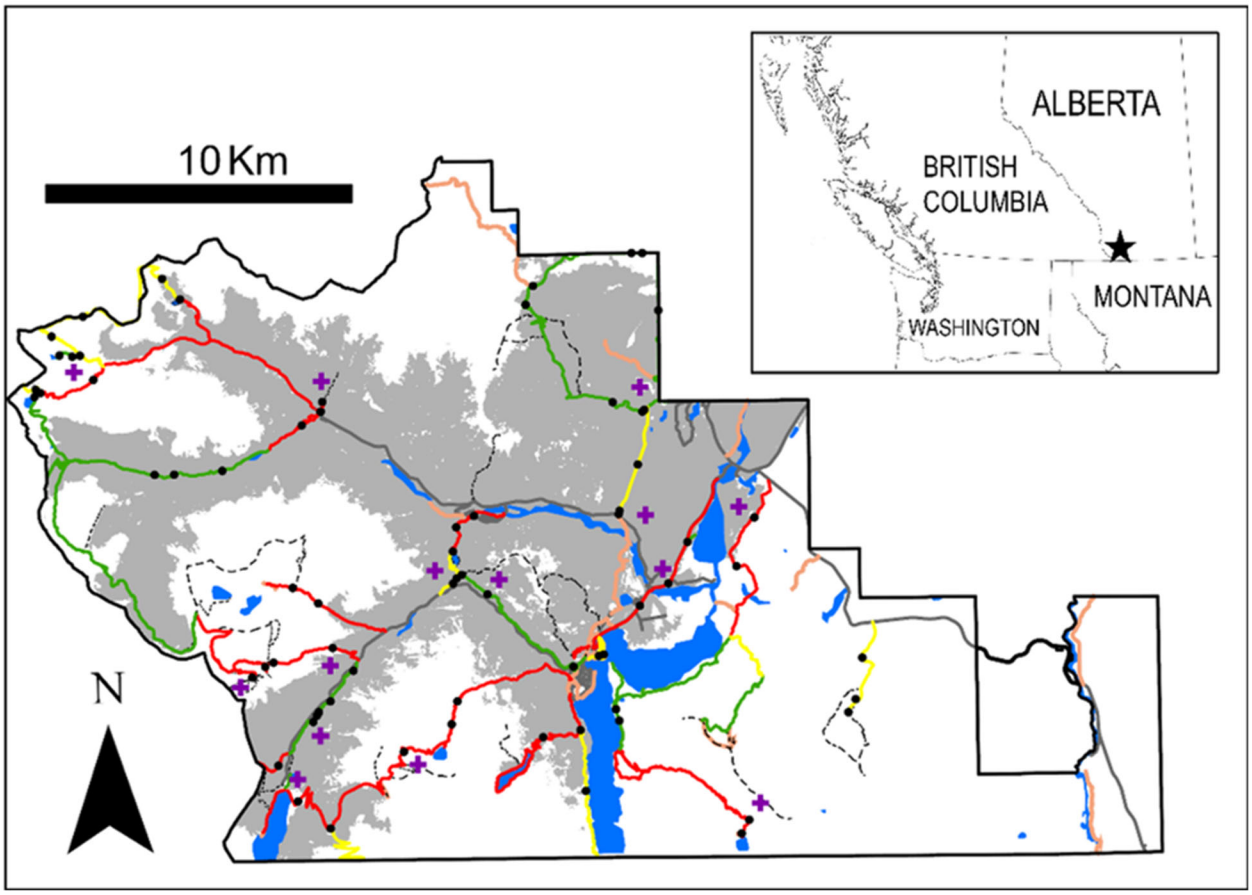

Figure 1. *Inset:* Western North America showing the location of Waterton Lakes National Park in southwestern Alberta (star). *Main map:* Waterton Lakes National Park. Park boundaries are solid black lines. Grey shading indicates the extent of the 2017 Kenow Wildfire. Official trails are shown as red (high use), yellow (medium use) or green (low use) lines. Informal routes determined by Strava are denoted by black dashed lines, and Parks Canada's informal trails are denoted by peach-coloured lines. Black points are surveyed trail transects and purple crosses indicate approximate locations of off-trail transects. Grey lines are roads. Waterbodies are blue.

became the first International Peace Park in the world with Glacier National Park, Montana in 1932 (Government of Canada, 2023). In 1995, it was designated a UNESCO World Heritage Site due to its unique ecologically diverse landscape (UNESCO, 1995). Over 50% of the vascular plant species found in Alberta grow within Waterton's 505 km^2 area (Government of Canada, 2025b), with 971 vascular plant species found during the Ecological Land Classification (ELC) survey in the 1990s (Achuff et al., 2002).

The park encompasses four ecoregions: the foothills parkland (FP), montane (MO), subalpine (SU = upper subalpine; SL = lower subalpine), and alpine (AL). The FP occurs between 1,025 and 1,525m elevation, and is defined by rolling to hilly native grasslands on south-facing slopes, with aspen woodlands and willow shrublands in low-lying areas or on northerly slopes (Alberta Parks, 2015). The MO occurs between 825 and 1,850m elevation and is characterized by forests such as lodgepole pine and aspen, and grasslands on south and west-facing slopes. The SU and SL occur between 1,300 and 2,300m. At higher elevations, open stands of Engelmann spruce and subalpine fir are common, with lodgepole pine forests at lower elevations. The AL occurs between 1,900 and 3,650m elevation and plant growth is limited with low-growing shrubs and herbs. While winters are long in Waterton, it is one of the warmest places in Alberta during the winter with temperatures as high as 10°C. Temperatures in the summer can get as high as 35°C. Waterton receives the highest average annual precipitation (1,072mm) in Alberta (Government of Canada, 2025d). A remarkable east-west gradient in precipitation also exists throughout Waterton with the western edge receiving three times more precipitation than the eastern edge (Kuchar, 1973).

Historically, wildfires of mixed severity were common in the area. It is estimated that a fire occurred somewhere in the park area on average every seven years until the early 1900s, when wildfires were suppressed (Barrett, 1996). Studies estimating fire history using cores from fire-scarred trees and early 1900s aerial photographs suggest that before the 1940s, a coniferous forest in the park would have burned on average every 84 years (Barrett, 1996). In September 2017, a high severity wildfire – known as the Kenow Wildfire - swept through the park, burning 50% of its vegetation (Government of Canada, 2025a).

Waterton has an extensive trail network with 202km of formal and well-maintained trails (Government of Canada, 2025a) used by hikers, horseback riders, and mountain bikers from Canada and around the world. Formal trails are maintained by Parks Canada and are published on government issued

maps. Parks Canada has designated each formal trail with allowable uses, with hiking allowed along every trail. In addition, informal trails and routes exist throughout the park and off-trail hiking is permitted when formal area closures are not in place. However, Parks Canada discourages off-trail hiking in areas such as the Front Range via strategies such as active restoration, minimal promotion and lack of signage (Parks Canada, 2022). I designated Parks Canada's non-official trails, which were shared with me via a geospatial layer, as "informal trails". In addition, exploring off-trail has become easier in recent years due to smart phone apps which allow users to follow routes uploaded by other adventurers. I designated routes obtained from smart phone apps as "informal routes". Informal trails and routes are not maintained by Parks Canada but can be used frequently, especially in the summer months. Formal trails and informal trails/routes are found in all ecoregions. In addition to trails, Waterton has three main parkways which provide vehicle access to trailheads. Roads and trails are the primary linear disturbances in the park, which contribute to a linear footprint density of 0.58km/km^2. In comparison, the linear footprint density in Banff National Park is 0.19km/km^2 and density in the Castle region, a provincial park directly north of Waterton, is 1.31km/km^2 (Farr et al., 2017).

2.3.2. Study Design

I focused the study on all formal trails and the informal Sofa Mountain trail. Parks Canada removed the Sofa Mountain trail from the formal trail network in the 1990s to reduce trail use in this area, but prior to that it was maintained as a formal trail. To categorize trail use, I first segmented all trails according to high, medium, and low use levels of recreational trail use based on a database provided by Parks Canada. This database divides trails into segments between major junctions and provides an estimate of the level of use (high, medium, or low) for each segment. This estimate is based mainly on staff knowledge. While Parks Canada has deployed trail counters from 2007 to present on a few high use trails, quantitative data on use levels are not available for most trails (C. Gustavison, personal communication, February 16, 2024). Almost all trail segments had an estimate of trail use level with exception of the Little Dipper Trail, some trails around the Prince of Wales Hotel, and the Kootenai Brown trail, including the spur trail going to Kootenai Brown's grave. When trail use was not available from the Parks Canada database, I used data from a popular app called Strava to estimate trail use levels. Recreationalists use Strava to help

navigate routes others have made public and to post their trip routes and statistics. Strava has a publicly available Global Heatmap assigning colours to their map to show how much the trail is used. It is important to note that this data is updated monthly based on all records from the previous 12 months and is based on data from trail users who use the app with their visibility settings set to 'Everyone' (Strava, 2024). To categorize trails into high, medium, and low use, I zoomed in to 300 feet (91m) on the map and then used the 'hot' colour spectrum provided by Strava to define all relevant trails. The map shows trails and routes varying in colours from white to yellow/orange to dark pink and 'heat' is only visible when multiple users have uploaded their data in the past year. Unfortunately, Strava does not show the actual number of trail users associated with these colours. However, white represents relatively high use, yellow/orange medium use, and dark pink low use. In most cases, I replicated the same trail segmentation as Parks Canada; however, in some cases I increased the number of segments. For example, Strava showed Blakiston Valley as being high use from Red Rock Parkway to Blakiston Falls, after the falls it was medium use until the trail reached an opening created by an avalanche pathway, then it was low use past the avalanche pathway. Meanwhile, Parks Canada segmented this section into two segments. I then created two maps to show the trail use levels based on Parks Canada and Strava's data and found that they agreed 82% of the time. Because the Parks Canada data is based on long-term manager experience, I used Parks Canada data on use level when available and supplemented the unknown segments with the data from Strava. The final trail use map had a total of 96km of high use trails, 36km of medium use trails, and 70km of low use trails.

I then used a Geographic Information System (GIS) (Esri Inc., 2023) to randomly select a set of points along the focal trails. To ensure representation of sample points throughout the park, I overlaid the park area with a grid made up of 5km x 5km cells. Using the 'select random points' tool, I selected four points at least 100m apart on trails of each use level, if present, in each grid cell. This process yielded 185 candidate survey sites.

2.3.3. Data Collection

From June to August 2024, my field assistants and I collected data on the vascular plant community at 70 trail transects from the randomly selected locations and 14 off-trail transects (**Figure 1**). I aimed to

ensure a relatively even representation of the ecoregions, trail use level, and burn status (burned and unburned) of the surveyed sites (**Table 1**). We surveyed low elevation sites first and moved to higher elevations as the summer progressed. We were mostly limited to sites we could reach on foot in one day, although we did camp overnight to reach some sites that were farther in the backcountry.

We navigated to each selected location using a handheld global positioning system (GPS). At each location, we set up a 15m transect perpendicular to the trail (**Figure 2**). We chose which side of the trail to survey based on safety and a good representation of the vegetation. For instance, if one side of the trail was near a creek or cliff, then we chose to survey the opposite side of the trail. If both sides of the trail were safe and unobstructed, then we randomly selected which side to survey by playing rock, paper, scissors. To measure changes in the understory plant community moving outwards from the trail, we surveyed five 1m x 1m quadrats (constructed with light-weight PVC pipe) placed at 0m (immediately beside the trail), 2m, 5m, 10m, and 15m from the trail edge (**Figure 2**). We placed the 0m transect where the bare trail edge ended and relatively continuous vegetation began. I noted disturbance such as loose soil or cut vegetation or trees from the trail which spilled over into the transect, presumably from trail maintenance. I chose to survey up to 15m from the trail edge because, while many studies have failed to find trail effects beyond 10m from trail edges (e.g. Dickens et al., 2005; Godefroid & Koedam, 2004; Ngugi et al., 2014; Watkins et al., 2003), Chisholm and McCune (2024) found that trail effects may extend beyond 10m in the Castle Provincial Parks, an area adjacent to Waterton.

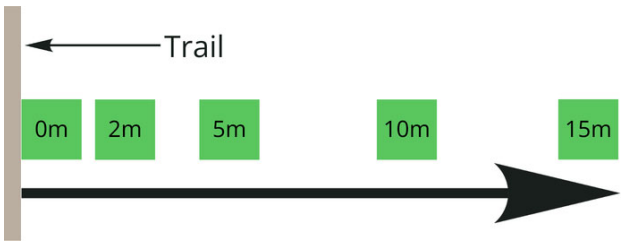

Figure 2. Diagram of trail transect and location of the 1m x 1m quadrats. Not to scale.

Within each quadrat, we identified every vascular plant under 2m in height and estimated the percent cover of each. We took photos or samples of specimens we could not identify in the field to identify later in the lab. In addition, at each trail transect we noted whether the transect was upslope or downslope from the trail, the trail direction, the slope angle and steepness, elevation, longitude/latitude, the dominant

tree species on both sides of the trail, vegetation type (coniferous, deciduous, mixed, grassland, or shrubland), and whether or not it had burned in the Kenow Fire (burned or unburned). We recorded elevation using the handheld GPS. We also measured trail width, depth, and soil compaction. We used a pocket spring-operated soil penetrometer (5DPJ8 Humboldt) to measure soil compaction in the centre of the trail and in the centre of each quadrat.

To estimate the natural fluctuations in plant community diversity and composition over 15m, I also surveyed 14 off-trail transects. Natural fluctuations will be present in all transects due to variations in light, moisture, topography, and other site-specific parameters found across any 15m distance, even if a trail is not present (Chisholm & McCune, 2024). To determine the location of the off-trail transects, I paired them with 14 of the trail transects selected strategically so there would be a relatively even representation of ecoregions and burn status (**Table 1**). When setting up the transect, I walked 50m from the end of a selected trail transect and placed a 15m transect running in the same direction as the trail transect moving away from the trail. I ensured the off-trail transect did not intersect with another disturbance, such as a road or another trail, by measuring distances on my phone using the Gaia GPS app (Gaia GPS, 2024). There was a minimum of 65m between any location along the transect and another anthropogenic disturbance. At each off-trail transect, we surveyed 1m x 1m quadrats at 0m, 2m, 5m, 10m, and 15m. We collected the same data as the trail transect with the exception of trail specific data, such as depth, width and compaction. Compaction was measured from the centre of each quadrat.

Table 1. Number of trail and off-trail transects surveyed within each trail use level, ecoregion, and burn status in Waterton Lakes National Park. Ecoregions are: SU = upper subalpine, SL = lower subalpine, MO = montane, FP = foothills parkland.

Trail use level	# trail transects	# off-trail transects	Ecoregion	# trail transects	# off-trail transects	Burn status	# trail transects	# off-trail transects
High	24	na	SU	15	4	Burned	37	7
Medium	18	na	SL	23	3	Unburned	33	7
Low	28	na	MO	22	3			
			FP	10	4			

I identified vascular plant species using keys in ‘Vascular Flora of Alberta: An Illustrated Guide’ (Kershaw & Allen, 2020), ‘Flora of Alberta Second Edition’ (Moss & Packer, 1959), ‘Common Plants of the

Western Rangelands: Volume 1 Grasses and Grass-like Species' (Tannas, 2001), and 'A Flora of Waterton Lakes National Park' (Kuijt, 1982). I used additional sources 'Flora of North America' (Flora of North America, 2025), 'iNaturalist' (iNaturalist, 2025), and 'Vascular Flora of Alberta: Illustrations and Maps' (Kershaw & Allen, 2024) to confirm my identifications. I based nomenclature on the Canadensys online Database of Vascular Plants of Canada (Brouillet et al., 2010+). I lumped all meadow rue species as *Thalictrum spp.* and snowberry species as *Symphoricarpos spp*. In addition, some specimens could be identified only to the genus level, and 25 plant specimens lacked diagnostic features. I categorized all known species as exotic or native as reported by the Alberta Conservation Information Management System (Government of Alberta, 2025). Non-native plants are often referred to as exotic or alien, and have been introduced to Alberta (Government of Alberta, 2026).

2.3.4. Statistical Analyses

2.3.4.1. Assessing characteristics of trails with different use levels

I first tested for significant differences in trail depth and width, and the change in soil compaction moving along the 15m transect for the four trail use levels (off-trail, low use, medium use, and high use). The trail depth data was skewed and there were several trails with depth of 0cm, so I applied a data transformation of ln(x+1) to the data. I also took the natural log of the trail width data due to a violation of the normality assumption for the analysis of variance (ANOVA) test. I then used an ANOVA for trail depth and one for trail width to test for differences among trail use levels. To test for differences in soil compaction extending outwards from trails of different use levels I used a linear mixed model (LMM) with the predictors distance (0m, 2m, 5m, 10m, and 15m), trail use level, vegetation type (grassland, mixed, coniferous), and the interactions between them. I specified transect identity as the random effect to account for the non-independence of quadrats within the same transect. I included vegetation type as a covariate because off-trail trampling (and thus soil compaction) may be more extensive in certain vegetation types. For example, going off the trail in a grassland is much easier for a trail user than a dense shrubland. To test the effect of each predictor or interaction while accounting for the other predictors, I used a *drop1* test to perform marginal fitting of terms. The *drop1* test compares a model without the predictor of interest to the full model. If interactions were not significant, I refit the model without them and repeated the *drop1* test. I made

distance from the trail a categorical predictor and used post-hoc pairwise Tukey tests to determine which pairs of distances differed significantly (Wright, 1992). To evaluate how much better the final model was compared to an intercept-only null model, I calculated the difference in Akaike Information Criterion (AIC) between the two models. AIC is a measure used to assess models by balancing goodness-of-fit and the number of variables included, computed using the log-likelihood and a penalizing term for parameters (Akaike, 1974). A model with an AIC of two units or more lower than the null model is considered to be better than the null model.

2.3.4.2. Modelling trail effects on plant communities

To test the effects of recreational trails on plant communities, I evaluated species richness, community composition, the presence or absence of at least one exotic species, and the relative abundance of exotic species in each quadrat. Species richness was the total number of vascular plant species in each quadrat. I measured shifts in community composition moving along each transect by calculating the dissimilarity of the community in each of the first four quadrats to the 15m quadrat. I used the 15m quadrat as the baseline for comparison, considering this distance to be the least affected by disturbance from trail effects. I calculated the Bray-Curtis dissimilarity metric based on the square-root transformed abundance (percent cover) of each species in each quadrat. This metric ranges between 0 and 1, where 0 indicates identical plant community composition with the same species present in equal abundances and 1 indicates that the two quadrats have no species in common (Bray & Curtis, 1957). I quantified the relative abundance of exotic species by dividing the summed abundance of all exotic species in each quadrat by the total cover of all species.

To explain changes in the plant communities moving out from the trail edge, I used distance from the trail (categorical: 0m, 2m, 5m, 10m, 15m), trail use level (off-trail, low, medium, high), vegetation type (grasslands, mixed, coniferous), and burn status (burned, unburned) as the predictor variables. I coded distance from the trail as a categorical predictor so that I could use post-hoc pairwise tests to determine which distances differed significantly. Due to low representation of transects in some vegetation types, I combined the mixed, deciduous, and shrubland vegetation types into one category called ‘mixed’. I

classified transects as ‘burned’ if they burned in the Kenow Fire and ‘unburned’ if they did not. If I was unsure about the burn status in the field, I confirmed the status using GIS. One transect was partly burned and I removed it from all analyses that included burn status as a predictor.

I used generalized linear mixed models (GLMMs) and linear mixed models (LMMs) to test for effects of distance from the trail edge, trail use level, vegetation type, burn status, and their interactions on species richness, community composition, exotic species presence or absence, and the relative abundance of exotic species. I included transect as a random effect in each model due to the non-independence of the quadrats within the same transect. I also considered interactions between the variables. For example, the magnitude of change in the relative abundance of exotics moving outwards from a trail might depend on the burn status (2-way interaction between distance and burn). It is also possible to have three-way interactions. For example, the change in plant communities moving outwards from a trail edge might depend on burn status in combination with the use level of the trail. I did not have enough data to include all the 3-way interactions (distance x use level x vegetation type, distance x use level x burn status, distance x burn status x vegetation type) in a single model. Therefore, I took a ‘subset models’ approach as follows: I created three models for each response variable excluding one predictor variable (vegetation type, trail use level, or burn status) each time. This allowed me to evaluate one 3-way interaction per model while including the associated 2-way interactions and predictors. Note that in the models excluding trail use level, I excluded off-trail transects so that the results represent trends near trails only. I used marginal fitting of terms (*drop1* test) to determine whether the 3-way interaction was statistically significant. If the 3-way interaction was not significant at $p<0.1$, I refit the model without it. A less stringent significance level for the 3-way interactions allowed detection of potential interactions when the sample size is small. I then repeated the marginal fitting of terms and eliminated any two-way interactions that were not significant at $p<0.1$, so that I could test the importance of each singular predictor alone. After building the final reduced model for each response variable, I ensured there were no model specification errors using scaled residuals for each model (Hartig & Hartig, 2017). I also ensured no spatial autocorrelation of the residuals using spline correlograms (Bjørnstad & Falck, 2001).

For species richness (count data) I used the Poisson family. I included elevation as a covariate because it is well documented that as elevation increases, species richness declines (Grytnes, 2003; McCain & Grytnes, 2010). For Bray-Curtis dissimilarity, I used LMMs. While the metric for dissimilarity ranges between 0 and 1, the model assumptions were not violated. I did not include elevation as a covariate in these models because there is no indication that elevation would alter the change in community composition moving from 0m to 15m along a transect. For the relative abundance of exotic species, I used a two-step 'hurdle model' approach due to the large quantity of quadrats with 0% relative abundance of exotic species. I first modeled the presence or absence of at least one exotic species with a binomial GLMM. I then modeled the relative abundance of exotic species in the set of all quadrats with at least one exotic species present using lognormal GLMMs. Relative abundance of exotic species had an approximate lognormal distribution with a low relative abundance of exotics in several quadrats and only a few quadrats with a high relative abundance of exotics. Rank deficiencies prevented the inclusion of 3-way interactions in models of relative abundance; therefore, I included only 2-way interactions in each model subset. I included elevation as a covariate in models for exotic species presence and abundance because fewer exotic species tend to be present at higher elevations (Chisholm & McCune, 2024). However, high use trails could spread exotic species to higher elevations (Chisholm & McCune, 2024); therefore, I included the interaction between trail use level and elevation in the models assessing exotic species. I standardized elevation prior to inclusion for all models by subtracting the elevation by the mean elevation, then dividing by the standard deviation.

To identify which categories differed for a significant predictor or interaction, I performed post-hoc pairwise comparisons of the estimated marginal means and used the Tukey adjustment for multiple tests (Wright, 1992). For example, when distance was a significant predictor or included in a significant interaction, I used pairwise tests to determine which distances were significantly different from the 15m distance. This allowed me to estimate the maximum distance over which trail impacts extend out from the trail. If distance was not significant, then the post-hoc tests determined which categories of trail use level, vegetation type, or burn status differed from each other. Lastly, I compared the null model with the intercept and random effects only to the final model by calculating the difference in AIC (deltaAIC).

I performed all statistical analysis using R software, version 4.5.1 (R Core Team, 2023). To calculate dissimilarly I used the ‘vegan’ package (Oksanen et al., 2020). I used packages ‘glmmTMB’ (Magnusson et al., 2017) to fit binomial and lognormal GLMMs, ‘lmertest’ (Kuznetsova et al., 2017) to fit LMMs, and ‘ncf’ (Bjørnstad & Falck, 2001) to build spline correlograms. To complete the post-hoc tests, I used the ‘emmeans’ package (Lenth, 2023). To visualize the model predictions, I created partial regression plots using ‘visreg’ (Breheny and Burchett, 2017).

2.3.4.3. Estimating total area of influence

To estimate the total area of influence of trails on each response variable, I used GIS to measure the total distance of trails with characteristics of each significant interaction and predictor. For example, if one of the plant community response metrics was found to be significantly different up to 2m along a low use trail in the burned area, I then tallied the total length of low use trails within the burn in Waterton. I excluded trail segments that do not bisect any vegetation, such as talus or rocky slopes, from the calculation. I then multiplied this total distance by four (to account for both sides of a trail) to determine the total area influenced.

The total extent of trail impacts should include informal trails and routes, especially as these areas increase in popularity. Parks Canada provided spatial data including informal trails. To determine informal routes, I collected data via Strava’s online Global Heatmapping and only included routes with more than one line segment along the same route. If an area had several routes spread out in the same area and it was hard to determine an exact route, such as the route to ascend Bertha Mountain summit, then I only assessed one route through the area. If it was easy to decipher multiple routes and they had multiple line segments, then I included all routes. I excluded routes located on roads and water. I decided not to assign use levels for the informal trails and routes as the informal trails could not be classified. Hence, I assumed all informal trails and routes as low use. It is important to note that I only captured informal routes which Strava has documented with heatmapping, but other informal routes certainly do exist in Waterton. From personal experience, I know other routes exist such as those summitting Galwey and Bellevue Hill, horseback riding routes through the eskers, routes to climbing crags along Pass Creek, and Crandell Lake trails that show on GEM Trek maps travelling from the townsite to Camp Canyon (Nelson et al., 2017).

Therefore, I consider my estimated length of informal trails and routes to be an underestimate of the actual length.

To estimate the total area of the park's vegetation influenced by informal trails and routes, I followed the same steps as for the formal trails. Lastly, I compared the total area of influence to the total vegetation cover in Waterton to give a percentage of the park's vegetated areas impacted by recreational trails. Note that Waterton covers 505km², but only 367km² is covered by vegetation (the remainder is unvegetated rock, developed land, or water).

To calculate these estimations based on vegetation type, burn status, and trail use levels, I used GIS layers. To determine vegetation type, I used a layer from Alberta Biodiversity Monitoring Institute called "Wall-to-Wall Land Cover Map 2010 Version 1.0" (Alberta Biodiversity Monitoring Institute, 2010). To determine the burned area, I obtained a GIS layer from Parks Canada that delineates the extent of the Kenow Wildfire (**Figure 1**).

2.4. Results

Overall, I observed 423 species of vascular plants in the 84 surveyed transects. The most frequently occurring species were fireweed (*Chamaenerion angustifolium;* 152 quadrats), shinyleaf spirea (*Spiraea lucida;* 129 quadrats), broadleaf arnica (*Arnica latifolia*; 127 quadrats), northern bedstraw (*Gallium borealis*; 110 quadrats), and meadow rue (*Thalictrum* spp.; 107 quadrats). The most abundant species were beargrass (*Xerophyllum tenax*; summed percent cover 2256.5), thimbleberry (*Rubus parviflorus;* 1463.0), shinyleaf spirea (*Spiraea lucida;* 1331.0), snowberry (*Symphoricarpos* species; 911.0), false azalea (*Menziesia ferruginea*; 805.5), and fireweed (*Chamaenerion angustifolium;* 770.5). The most frequent exotic species were common dandelion (*Taraxacum officinale;* 75 quadrats), Kentucky bluegrass (*Poa pratensis*; 73 quadrats), timothy (*Phleum pratense;* 50 quadrats), pale madwort (*Alyssum alyssoides*; 29 quadrats), and smooth brome (*Bromus inermis;* 20 quadrats). The most abundant exotic species were Kentucky bluegrass (*Poa pratensis*; summed percent cover 551.5), Canada bluegrass (*Poa compressa*; 244.5), timothy (*Phleum pratensis*; 232.0), smooth brome (*Bromus inermis*; 193.0), and common dandelion (*Taraxacum officinale*; 178.0).

2.4.1. Characteristics of Trails for Different Use Levels

When assessing trail width and depth, I found only trail width differed significantly with trail use. Trail width increased as trail use level increased (**Table 2**; **Figure 3A; Appendix 1, Table A1.1**); yet, trail depth was similar across all trail use levels (**Table 2; Figure 3B; Appendix 1, Table A1.2**). As expected, soil compaction along the transect was highest at the trail edge and then declined moving out from the trail; however, soil compaction moving out from the trail did not vary based on trail use level, vegetation type, or the interactions between them. Only the 0m quadrat had significantly greater soil compaction than the 15m quadrat (**Table 3**; **Figure 3C; Appendix 1, Table A1.3**).

Table 2. Summaries of the linear mixed models for trail width and depth with trail use levels. Coefficients for trail use levels are in comparison to the reference category 'low use'. Residual standard error is 0.48 (trail width) and 0.68 (trail depth) on 347 degrees of freedom (df).

Predictor	Coefficient	SE	df	t value	p‡
trail width					
intercept	4.11	0.04	347	93.05	**<0.001**
use level (medium)	0.22	0.07	347	3.28	**0.001**
use level (high)	0.69	0.06	347	11.53	**<0.001**
trail depth					
intercept	1.49	0.06	347	23.83	**<0.001**
use level (medium)	-0.14	0.10	347	-1.45	0.147
use level (high)	-0.15	0.09	347	-1.77	0.078

‡ p-value based on an ANOVA test with a 95% confidence level.

Table 3. Summary of linear mixed model for soil compaction moving out from the trail edge including trail use and vegetation type as predictors. I included transect ID as a random effect to account for non-independence of quadrats within the same transect. Coefficients for distance are in comparison to the reference category '0m', for use level to the reference category 'low use', and for vegetation type to the reference category 'grassland'.

Predictor	Coefficient	SE	df	F value	p‡
intercept	-0.15	0.22	na	na	na
distance (2m)	-0.55	0.15	276	8.18	**<0.001**
distance (5m)	-0.48	0.15			
distance (10m)	-0.71	0.15			
distance (15m)	-0.73	0.15			
use level (medium)	0.10	0.25	65	0.82	0.445
use level (high)	-0.19	0.22			
vegetation type (mixed)	0.08	0.21	65	0.91	0.409
vegetation type (coniferous)	0.35	0.26			

‡ p-value based on term deletions using Satterthwaite's method in a *drop1* test.

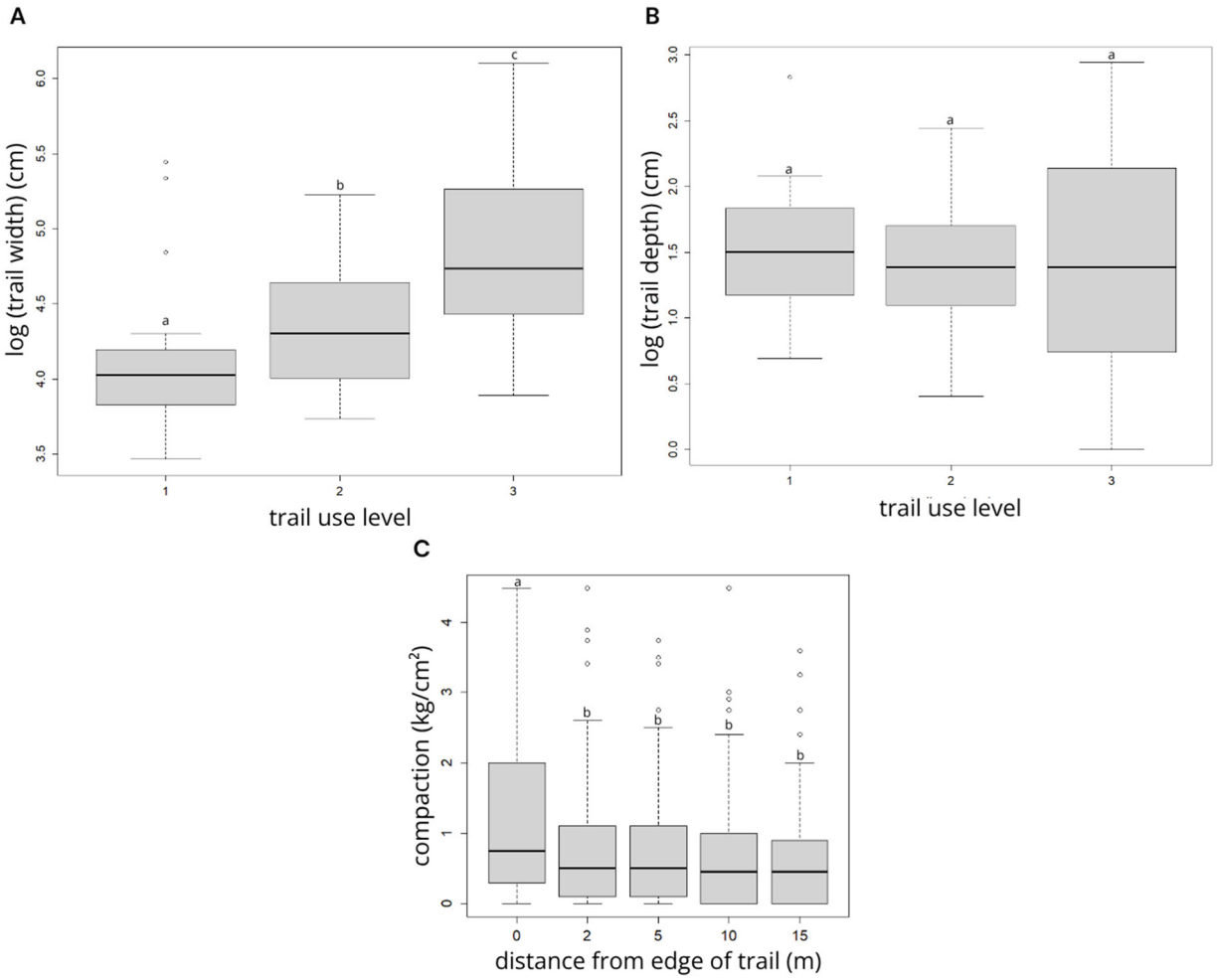

Figure 3. Boxplots showing the raw data assessing trail use level with log (trail width) (cm) (A), trail use level with log (trail depth) (cm) (B), and distance from the edge of the trail (m) with compaction (kg/cm^2) (C). Use levels are coded as 1 (low use), 2 (medium use), or 3 (high use). Letters above the bars in A-B indicate significant differences between use levels, where bars sharing a letter have no significant difference in trail width (A) and trail depth (B). Letters above the bars in C indicate significant differences between 0m and 15m quadrats, where bars sharing a letter have no significant difference in soil compaction.

2.4.2. Species Richness

Species richness in each quadrat ranged from 0 to 35, with a mean of 12 species. The GLMMs showed that species richness tended to decline moving outwards from a trail edge, but this effect differed depending on trail use level and vegetation type (**Table 4; Figure 4A-G; Appendix 1, Tables A1.4 & A1.5**). As expected, species richness did not change significantly moving from 0m to 15m along off-trail transects, whereas species richness was elevated at the 0m quadrat compared to the 15m quadrat along low and

high use trails, but not medium use trails (**Figure 4A-D**). Species richness was significantly higher at 0m than at 15m from trails in coniferous and mixed vegetation, but did not change significantly with distance from trails in grasslands (**Figure 4E-G**).

The burn caused a reduction in species richness, but only in grasslands, where unburned quadrats had approximately twice as many species compared to burned sites (**Figure 4J; Appendix 1, Table A1.6**). Species richness was slightly lower in burned than unburned quadrats in mixed vegetation, but this difference was not statistically significant (**Figure 4I; Appendix 1, Table A1.6**). Species richness was greater in low and medium use trails compared to high use trails and off-trail transects, but this pattern was driven mainly by transects in mixed vegetation (**Figure 4L; Appendix 1, Table A1.7**). In coniferous vegetation, there were no significant differences in species richness between use levels (**Figure 4K; Appendix 1, Table A1.7**). In grasslands, species richness was significantly higher in medium use trails than in high use trails, but there were no other significant differences (**Figure 4M; Appendix 1, Table A1.7**). We found no evidence for significant interactions between use level and burn status or distance from trail and burn status.

All the subset models were significantly better than a model with only the intercept and the random effect, with deltaAIC of 77.6, 72.2, and 83.0 (**Appendix 1, Table A1.8**).

Table 4. Summaries of the three subset generalized linear mixed models for species richness within each quadrat. I included transect ID as a random effect to account for non-independence of quadrats within the same transect. Coefficients for distance are in comparison to the reference category '0m', for burn to the reference category 'unburned', for use level to the reference category 'off-trail', and for vegetation type to the reference category 'coniferous'.

Predictor	Coefficient	SE	df	AIC*	LRT†	p‡
subset 1 – use level excluded						
intercept	2.51	0.09	na	1968.7	na	na
elevation	-0.24	0.05	1	1985.3	18.59	**<0.001**
distance (2m)	-0.30	0.08	na	na	na	na
distance (5m)	-0.29	0.08				
distance (10m)	-0.34	0.08				
distance (15m)	-0.29	0.08				
vegetation type (mixed)	0.38	0.17	na	na	na	na
vegetation type (grassland)	0.58	0.19				
burn status	-0.04	0.14	na	na	na	na
distance (2m) x vegetation type (mixed)	0.11	0.11	8	1968.2	15.54	**0.049**
distance (5m) x vegetation type (mixed)	0.01	0.11				
distance (10m) x vegetation type (mixed)	-0.01	0.11				
distance (15m) x vegetation type (mixed)	-0.09	0.11				
distance (2m) x vegetation type (grassland)	0.22	0.12				
distance (5m) x vegetation type (grassland)	0.25	0.12				
distance (10m) x vegetation type (grassland)	0.34	0.12				
distance (15m) x vegetation type (grassland)	0.23	0.12				
burn status (burned) x vegetation type (mixed)	-0.16	0.20	2	1973.0	8.34	**0.015**
burn status (burned) x vegetation type (grassland)	-0.66	0.22				
subset 2 – vegetation type excluded						
intercept	2.38	0.13	na	2350.0	na	na
elevation	-0.31	0.04	1	2389.3	41.33	**<0.001**
distance (2m)	0.05	0.11	na	na	na	na
distance (5m)	0.03	0.11				
distance (10m)	-0.11	0.12				
distance (15m)	0.03	0.11				
use level (low)	0.45	0.14	na	na	na	na
use level (medium)	0.33	0.15				
use level (high)	0.19	0.14				
burn status	-0.16	0.09	1	2351.5	3.52	0.061
distance (2m) x use level (low)	-0.25	0.14	12	2344.8	18.84	0.092
distance (5m) x use level (low)	-0.22	0.14				
distance (10m) x use level (low)	-0.16	0.14				
distance (15m) x use level (low)	-0.39	0.14				
distance (2m) x use level (medium)	-0.15	0.14				
distance (5m) x use level (medium)	-0.11	0.14				
distance (10m) x use level (medium)	0.00	0.15				
distance (15m) x use level (medium)	-0.11	0.14				
distance (2m) x use level (high)	-0.33	0.14				
distance (5m) x use level (high)	-0.39	0.14				
distance (10m) x use level (high)	-0.25	0.14				
distance (15m) x use level (high)	-0.34	0.14				

Predictor	Coefficient	SE	df	AIC*	LRT†	p‡
subset 3 – burn status excluded						
intercept	2.37	0.11	na	2339.2	na	na
elevation	-0.21	0.04	1	2360.4	23.22	**<0.001**
distance (2m)	-0.17	0.04	4	2370.3	39.13	**<0.001**
distance (5m)	-0.18	0.04				
distance (10m)	-0.24	0.04				
distance (15m)	-0.22	0.04				
use level (low)	0.15	0.14	na	na	na	na
use level (medium)	0.03	0.16				
use level (high)	-0.03	0.14				
vegetation type (mixed)	0.08	0.19	na	na	na	na
vegetation type (grassland)	0.45	0.24				
use level (low) x vegetation type (mixed)	0.30	0.23	6	2339.2	12.07	0.060
use level (medium) x vegetation type (mixed)	0.28	0.28				
use level (high) x vegetation type (mixed)	0.06	0.22				
use level (low) x vegetation type (grassland)	-0.39	0.30				
use level (medium) x vegetation type (grassland)	0.19	0.28				
use level (high) x vegetation type (grassland)	-0.42	0.28				

* AIC values include all factors in the model except the one being tested. In marginal fitting of terms, main effects also included in an interaction were excluded.

† Likelihood ratio test (LRT) compares the model without the predictor to the full model, using *drop1*.

‡ p-values indicate the significance of each predictor using a *drop1* test. I did not drop individual predictors that were also in a significant interaction. Predictors with $p < 0.05$ are indicated in bold text.

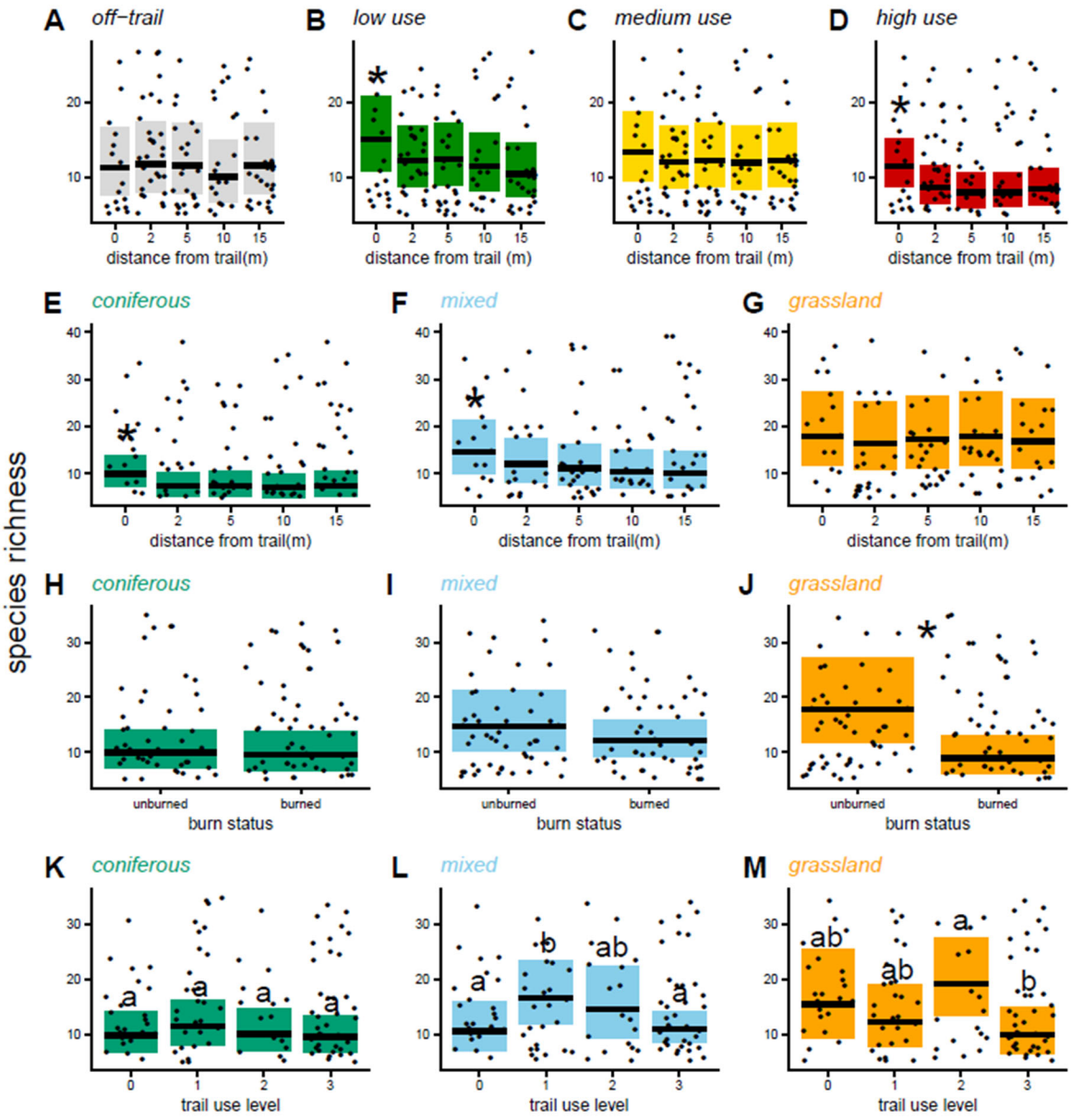

Figure 4. Partial regression plots showing predicted species richness with distance from the trail edge depending on trail use level (A-D) and vegetation type (E-G), predicted species richness along unburned and burned trails depending on vegetation type (H-J), and predicted species richness along trails of different use levels depending on vegetation type (K-M). Use levels are coded as 0 (off-trail), 1 (low use), 2 (medium use), or 3 (high use). In each panel, elevation is held constant at the median. In A-G and K-M, burn status is set to unburned. Asterisks in A-G indicate distances that were significantly different from the 15m distance based on post-hoc pairwise tests. The asterisk in J indicates a significant difference between unburned and burned quadrats based on post-hoc pairwise tests. Letters above the bars in K-M indicate significant differences between use levels, where bars sharing a letter have no significant difference in species richness.

2.4.3. Community Composition

Bray-Curtis dissimilarity of 0m, 2m, 5m and 10m quadrats from the 15m quadrat on the same transect ranged from 0.17 to 1. Quadrats from transects adjacent to low use trails had the greatest dissimilarity to the 15m reference quadrat, while high use and off-trail transects had the lowest dissimilarities. However, use level was not a significant predictor of dissimilarity (**Table 5**; **Figure 5B**). The distance from the trail edge was the only significant predictor in all subset models (**Table 5**; **Figure 5A; Appendix 1, Table A1.9**). As expected, the plant communities were more similar the closer the quadrats became to the 15m quadrat.

All the subset models were significantly better than a model with only the intercept and the random effect, with deltaAIC of 43.6, 48.9, and 48.1 (**Appendix 1, Table A1.10**).

Table 5. Summaries of the three subset linear mixed models for community composition within each quadrat. I included transect ID as a random effect to account for non-independence of quadrats within the same transect. Coefficients for distance are in comparison to the reference category '0m', for burn to the reference category 'unburned', and for use level to the reference category 'off-trail'.

Predictor	Coefficient	SE	df	REML*	F-value†	p‡
subset 1 – use level excluded						
intercept	0.63	0.03	na	-269.4	na	na
distance (2m)	-0.07	0.02	3	na	20.36	**<0.001**
distance (5m)	-0.09	0.02				
distance (10m)	-0.15	0.02				
vegetation type (mixed)	0.02	0.04	2	na	0.47	0.63
vegetation type (grassland)	-0.03	0.05				
burn status	0.02	0.04	1	na	0.38	0.54
subset 2 – vegetation type excluded						
intercept	0.60	0.04	na	-337.5	15.09	**<0.001**
distance (2m)	-0.07	0.02	3	na	20.84	**<0.001**
distance (5m)	-0.08	0.02				
distance (10m)	-0.13	0.02				
use level (low)	0.09	0.04	3	na	2.00	0.12
use level (medium)	0.01	0.05				
use level (high)	0.00	0.04				
burn status	0.00	0.03	1	na	0.00	0.94

Predictor	Coefficient	SE	df	REML*	F-value†	p‡
subset 3 – burn status excluded						
intercept	0.60	0.04	na	-334.1	15.32	**<0.001**
distance (2m)	-0.07	0.02	3	na	20.84	**<0.001**
distance (5m)	-0.08	0.02				
distance (10m)	-0.13	0.02				
use level (low)	0.08	0.04	3	na	1.86	0.14
use level (medium)	0.02	0.05				
use level (high)	0.00	0.04				
vegetation type (mixed)	0.03	0.03	2	na	0.54	0.58
vegetation type (grassland)	-0.02	0.04				

* Restricted maximum likelihood (REML) values include all factors in the model except the one being tested. In marginal fitting of terms, main effects also included in an interaction were excluded.

† F-value compares the model without the predictor to the full model, using *drop1*.

‡ p-values indicate the significance of each predictor using a *drop1* test. I did not drop individual predictors that were also in a significant interaction. Predictors with p <0.05 are indicated in bold text.

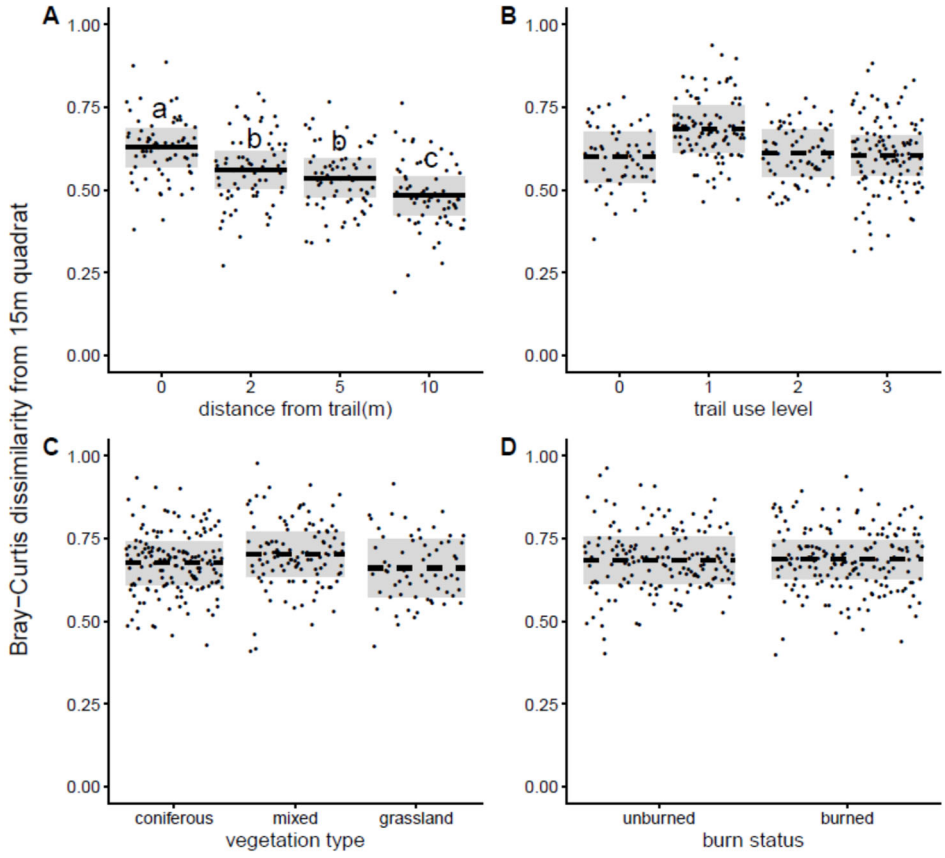

Figure 5. Partial regression plots showing predicted dissimilarity with distance from the trail edge (A), trail use level (B), vegetation type (C) and burn status (D). Only distance was a significant predictor, and there were no interactions between predictors. Dissimilarity ranges between 0 to 1, where 0 indicates identical plant community composition with the same species present in equal abundances and 1 indicated that the two quadrats have no species in common. Use levels are coded as 0 (off-trail), 1 (low use), 2 (medium use), or 3 (high use). Letters above the bars in A indicate significant differences between distances, where bars sharing a letter have no significant difference in dissimilarity.

2.4.4. Exotic Species

I found at least one exotic species in 154 quadrats (37%). On trail transects, 61% of quadrats had at least one exotic species, while 30% of quadrats on non-trail transects had at least one exotic. There were 27 different exotic species represented in the dataset, with a maximum of eight different exotic species found in a quadrat near the townsite along the Crandell Lake trail. In quadrats with at least one exotic species, the relative abundance of exotic species ranged from less than 1% to 91%. The mean relative abundance of exotic plants in quadrats with at least one exotic was 14.3% (median: 6.5%).

2.4.4.1. Presence/ Absence

The probability of at least one exotic species occurring in a quadrat was significantly higher in the 0m quadrat than the 15m quadrat regardless of trail use level, vegetation type, or burn status (**Table 6**; **Figure 6A; Appendix 1, Table A1.11**). As expected, the probability of finding exotic species declined as elevation increased. Interestingly, all transects, including the off-trail transects, had a high probability of containing at least one exotic species at low elevations (**Figure 6H**), and a low probability of exotics at high elevations (**Figure 6J**). However, at median elevations, off-trail and high use trail transects had a low probability of exotic presence compared to low and medium use trail transects (**Figure 6I**). Despite these trends, no pairwise differences between use levels were significant after correction for multiple tests (**Appendix 1, Table A1.14**).

The interaction between level of trail use and vegetation type was nearly significant ($p = 0.049$; **Table 6**; **Figure 6E-G; Appendix 1, Table A1.13**). In mixed forests and grassland vegetation there was a pattern of higher probabilities of exotic species presence in low and medium use trails compared to high use trails and off-trail transects, whereas in coniferous forests the probability was more variable across use levels. Quadrats near high use trails did not have the highest predicted probability of exotic species occurrence, regardless of vegetation type (**Table 6**; **Figure 6E-G; Appendix 1, Table A1.13**). The interaction between burn status and vegetation type was not quite significant in the final model, however it shows an interesting trend in which the probability of exotic species presence near trails is elevated in burned sites in coniferous forests only (**Table 6; Figure 6B-D; Appendix 1, Table A1.12**).

All the subset models were significantly better than a model with only the intercept and the random effect, with deltaAIC of 70.4, 88.3, and 89.1 (**Appendix 1, Table A1.15**).

Table 6. Summaries of the three subset generalized linear mixed models for exotic species presence / absence within each quadrat. I included transect ID as a random effect to account for non-independence of quadrats within the same transect. Coefficients for distance are in comparison to the reference category '0 m', for burn to the reference category 'unburned', and for use level to the reference category 'off-trail.

Predictor	Coefficient	SE	df	AIC*	LRT†	p‡
subset 1 – use level excluded						
intercept	-2.98	1.13	na	255.22	na	na
elevation	-2.79	0.62	1	286.63	33.41	**<0.001**
distance (2m)	-1.40	0.62	4	261.21	13.99	**0.008**
distance (5m)	-1.23	0.61				
distance (10m)	-2.10	0.65				
distance (15m)	-1.75	0.63				
vegetation type (mixed)	4.12	1.62	na	na	na	na
vegetation type (grassland)	4.20	1.69				
burn status (burned)	2.77	1.32	na	Na	na	na
vegetation types (mixed) x burn status (burned)	-3.05	1.83	2	255.22	3.98	0.137
vegetation types (grassland) x burn status (burned)	-3.37	2.09				
subset 2 – vegetation type excluded						
intercept	-3.57	1.73	na	295.33	na	na
elevation	-5.21	1.77	na	na	na	na
distance (2m)	-1.19	0.56	4	302.82	15.49	**0.004**
distance (5m)	-1.19	0.56				
distance (10m)	-2.09	0.60				
distance (15m)	-1.64	0.58				
use level (low)	3.21	1.62	na	na	na	na
use level (medium)	3.32	1.72				
use level (high)	-0.81	2.30				
burn status (burned)	1.10	0.77	1	295.46	2.14	0.143
elevation x use level (low)	2.67	1.88	3	301.61	12.28	**0.006**
elevation x use level (medium)	2.90	1.83				
elevation x use level (high)	-2.80	2.93				

Predictor	Coefficient	SE	df	AIC*	LRT†	p‡
subset 3 – burn status excluded						
intercept	-2.57	1.60	na	294.48	na	na
elevation	-9.31	3.49	na	na	na	na
distance (2m)	-1.19	0.56	4	301.97	15.49	**0.004**
distance (5m)	-1.19	0.56				
distance (10m)	-2.09	0.60				
distance (15m)	-1.64	0.58				
use level (low)	2.23	1.70	na	na	na	na
use level (medium)	0.61	1.90				
use level (high)	0.43	2.29				
vegetation type (mixed)	-4.83	3.22	na	na	na	na
vegetation type (grassland)	-6.21	3.65				
elevation x use level (low)	7.57	3.54	3	304.67	16.19	**0.001**
elevation x use level (medium)	6.94	3.52				
elevation x use level (high)	0.99	4.21				
use level (low) x vegetation type (mixed)	6.54	3.38	6	295.12	12.64	**0.049**
use level (medium) x vegetation type (mixed)	10.22	3.92				
use level (high) x vegetation type (mixed)	2.88	3.83				
use level (low) x vegetation type (grassland)	7.60	3.98				
use level (medium) x vegetation type (grassland)	8.94	3.91				
use level (high) x vegetation type (grassland)	5.08	4.28				

* AIC values include all factors in the model except the one being tested. In marginal fitting of terms, main effects also included in an interaction were excluded.

† Likelihood ratio test (LRT) compares the model without the predictor to the full model, using *drop1*.

‡ p-values indicate the significance of each predictor using a *drop1* test. I did not drop individual predictors that were also in a significant interaction. Predictors with $p < 0.05$ are indicated in bold text.

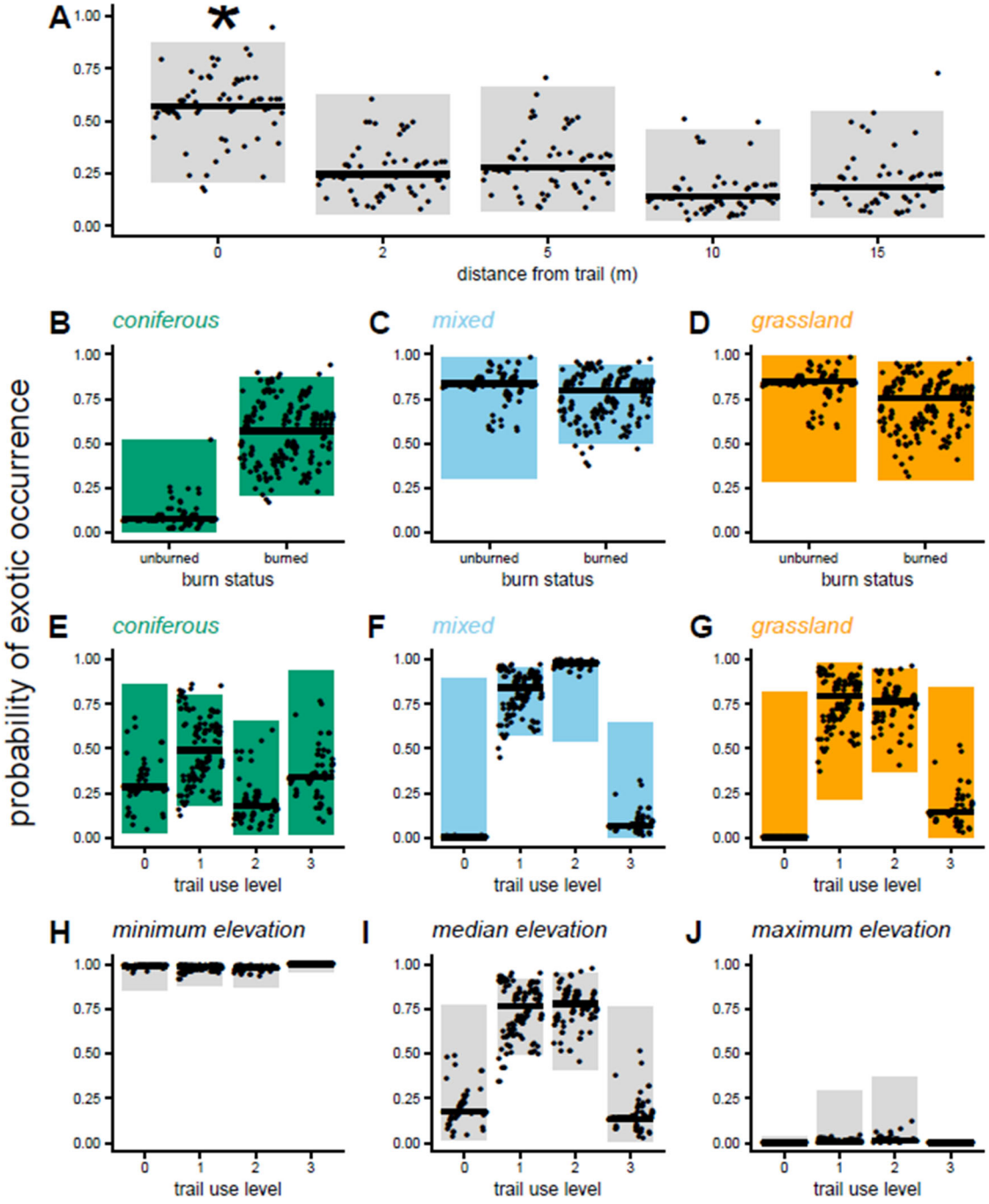

Figure 6. Partial regression plots showing predicted probability of at least one exotic species presence with distance from the trail edge (A), burn status and vegetation type (B, C, D), trail use level with vegetation type (E, F, G), and trail use level with elevation (H, I, J). In (A) burn status is set to 'burned' and vegetation type 'coniferous'. In (B) through (G) distance is set to 0m. In (A) through (G) elevation is held at the median. Use levels are coded as 0 (off-trail), 1 (low use), 2 (medium use), or 3 (high use). Asterisks above the bars in A indicate distances with probability of exotic presence significantly different than the 15m distance.

2.4.4.2. Relative Abundance

In quadrats with at least one exotic species (n=154), the relative abundance of exotic species declined as elevation increased (**Table 7**). Interestingly, the effect of distance from the trail edge depended on trail use level, with abundance significantly elevated at 0m compared to 15m only on low use trails (**Table 7**; **Figure 7A-D; Appendix 1, Table A1.16**). The *drop1* test on the final model indicated a nearly significant (p=0.078) interaction of distance with burn status: a pairwise test indicated that the relative abundance of exotic species was significantly higher in burned than unburned quadrats at the 5m and 15m distance (**Table 7; Figure 7E-I; Appendix 1, Table A1.17**).

The relative abundance of exotic species was significantly higher in burned quadrats, but only in grasslands (**Table 7; Figure 7J-L**). Burned grassland quadrats had an estimated marginal mean of 25% relative abundance of exotics, while unburned grassland quadrats had a mean of 7% (**Appendix 1, Table A1.18**). Vegetation type also interacted with use level in the models of exotic species abundance. Exotic abundance did not differ significantly with trail use level in coniferous or mixed vegetation, but was significantly elevated near low and high use trails relative to off-trail and medium use trails in grasslands (**Table 7; Figure 7M-O; Appendix 1, Table A1.19**).

All the subset models were significantly better than a model with only the intercept and the random effect, with deltaAIC of 24.7, 12.0, and 27.2 (**Appendix 1, Table A1.20**).

Table 7. Summaries of the three subset generalized linear mixed models for relative abundance of exotic species within each quadrat. Only quadrats with at least one exotic species are included in these models. We included transect ID as a random effect to account for non-independence of quadrats within the same transect. Coefficients for distance are in comparison to the reference category '0 m', for burn to the reference category 'unburned', and for use level to the reference category 'off-trail.

Predictor	Coefficient	SE	df	AIC*	LRT†	p‡
subset 1 – use level excluded						
intercept	-2.85	0.49	na	-303.55	na	na
elevation	-0.29	0.16	1	-302.30	3.25	0.071
distance (2m)	0.07	0.13	4	-299.05	12.51	**0.014**
distance (5m)	-0.28	0.14				
distance (10m)	-0.44	0.17				
distance (15m)	-0.13	0.16				
vegetation type (mixed)	0.54	0.50	2	-301.20	6.35	**0.042**
vegetation type (grassland)	0.14	0.56				
burn status	0.28	0.52	na	na	na	na
vegetation type (mixed) x burn status	-0.21	0.57	na	na	na	na
vegetation type (grassland) x burn status	0.98	0.65				
subset 2 – vegetation type excluded						
intercept	-3.17	0.43	na	-348.19	na	na
elevation	-0.80	0.18	1	-330.05	20.14	**<0.001**
distance (2m)	-0.69	0.40	na	na	na	na
distance (5m)	-0.18	0.39				
distance (10m)	-0.27	0.65				
distance (15m)	-1.08	0.49				
use level (low)	0.76	0.36	na	na	na	na
use level (medium)	0.10	0.41				
use level (high)	0.48	0.38				
burn status	0.09	0.25	na	na	na	na
distance (2m) x use level (low)	0.34	0.38	12	-347.32	24.88	**0.015**
distance (5m) x use level (low)	-1.09	0.37				
distance (10m) x use level (low)	-0.42	0.60				
distance (15m) x use level (low)	-0.16	0.50				
distance (2m) x use level (medium)	0.72	0.46				
distance (5m) x use level (medium)	-0.24	0.42				
distance (10m) x use level (medium)	-0.12	0.65				
distance (15m) x use level (medium)	0.77	0.51				
distance (2m) x use level (high)	0.41	0.42				
distance (5m) x use level (high)	-0.77	0.39				
distance (10m) x use level (high)	-0.48	0.65				
distance (15m) x use level (high)	0.85	0.46				
distance (2m) x burn status	0.37	0.28	4	-347.81	8.38	0.078
distance (5m) x burn status	0.80	0.30				
distance (10m) x burn status	0.16	0.35				
distance (15m) x burn status	0.55	0.29				

Predictor	Coefficient	SE	df	AIC*	LRT†	p‡
subset 3 – burn status excluded						
intercept	-3.09	0.40	na	-363.41	na	na
elevation	-0.32	0.12	1	-357.95	7.46	**0.006**
distance (2m)	-0.04	0.13	4	-358.12	13.29	**0.010**
distance (5m)	-0.27	0.13				
distance (10m)	-0.49	0.15				
distance (15m)	-0.21	0.15				
use level (low)	0.51	0.45	na	na	na	na
use level (medium)	0.42	0.55				
use level (high)	0.61	0.58				
vegetation type (mixed)	0.71	0.48	na	na	na	na
vegetation type (grassland)	0.83	0.48				
use level (low) x vegetation type (mixed)	-0.37	0.55	6	-356.90	18.51	**0.005**
use level (medium) x vegetation type (mixed)	-0.03	0.65				
use level (high) x vegetation type (mixed)	-0.62	0.66				
use level (low) x vegetation type (grassland)	0.65	0.57				
use level (medium) x vegetation type (grassland)	-0.51	0.64				
use level (high) x vegetation type (grassland)	0.43	0.67				

* AIC values include all factors in the model except the one being tested. In marginal fitting of terms, main effects also included in an interaction were excluded.

† Likelihood ratio test (LRT) compares the model without the predictor to the full model, using *drop1*.

‡ p-values indicate the significance of each predictor using a *drop1* test. I did not drop individual predictors that were also in a significant interaction. Predictors with $p < 0.05$ are indicated in bold text.

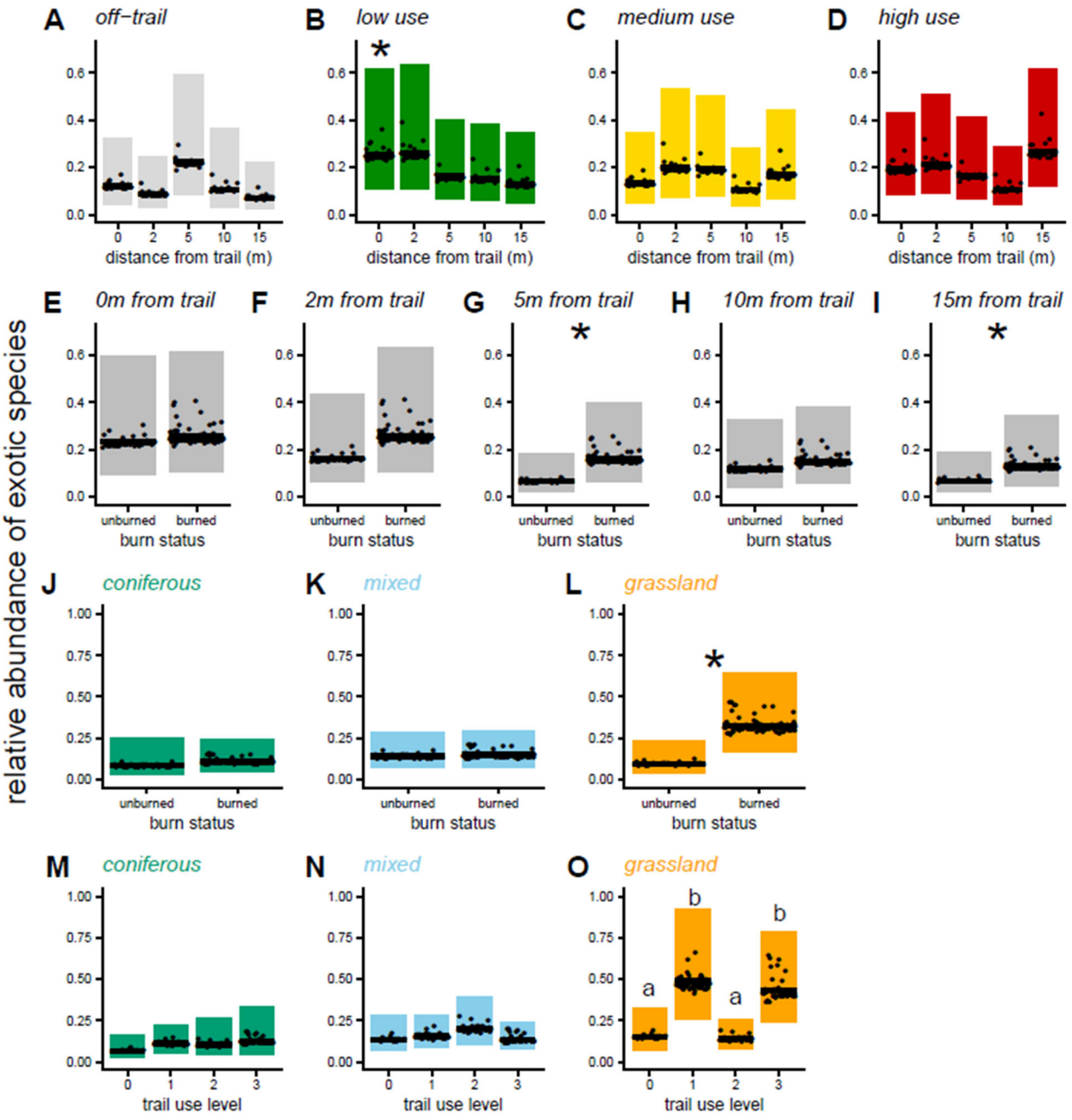

Figure 7. Partial regression plots showing predicted exotic species relative abundance with distance from the trail edge with trail use levels (A - D), burn status with distance from the trail edge (E - I), burn status with vegetation type (J, K, L), and trail use level with vegetation type (M, N, O). In (A) through (D) burn status is held at 'burned', in (E) through (I) use level is held at low use, and in (J) through (O) distance is held at 0m. Use levels are coded as 0 (off-trail), 1 (low use), 2 (medium use), or 3 (high use). The asterisk above the bar in B indicates distances with exotic species abundance significantly different than the 15m distance. Asterisks above the bars in G and I indicate distances with exotic species abundance significantly different between burn and unburned transects. The asterisk above the bar in L indicates grassland with exotic species abundance significantly different between burn and unburned transects. Letters above the bars in O indicate significant differences between use levels, where bars sharing a letter have no significant difference in exotic species abundance.

2.4.5. Total Area of Influence

To calculate the total area of influence, I accounted for formal trails (202km), informal trails (34km), and informal routes (81km) for a grand total of 317km trails and routes. I found species richness was elevated up to 2m along low and high use trails, except in grasslands. Therefore, I calculated the length of low and high use trails through coniferous and mixed forests only, and multiplied by 4m. Community composition does shift moving from 0m to 15m, but it shifts about the same whether it was near a trail or not. Therefore, I did not calculate total area of trail effects on community composition. The probability of exotic species presence was elevated up to 2m along all trails.

Finally, when exotic species were present, their relative abundance was elevated up to 2m, but only along low use trails. However, in the burn, it was elevated at 5m and 15m, suggesting that the trail impact may extend up to at least 15m. Consequently, in the unburned areas I multiplied the length of low use trails by 4m, and in the burn, I multiplied by 30m calculated for all trails. This estimate for exotic species relative abundance may be an overestimate or underestimate. It may be an overestimate because exotics were only present in 37% of the quadrats, and obviously abundance of exotics can only be elevated if exotics are present. Alternatively, it may be an underestimate because the relative abundance of exotics 15m from high use trails is elevated compared to off-trail transects, and I only included low use trails.

The estimated total area of influence of trails on species richness was 0.67km², exotic species presence/ absence was 0.91km², and exotic species relative abundance was 4.55km² (**Table 8**). Therefore, the estimated total percentage of Waterton's vegetated area affected by trails and routes is between 0.18% and 1.24% (**Table 9**). I recognize that my calculations are speculations as I did not collect data at informal areas and it is possible they do not have similar effects on plant communities as the formal trails. However, this calculation gives an opportunity to estimate the impact from informal routes, especially if they have become established routes.

Table 8. Calculations of area of impact of both formal and informal trails and routes. The total area of influence (km²) is calculated for species richness, exotic species presence/ absence, and exotic species relative abundance.

Trail type	Extent from trail (m)	Formal trails		Informal trails/ routes		Total area of influence (km²)
		Length of trail (m)	Total area (m^2)	Length of trail (m) (Strava + informal)	Total area (m^2)	
Species richness						
coniferous x low use	2 x 2	29,353	117,412	8,321 + 10,128	73,796	
coniferous x high use	2 x 2	44,057	176,228			
mixed x low use	2 x 2	28,448	113,792	14,273 + 7,917	88,760	
mixed x high use	2 x 2	24,410	97,640			
total extent of impact			505,072		162,556	**0.668**
Exotic species presence/ absence						
all trails	2 x 2	167,266	668,904	27,493 + 31,801	237,176	
total extent of impact			668,904		237,176	**0.906**
Exotic species relative abundance						
low use x unburned	2 x 2	27,339	109,356	57,714 + 22,869	322,332	
all trails x burned	15 x 2	100,035	3,001,050	23,083 + 14,093	1,115,280	
Total extent of impact			3,110,406		1,437,612	**4.548**

Table 9. The estimated percentage (%) of vegetation impacted by formal and informal trails and routes based on species richness, exotic species presence/ absence, and exotic species relative abundance. Calculations include total vegetated area in Waterton Lakes National Park (367km²).

Response variable	Formal trails	Informal trails/ routes	**Total**
species richness	0.14%	0.04%	**0.18%**
exotic species presence	0.18%	0.06%	**0.25%**
exotic species abundance	0.85%	0.39%	**1.24%**

2.5. Discussion

Conservation objectives will continue to be challenged as visitation to Canada's parks and protected areas increase in combination with projected increases in the frequency of natural disturbances such as wildfire. The extent and magnitude of impacts caused by recreational trails on plant diversity and composition is not well-studied in the Canadian Rockies, a popular tourist destination. It is also not known whether these effects are greater when trails are used more frequently, or whether these effects are magnified by wildfire. While previous research does show trails impact plant communities, the spatial extent of these effects moving out from the trail is often unknown and the overall proportion of the area influenced is not documented. My research shows that recreational trails increase species richness and exotics species presence and abundance, but these effects depend on the intensity of trail use, vegetation type,

and whether the area burned or not. Currently, I estimate that a relatively small percentage of Waterton's vegetation is influenced by trails.

Overall, the influence of trails in Waterton on plant species richness aligned with other studies. I found species richness to be elevated at the trail edge relative to 15m away, in particular along low and high use trails. Other research indicates species richness is elevated at disturbance edges (Willmer et al., 2022). Species richness often increases at the disturbance edge due to spill over when species disperse into other habitats by crossing the boundary from their preferred habitat (Ries & Sisk, 2004). This occurs along the trailside when some species from the pre-existing plant community continue to grow, along with additional disturbance-associated and/or sun-loving species dispersed by trail users. The probability of finding an exotic species is highest at 0m and declines moving out from the trail edge. This is also consistent with other research reporting trails as facilitators of exotic plant species movement (Benninger-Truax et al., 1992; Chisholm & McCune, 2024; Potito & Beatty, 2005). This is due to trail users dispersing seeds on clothing and gear (Pickering et al., 2011), combined with higher light and trampling near trail edges that favours species adapted to disturbance, as many exotic species are. Although my findings generally match other studies, my research shows that the magnitude of these effects of trails vary depending on trail use level, the vegetation type, and are affected by recent wildfire.

2.5.1. The Influence of Trail Use Level

It is common to find elevated species richness along trails; however, the magnitude of this effect may depend on the degree of disturbance the trail edge receives. At the edge of the trail, more resources such as light and rainfall are available for light-tolerant colonizers to grow (Davis et al., 2000). This allows more species adapted to these conditions to colonize, increasing the species richness. However, this boost in resources could be counteracted with a high intensity of trampling or erosion. For example, Parikesit et al. (1995) found species richness to be highest along trails with intermediate levels of use and lower along low use and high use trails. They explained this using the Intermediate Disturbance Hypothesis (Connell, 1979) which states that at low disturbance levels, the best competitors are able to dominate, reducing species richness, whereas at high disturbance levels, only a few species are able to withstand the high frequency of trampling. Thus, intermediate disturbance levels have the highest species richness. My

findings align with this trend, although across all distances this pattern occurred in mixed forests only, with species richness elevated at low and medium transects relative to off-trail and high use trails.

The use level of trails also influences the presence of exotic plant species. Exotic species are relatively rare at the highest elevations, and very common at the lowest elevations, regardless of trail use level. However, at median elevations low and medium use trails had the highest probability of having exotic species present while off-trail transects and high use trails had a lower probability. Several research studies have found the higher the disturbance rate the more exotic species exist (Siderhurst et al., 2012; Vujnovic et al., 2002). Therefore, I was surprised by the higher probability of occurrence of exotic species along low use trails relative to high use trails. I suspect the increase in exotic species occurrence is attributable to the trail locations and park managers' focus on high use trails for exotic species detection and control efforts. Many low use trail segments occur in close proximity to roads, the townsite, and along the park boundary adjacent to ranch lands and include the trails: The Dipper, Crandell Lake via Akamina, Crandell Lake via the townsite, and the Park Boundary. The sample locations along these trail segments were often less than 150m from roads, the townsite, or adjacent land uses. It is possible that the close proximity to other uses allows wind-dispersed and agronomic exotic species to grow along these trails at a high frequency, even though use of the trails themselves is infrequent. I also suspect that early detection of exotic species is less likely on trails not frequented often. For example, detection of exotic species can also occur by educated trail users, as well as park staff who likely monitor the high use locations. On low use trails, early detection may not occur, allowing these exotic species more time to spread before being detected.

When exotics were present, the level of trail use also affected their relative abundance. Low use trails had elevated abundance at 0m compared to 15m. Interestingly, medium and high used trails did not have elevated abundance at 0m compared to 15m, but high use trails had relatively high abundance throughout the 15m transect. It is possible that disturbance along low use trails does not extent much beyond 2m and the existing native communities prevent exotics from becoming abundant beyond that distance, even if present. The medium use trails had a relatively low abundance of exotics, with levels similar to the off-trail transects. This may be due to their far proximity to both the trailhead and other land uses; therefore, any exotics present have had less time to establish. Bella (2011) found a significant reduction in exotic species beyond 500m from the trailhead, and exotics were found farthest along high use

trails. Several of the medium use trails in my research were located much farther than 500m from the trailhead, and Parks Canada may prioritize locations near trailheads for invasive species treatment. When considering the abundance of exotics across all distances (0m – 15m), the influence of trail use level varied with vegetation type. Exotic species abundance was significantly higher near low and high use trails compared to off-trail and medium use trails only in grassland. The tendency for a lower abundance of exotic species in grasslands along medium use trails compared to low and high use trails is puzzling. It may have occurred because the low and high use trails I sampled in grasslands tended to be near (<150m) other land uses, such as roads or agricultural land. Only two medium use transects in grasslands are located near a road, and the rest are located >150m from another anthropogenic disturbance.

2.5.2. The Influence of Vegetation Type and Wildfire

Different vegetation types can be more or less responsive to trail effects depending on the available resources. For example, a closed-canopy forest does not have as much light and rainfall penetrating to the forest floor, and the nutrients in the soil are taken up by the existing plant community (Davis et al., 2000; Pausas & Austin, 2001). A closed-canopy forest may resist colonization by new species due to fewer available resources. If light is more available, such as in a mixed forest or grassland, this can support greater species richness, including light-loving exotic species (Yang et al, 2021). When a wildfire goes through the area, the forest can go from a closed-canopy to an open-canopy allowing light and rainfall to reach the forest floor, and limited vegetation exists to take up nutrients released during the burn. Therefore, how plant communities respond to wildfire can depend on the change in resource availability (Davis et al., 2000; Maxwell et al., 2026). In addition, when the canopy cover is removed it can allow wind-dispersed seeds to spread farther across a landscape. In Waterton, records indicate wind speeds over 150km/hr and a daily average wind speed of 30km/hr (Government of Canada, 2025d). I found important interactions between wildfire and vegetation type, with trailside plant communities being affected depending on what vegetation type they are in.

Firstly, vegetation type influenced trail effects on species richness. Coniferous and mixed forests had elevated species richness up to 2m from the trail edge, whereas in grasslands species richness in each quadrat was higher on average than the other vegetation types and relatively unchanged moving from 0m

to 15m from a trail edge. This makes sense because grasslands do not have a forest canopy and when a trail is constructed in a grassland, the changes in light and rainwater are minimal compared to a forest with a closed-canopy (Cole, 1979; Dale & Weaver, 1974; Hill & Pickering, 2009; Stohlgren et al., 1999). Willmer et al. (2022) found plant communities typically have a higher species richness when there is a high contrast at the disturbance edge. When a trail traverses through a coniferous or mixed forests, the trail introduces more light and rainwater to the edge of the trail allowing light-tolerant colonizers to establish.

I found an interesting interaction between vegetation type and wildfire resulting in differences in species richness. Within 15m of trails (regardless of trail use level), species richness was significantly lower in burned sites, but only in grasslands. This is actually the opposite of what other research studies have found as species richness is generally higher in grasslands post-wildfire (Kertész et al., 2017; Loydi et al., 2020). However, in a study of grassland plant responses to fire in Golestan National Park, Iran, Zaki et al. (2021) found that their study species tolerated low fire severities, yet high severities were lethal. In Waterton, the Kenow Fire severity was rated high throughout the burned area, including grasslands (Greenaway et al., 2018). Another factor I did not measure which may have influenced species richness following the fire is herbivory on grassland species post-fire. A large elk herd and other ungulates frequent the grasslands in Waterton (Government of Canada, 2025e). It is possible that the grasslands post-fire were over-browsed by ungulates due to the burnt shrubs and trembling aspen not being available and an abundance of young, lush herbaceous vegetation post-fire (Biggs et al., 2010). Additionally, plant species traits such as fire-tolerance could contribute to these patterns. Historically, fires occurred more frequently in Waterton, especially in the grasslands (Reeves & Peacock, 1992). Due to fire suppression since the early 1900s, several grassland species pre-Kenow Fire may have been fire-intolerant species and unable to regenerate post-fire. Lastly, the decline in species richness in grasslands post-fire could be due to the increase in exotic species abundance (see below), which could be restricting some competitively inferior native species from establishing, resulting in a lower species richness post-fire.

The spread of exotic species along trails could be magnified by wildfire. We already know that trail users disperse seeds, and sometimes these seeds are exotic species. However, we do not know if - once a wildfire has burned the vegetation and more resources are available - trails may facilitate the movement of exotics into a burned area. My results show that wildfire effects on the frequency of occurrence of exotic

species near trails varies depending on the vegetation type. Coniferous forests were the only vegetation type with a low occurrence of exotic species pre-fire. Yet, post-fire coniferous forest transects tended to have an increased probability of exotic species presence. This aligns with the theory that a plant community's invasibility increases once more resources are available such as light, rainwater, and soil nutrients (Davis et al., 2000). Many other studies in forestry have also found when more trees are removed, a higher rate of exotics invade and persist (Butler et al., 2025; Selmants & Knight, 2003). However, this may not be a long-lasting effect and exotic occurrence may decline again once the forest recovers (Deferrari & Naiman, 1994; Romme et al., 2011).

Even though coniferous forests had an increased probability of having an exotic species post-wildfire, the overall abundance of exotic plant species was not greater in burned than in unburned coniferous forests. However, the relative abundance of exotics more than doubled from 7% to 25% on average in trailside grassland quadrats in burned transects (regardless of trail use level). It is interesting that exotic species abundance is increasing post-fire in grassland as prescribed burns are often used to reduce the abundance of exotic species in grasslands (Ratcliffe et al., 2022). Other research has found that the timing of the wildfire influences which species grow post-fire (Zaki et al., 2021) and is dependent on plant traits such as fire-tolerance and when the plant reaches maturity. For example, if a plant fails to reach full maturity before a fire occurs, it will not contribute its seeds to the seed bank. In my research, within the top five species (in terms of abundance post-fire in grasslands) three exotic species were found: Canada bluegrass (*Poa compressa*), Kentucky bluegrass (*Poa pratensis*), and smooth brome (*Bromus inermis*). Early-season burning does decrease the cover of exotic species including Kentucky bluegrass and promotes native plant diversity (Kral et al., 2018). However, the Kenow Fire occurred in September and it is possible it promoted the spread of exotic species which had already produced seed by this time.

Across all vegetation types, the relative abundance of exotic species was significantly higher at 5m and 15m in the burned areas compared to unburned areas. This suggests that wildfire may promote the increased abundance of exotic species farther out from the trail edge. The increased relative abundance of exotics post-fire may occur due to the removal of established native plant species (Bennett et al., 2011; Levine, 2003). Some exotics maybe more resilient to fire, and if they are already present in the seedbank then they can recolonize before native species, increasing their abundance post-fire. It may be possible

this effect extends farther than 15m. While this may be concerning, it is important to note that exotic species were often absent. Throughout my research study, 67% of the quadrats did not have an exotic species present. Other research has shown that the abundance of exotic species decreases as succession continues and native plant communities establish post-fire (Romme et al., 2011; Selmants & Knight, 2002). It is important to continue to monitor plant communities in Waterton to determine whether the elevated abundance of exotics post-fire declines with time, especially in the burned grasslands and along all trail use levels.

Surprisingly, I found shifts in plant community composition moving towards trail edges were not greater than the natural shifts moving along any 15m distance. To the contrary, in the Castle region just north of Waterton, Chisholm and McCune (2024) found the greatest community shifts near roads, then along off-highway vehicle trails, and the least shifts along footpaths. This may be because even the high use trails in Waterton have relatively low disturbance levels compared to trails used by off-highway vehicles. It is also possible that the management style (e.g. active management with enforcement versus limited management resources and funding), historical use (e.g. cattle grazing and mineral exploration), and social behaviours impact the plant communities. For example, the Castle was historically designated as public land and conservation was not a high priority or enforced. The social behaviour cultivated for the protection and appreciation for the natural beauty of a national park may influence how people use the trails and respect the environment. In addition, I used to work in the Castle region and would often see new trails being developed by recreational users, which was rarely discouraged. There is a culture of “roughing-it” and “machine versus nature” in places such as public land. While I see people travelling off-trail in a national park, I have never seen people actively removing vegetation to create a new trail.

2.5.3. Total Area of Influence

The trail effects occurred over relatively short distances, and Waterton has among the lowest densities of official trails compared to other nearby provincial parks in the Rocky Mountains. Yet, the estimated total area of influence on plant communities along formal trails in Waterton is 0.51km² (species richness), 0.67km² (exotic species presence), and 3.11km² (relative abundance of exotic species). The extent of trail impacts in Waterton varied between 0m to 15m depending on the measured response

variable. In other literature, trail and road impacts on plant communities vary greatly (Wolf & Croft, 2014), with some studies finding effects extending farther than 50m (Angold, 1997; Gelbard & Belnap, 2003; Hansen & Clevenger, 2005) whereas others find effects only as wide as the trail tread (Benninger-Traux et al., 1992; Dale & Weaver, 1974). The impact on plant communities in Waterton is relatively small; however, it may increase in the future.

It is important to recognize that the formal trails do not account for the full extent of trail use in Waterton. I recognize that I surveyed only the formal trails, but if effects are similar on informal trails and routes, then the total area of influence increases to 1.24% of the plant communities. This is a relatively low area of influence that likely reflects a well-managed national park with scientists and trail crews who have actively worked toward conservation for decades. Not all areas in the Canadian Rockies are protected in this way, nor do they have the same level of funding for conservation which may lead to very different trail impact results.

The area of influence of recreation on plant community diversity and composition may expand beyond the areas adjacent to trails (formal/informal) and routes (informal) as trail users continue to explore deeper into the backcountry. Several informal routes do occur along rocky surfaces, but when they traverse through vegetated landscapes, these impacts may be accelerated due to no obvious path and more people recreating. The full spatial extent of recreation use in Waterton is difficult to quantify; however, the crowdsourcing data from smart phone apps can be a good tool to decipher where people are recreating and how often.

2.5.4. Limitations/ Future Research

My research provides baseline data for Parks Canada to continue to monitor how plant communities change over time with trail use. It is projected that tourism and outdoor recreation will continue to increase in Waterton; in 2025, Waterton saw nearly a 7% visitation increase from 2024 levels (statista, 2026). There has been relatively little research in Canadian national parks on how trails affect plant communities, and some national parks such as Banff see visitation numbers much higher than Waterton. It would be interesting to determine whether similar impacts are found in parks that are more highly utilized.

In addition, this research can help inform studies of other areas which have recently seen vast wildfires such as Jasper, where the combined effects of wildfire and recreational disturbance are also of interest.

While the extent of trail impacts is not vast, the addition of more trails and continued use of informal trails and routes must be considered, managed and monitored. In some areas, the informal routes are not refined to a single trail and can spread out over a larger area causing trail braiding and more dispersed impacts to the surrounding vegetation. These areas must be managed, especially when traversing vegetation types with closed canopies. To determine if informal routes influence plant communities, I suggest a similar research study at frequently-used informal routes. Additionally, it would have been ideal to have more quantitative estimates of trail use levels. Many organizations utilize trail counters to understand trail use levels (e.g. Pettebone et al, 2010; Ziesler & Pettebone, 2018), but this comes with limitations such as distinguishing between human and wildlife use, and the available resources to install and monitor the trail counters. While Strava's Global Heatmapping comes with its own set of limitations, it does appear to be a good resource to understand trail use levels both on formal and informal trails and routes. Crowdsourcing data coupled with additional trail counters at strategic junction points can help Parks Canada understand where and how much outdoor recreation occurs throughout the park.

Another limitation of my work is the length of the transects that I used. Fifteen metres may not be far enough to know the full extent of trail effects, particularly in the burned area and in grasslands. Additionally, my research did not incorporate the effects of adjacent land uses or other current or historical anthropogenic disturbances and their proximity to transects. I also did not measure herbivory. Future studies on interactions between fire and recreation on grassland plant communities should also extend transects farther than 15m and consider herbivory, the maturity stage of plants when the fire occurred, and the successional stage of the plant community. Continued research post-fire should continue to assess how exotic species occurrence and frequency change with ongoing succession.

Recreational trails can have positive effects on plant communities, such as species richness, yet a closer look at other plant community characteristics may change the outlook. For example, if a higher local species richness is considered good, then trails can be beneficial. However, not just the number of species present but their identity is also of interest, and if exotic species presence and abundance is high, then trail

effects can be considered detrimental. Trails do facilitate the spread of exotic species, but they are not the only contributor. Even low use trails had a high probability of finding an exotic species, and this may be due to the close proximity to roads, developed areas and adjacent land uses. Trail users could be an asset to early detection of exotic species if they are educated on identification and reporting. Parks Canada has several educational signs in Waterton showcasing problematic species and this likely helps with early detection. However, based on my findings, education and attempts to encourage early reporting of exotics along less popular trails are just as important as high use trails. Vegetation types with more canopy cover, such as coniferous forests, were more susceptible to an increase in the occurrence rate of exotics post-fire regardless of trail use levels. While exotic species frequency may decline with succession, it is important to monitor these forests to ensure exotic species do not hinder the ability for these forests to regenerate.

2.5.5. Conclusion

It is important to understand how trails influence plant communities, especially where recreation is being balanced with conservation values in protected areas. My study showed trail effects largely similar to previous studies, including increased species richness, and increased occurrence and abundance of exotic species near trails. More importantly, the magnitude and extent of these effects depend on how much the trail is used, the vegetation type surrounding the trail, and whether the area burned or not. The extent of effect is relatively small, often only up to 2m from the trail, but this does add up to hundreds of hectares. Land managers can use this information to decide where to focus ongoing monitoring and to make decisions about monitoring or managing unofficial trails.

CHAPTER 3: CONCLUSION

The balance between outdoor recreation and conservation is complex. Increases in visitation to protected areas coupled with natural disturbances make it challenging to meet both goals of conserving biodiversity and inspiring connection with the natural world. Exploring outdoors allows people to feel connected to nature and inspires them to protect it (e.g. Heidari & Gravelle, 2025). However, protected area managers are faced with determining how much recreation is compatible with maintaining the diversity and wildness of the natural areas. Because ecological integrity is the mandate for Canada's protected areas (Government of Canada, 2026), I aimed to grow our understanding of how trails impact their surrounding plant communities.

It is well known that trails can impact both abiotic (e.g. soil erosion, water displacement) and biotic factors (e.g. wildlife movement, bird nesting, and plant communities). Yet, the influence of trail use frequency, the vegetation types the trails traverse through, and wildfire on these impacts is less certain. For example, land managers are concerned that people entering burned areas after a wildfire could facilitate the invasion of exotic species by dispersing the seeds of exotic plants on their clothing and gear. Surprisingly, no published studies have quantified trail effects on plant communities in Canada's Rocky Mountain National Parks, even though they are highly-valued tourism destinations.

Meanwhile, how people recreate is evolving due to digital apps linked to satellites (Hamza-Mayora et al., 2025). For example, Apple's app store contains over 100 different hiking and trail apps, with several focusing on specific tourist attractions. Hamza-Mayora et al. (2025) highlights Strava, AllTrails, Komoot, Wikiloc, and Maps.me as the most popular apps. AllTrails is recommended as the most popular on Apple's iPhone store and has over 120,000 ratings (Apple Inc., 2026). These apps allow even novice explorers to venture off formal trails into less managed areas. The influx of people recreating off-trail can potentially undermine conservation values, and collaboration between protected area managers and app developers is essential to improve quality, diversity, and sustainability (Hamza-Mayora et al., 2025). While formal trails are managed with clear objectives and maintained by trail crews, informal trails and routes do not receive the same attention. Even less is known about how recreational use away from the formal trails is impacting plant communities.

My research quantified effects of recreational trails on the surrounding plant community's diversity and composition in Waterton Lakes National Park. I also asked whether impacts differ based on trail use level, vegetation type, whether the area recently burned or not, and interactions between these. I expected high use trails would have the greatest impact on plant communities, yet higher use trails did not always elevate trail effects. For example, high use trails actually had a lower probability of supporting exotic species than low and medium use trails. I found that trail effects on the occurrence and abundance of exotic species post-fire depended on vegetation type. Exotic species were infrequent near trails in coniferous forests pre-fire, but elevated post-fire, while exotic species presence was equally high both before and after wildfire in mixed forests and grasslands. The relative abundance of exotic species near trails was elevated post-fire mainly in grasslands. Trail effects clearly vary with trail use level and vegetation type, but not always in a predictable way.

To capture the extent of trail impacts, I estimated how far from trail edges trail effects were evident, and then estimated the total area of trail influence on plant communities throughout the park. I also calculated what this area of influence would be if informal trails and routes have similar effects as formal trails. The extent of impact from the trail is relatively small, but once the total area is calculated throughout the park the impact equals hundreds of hectares, and even more if informal trails and routes are included.

Now that this study is complete, a baseline is established for trail impacts on plant communities in Waterton. Resurveying these transects in the future will allow ecologists and park managers to determine how trail effects on plant communities change over time, particularly in the burned areas as the plant communities recover. Consistent monitoring and installation of trail counters paired with online assessments of trail use can provide more quantitative data on how much recreation is occurring and where it is occurring on the landscape. This study can also be replicated in other areas of the Canadian Rockies, and especially areas such as Banff which has higher use levels (Government of Canada, 2025f) and Jasper which recently had a major wildfire (Government of Canada, 2025g). Additional research should include the impacts of informal trails and routes to understand if more management is needed at these locations; for example, these locations may require reclamation if they are not suitable routes, or Parks Canada may want to maintain these routes by doing trail maintenance or marking the preferred path. Also, land managers

should work with the app developers to ensure that only routes that align with their conservation goals are available to the public. In addition, subalpine and alpine ecoregions should be monitored. While I excluded informal routes traversing rock or rubble from my calculations of the potential area of influence, plants do grow in these environments and recreation in these areas tends to be spread-out with multiple routes. While there are fewer plants in these locations, it is unknown how these plants are responding to trampling.

This study can also provide a basis to compare trail effects on vegetation between areas with different recreation and management backgrounds. It is possible that management decisions over the history of a protected area and the social behaviour of recreationalists differ between more highly regulated areas (like long-established national parks) versus less regulated areas such as public land or recently designated protected areas. Not all areas in the Canadian Rockies are protected to the same extent, or have programs to educate recreational visitors, or are able to mitigate trail effects. A comparison between areas with different land designations could clarify how land management practices and the ways in which trails are used (e.g. motorized versus non-motorized) affect the magnitude and total area of trail effects on plant communities.

Very little research in the Canadian Rockies assesses how plant communities are impacted by trail use and the magnitude of these impacts. While many studies from around the world have measured trail impacts on plant communities (e.g. Ballantyne & Pickering, 2015; Bates, 1935; Chisholm & McCune, 2024, Dale & Weaver, 1974), most have not considered interactions between trail use levels, vegetation type, and wildfire. Some research has examined informal trails and routes (e.g. Ballantyne & Pickering, 2015; Pickering & Norman, 2017; Hamza-Mayora et al., 2025), but there is still a gap in our understanding of the extent of impacts from informal trails on the landscape. Finally, the total area of influence of trails on vegetation is not often calculated. These estimates give quantitative reference points to help decision makers comprehend the full impact of trails and to measure changes in trail impacts moving forward.

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APPENDIX 1: SUPPLEMENTARY MATERIALS FOR CHAPTER 2

Table A1.1. Results of pairwise comparisons of estimated marginal mean (emmean) trail width with trail use levels, excluding off-trail transects. Intervals are back-transformed from the log scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean trail widths between trail use levels the Tukey adjustments for multiple tests.

trail use level	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
low	61.1	2.70	347	56.0	66.6	a
medium	76.2	3.89	347	68.9	84.2	b
high	122.3	5.00	347	112.8	132.5	c

Table A1.2. Results of pairwise comparisons of estimated marginal mean (emmean) trail depth with trail use levels, excluding off-trail transects. Intervals are back-transformed from the log scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean trail depths between trail use levels the Tukey adjustments for multiple tests.

trail use level	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
low	1.49	0.062	347	1.36	1.61	a
medium	1.35	0.072	347	1.21	1.49	a
high	1.34	0.058	347	1.22	1.45	a

Table A1.3. Results of pairwise comparisons of estimated marginal mean (emmean) soil compaction at each distance from the trail. Results are averaged over the levels of trail use and vegetation type. Degrees of freedom (df) are determined using Kenward-Roger method. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean soil compaction between quadrats at different distances with the Tukey adjustments for multiple tests.

distance (m)	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
0	-0.06	0.135	196	-0.329	0.202	a
2	-0.61	0.135	196	-0.880	-0.349	b
5	-0.54	0.135	196	-0.807	-0.276	b
10	-0.77	0.135	196	-1.037	-0.506	b
15	-0.79	0.135	196	-1.059	-0.528	b

Table A1.4. Results of pairwise comparisons of estimated marginal mean (emmean) species richness at each distance for each trail use level. Results are averaged over the burned status. Intervals are back-transformed from the log scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean species richness between quadrats at different distances and trail use level with the Tukey adjustments for multiple tests.

use level	distance (m)	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
off-trail	0	9.96	1.170	Inf	7.92	12.54	a
	2	10.42	1.210	Inf	8.30	13.09	a
	5	10.23	1.190	Inf	8.14	12.85	a
	10	8.91	1.070	Inf	7.03	11.28	a
	15	10.23	1.190	Inf	8.14	12.85	a
low	0	15.65	1.290	Inf	13.31	18.39	a
	2	12.72	1.090	Inf	10.76	15.05	b
	5	12.87	1.100	Inf	10.89	15.22	b
	10	11.89	1.030	Inf	10.03	14.09	b
	15	10.86	0.963	Inf	9.13	12.92	b
medium	0	13.89	1.370	Inf	11.45	16.84	a
	2	12.47	1.260	Inf	10.24	15.19	a
	5	12.73	1.280	Inf	10.46	15.50	a
	10	12.42	1.250	Inf	10.19	15.13	a
	15	12.79	1.280	Inf	10.51	15.56	a
high	0	12.00	0.964	Inf	10.25	14.05	a
	2	9.07	0.779	Inf	7.66	10.73	b
	5	8.32	0.731	Inf	7.00	9.88	b
	10	8.35	0.733	Inf	7.03	9.92	b
	15	8.80	0.761	Inf	7.42	10.42	b

Table A1.5. Results of pairwise comparisons of estimated marginal mean (emmean) species richness at each distance for each vegetation type. Results are averaged over the levels of burned status. Intervals are back-transformed from the log scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean species richness between quadrats and different vegetation types with the Tukey adjustments for multiple tests.

vegetation	distance (m)	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
coniferous	0	12.17	0.981	Inf	10.39	14.3	a
	2	8.97	0.777	Inf	7.57	10.6	b
	5	9.11	0.786	Inf	7.69	10.8	b
	10	8.63	0.755	Inf	7.27	10.2	b
	15	9.11	0.786	Inf	7.69	10.8	b
mixed	0	16.57	1.390	Inf	14.06	19.5	a
	2	13.60	1.180	Inf	11.47	16.1	b
	5	12.59	1.110	Inf	10.59	15.0	b
	10	11.65	1.040	Inf	9.77	13.9	b
	15	11.35	1.020	Inf	9.51	13.5	b
grassland	0	15.70	1.730	Inf	12.65	19.5	a
	2	14.49	1.620	Inf	11.64	18.0	a
	5	15.16	1.680	Inf	12.20	18.8	a
	10	15.70	1.730	Inf	12.65	19.5	a
	15	14.83	1.650	Inf	11.92	18.4	a

Table A1.6. Results of pairwise comparisons of estimated marginal mean (emmean) species richness within burned or unburned areas for each vegetation type. Results are averaged over the levels of distance. Intervals are back-transformed from the log scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean species richness between burned or unburned transects and vegetation type with the Tukey adjustments for multiple tests.

vegetation	burned status	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
coniferous	unburned	9.69	0.790	Inf	8.26	11.4	a
	burned	9.35	1.000	Inf	7.57	11.5	a
mixed	unburned	14.34	1.740	Inf	11.31	18.2	a
	burned	11.84	0.915	Inf	10.17	13.8	a
grassland	unburned	21.45	3.240	Inf	15.95	28.8	a
	burned	10.73	1.190	Inf	8.63	13.3	b

Table A1.7. Results of pairwise comparisons of estimated marginal mean (emmean) species richness at each vegetation type for each trail use level. Results are averaged over the levels of distance. Intervals are back-transformed from the log scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean species richness between trail use levels and vegetation type with the Tukey adjustments for multiple tests.

vegetation type	use level	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
coniferous	off-trail	9.05	1.000	Inf	7.29	11.2	a
	low	10.53	1.000	Inf	8.74	12.7	a
	medium	9.32	1.090	Inf	7.40	11.7	a
	high	8.82	0.787	Inf	7.41	10.5	a
mixed	off-trail	9.78	1.470	Inf	7.28	13.1	a
	low	15.34	1.350	Inf	12.91	18.2	b
	medium	13.35	2.250	Inf	9.60	18.6	ab
	high	10.09	0.964	Inf	8.37	12.2	a
grassland	off-trail	14.21	2.940	Inf	9.47	21.3	ab
	low	11.23	1.930	Inf	8.02	15.7	ab
	medium	17.70	1.920	Inf	14.31	21.9	a
	high	9.09	1.400	Inf	6.72	12.3	b

Table A1.8. Results of ANOVA test comparison between the null (intercept and random effects only) and the final models for species richness.

model	df	AIC	BIC	logLik	deviance	p
subset 1 – use level excluded						
null	2	2046.3	2054.0	-1021.18	2042.3	**<0.001**
final	20	1968.7	2045.6	-964.34	1928.7	
subset 2 – vegetation type excluded						
null	2	2422.2	2430.3	-1209.1	2418.2	**<0.001**
final	23	2350.0	2442.6	-1152.0	2304.0	
subset 3 – burn status excluded						
null	2	2422.2	2430.3	-1209.1	2418.2	**<0.001**
final	18	2339.2	2411.7	-1151.6	2303.2	

Table A1 9. Results of pairwise comparisons of estimated marginal mean (emmean) dissimilarity using the 15m quadrat with each distance. Results are averaged over the levels of vegetation type and burned status. Degrees of freedom (df) are determined using Kenward-Roger method. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean dissimilarity between quadrats at different distances with the Tukey adjustments for multiple tests.

distance (m)	emmean	SE	df	lower	upper	Diff. (Tukey adjusted)
0	0.638	0.0211	125	0.596	0.679	a
2	0.569	0.0211	125	0.527	0.611	b
5	0.544	0.0211	125	0.502	0.586	b
10	0.491	0.0211	125	0.450	0.533	c

Table A1.10. Results of ANOVA test comparison between the null (intercept and random effects only) and the final models for dissimilarity.

model	npar	AIC	BIC	logLik	-2*log(L)	p
subset 1 – use level excluded						
null	3	-247.30	-236.48	126.65	-253.30	**<0.001**
final	9	-290.89	-258.44	154.45	-308.89	
subset 2 – vegetation type excluded						
null	3	-314.33	-302.95	160.17	-320.33	**<0.001**
final	10	-363.22	-325.29	191.61	-383.22	
subset 3 – burn status excluded						
null	3	-314.33	-302.95	160.17	-320.33	**<0.001**
final	11	-362.38	-320.65	192.19	-384.38	

Table A1.11. Results of pairwise comparisons of estimated marginal mean (emmean) probability of presence of exotic species using distance moving out from the trail. Results are averaged over the levels of vegetation type and burned status. Tests are performed on the log odds ratio scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean exotic species presence or absence between quadrats at different distances with the Tukey adjustments for multiple tests.

distance (m)	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
0	0.500	0.1380	Inf	0.252	0.747	a
2	0.198	0.0923	Inf	0.073	0.436	a
5	0.228	0.1010	Inf	0.087	0.477	b
10	0.107	0.0582	Inf	0.035	0.283	b
15	0.147	0.0745	Inf	0.051	0.356	b

Table A1.12. Results of pairwise comparisons of estimated marginal mean (emmean) probability of presence of exotic species using vegetation type and burned status. Results are averaged over the levels of distance. Intervals are back-transformed from the log scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean exotic species relative abundance between vegetation type and burned status with the Tukey adjustments for multiple tests.

vegetation	burned status	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
coniferous	unburned	0.0143	0.0157	Inf	0.002	0.114	a
	burned	0.1869	0.1180	Inf	0.048	0.513	b
mixed	unburned	0.4719	0.2910	Inf	0.083	0.898	a
	burned	0.4026	0.1420	Inf	0.175	0.682	a
grassland	unburned	0.4909	0.3140	Inf	0.076	0.919	a
	burned	0.3454	0.2240	Inf	0.071	0.786	a

Table A1.13. Results of pairwise comparisons of estimated marginal mean (emmean) probability of presence of exotic species using trail use level and vegetation type. Results are averaged over the levels of distance. Tests are performed on the log odds ratio scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean exotic species presence or absence between transects at different trail use levels and vegetation types with the Tukey adjustments for multiple tests.

vegetation	use level	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
coniferous	off-trail	2.20e-02	0.0342	Inf	9.99e-04	0.337	a
	low	1.73e-01	0.0951	Inf	5.35e-02	0.435	a
	medium	3.97e-02	0.0429	Inf	4.55e-03	0.273	a
	high	3.33e-02	0.0549	Inf	1.22e-03	0.493	a
mixed	off-trail	1.79e-04	0.0007	Inf	7.00e-08	0.304	a
	low	5.35e-01	0.1600	Inf	2.45e-01	0.803	ab
	medium	9.01e-01	0.1480	Inf	2.61e-01	0.996	ab
	high	4.88e-03	0.0094	Inf	1.09e-04	0.181	ac
grassland	off-trail	4.52e-05	0.0002	Inf	1.00e-08	0.216	a
	low	4.56e-01	0.3430	Inf	5.29e-02	0.927	a
	medium	3.87e-01	0.2000	Inf	1.08e-01	0.768	a
	high	1.11e-02	0.0223	Inf	2.03e-04	0.381	a

Table A1.14. Results of pairwise comparisons of estimated marginal mean (emmean) probability of presence of exotic species using elevation and trail use level. Results are averaged over the levels of distance and burned status. Elevation was split into min (-1.38), median (-0.178), and max (2.246) levels. Tests are performed on the log odds ratio scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean exotic species presence or absence between transects at different trail use levels and elevation with the Tukey adjustments for multiple tests.

elevation	use level	emmean	SE	df	lower	upper	Diff. (Tukey adjusted)
min	off-trail	9.50e-01	6.68e-02	Inf	5.43e-01	0.997	a
	low	9.23e-01	7.45e-02	Inf	6.06e-01	0.989	a
	medium	9.07e-01	8.55e-02	Inf	5.73e-01	0.986	a
	high	9.98e-01	4.86e-03	Inf	8.91e-01	1.000	a
median	off-trail	3.54e-02	4.59e-02	Inf	2.64e-03	0.338	a
	low	3.60e-01	1.19e-01	Inf	1.70e-01	0.608	a
	medium	3.77e-01	1.49e-01	Inf	1.48e-01	0.678	a
	high	2.65e-02	3.80e-02	Inf	1.50e-03	0.330	a
high	off-trail	1.00e-07	6.50e-07	Inf	0.00e+00	0.004	a
	low	1.18e-03	2.59e-03	Inf	1.63e-05	0.079	a
	medium	2.24e-03	4.17e-03	Inf	5.73e-05	0.081	a
	high	0.00e+00	0.00e+00	Inf	0.00e+00	0.000	a

Table A1.15. Results of ANOVA test comparison between the null (intercept and random effects only) and the final models for presence or absence of exotic species.

model	npar	AIC	BIC	logLik	-2*log(L)	p
subset 1 – use level excluded						
null	2	325.61	333.30	-160.81	321.61	**<0.001**
final	10	255.24	301.36	-115.62	234.24	
subset 2 – vegetation type excluded						
null	2	383.62	391.67	-189.81	379.62	**<0.001**
final	14	295.33	351.72	-133.66	267.33	
subset 3 – burn status excluded						
null	2	383.62	391.67	-189.81	379.62	**<0.001**
final	21	294.48	379.07	-126.24	252.48	

Table A1.16. Results of pairwise comparisons of estimated marginal mean (emmean) relative abundance of exotic species using distance from the trail edge and trail use level. Results are averaged over the levels of burned status. Intervals are back-transformed from the log scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean exotic species relative abundance between different quadrats and trail use level with the Tukey adjustments for multiple tests.

use level	distance (m)	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
off-trail	0	0.083	0.0274	Inf	0.043	0.159	a
	2	0.050	0.0180	Inf	0.025	0.101	a
	5	0.104	0.0343	Inf	0.055	0.199	a
	10	0.069	0.0363	Inf	0.024	0.193	a
	15	0.037	0.0165	Inf	0.016	0.089	a
low	0	0.178	0.0328	Inf	0.124	0.255	a
	2	0.150	0.0315	Inf	0.100	0.226	b
	5	0.075	0.0180	Inf	0.047	0.120	b
	10	0.100	0.0237	Inf	0.060	0.156	b
	15	0.068	0.0196	Inf	0.039	0.120	b
medium	0	0.092	0.0247	Inf	0.054	0.156	a
	2	0.114	0.0323	Inf	0.066	0.199	a
	5	0.090	0.0247	Inf	0.053	0.154	a
	10	0.067	0.0214	Inf	0.036	0.125	a
	15	0.090	0.0262	Inf	0.051	0.159	a
high	0	0.134	0.0317	Inf	0.084	0.213	a
	2	0.122	0.0327	Inf	0.072	0.206	a
	5	0.078	0.0227	Inf	0.044	0.138	a
	10	0.069	0.0220	Inf	0.037	0.129	a
	15	0.142	0.0315	Inf	0.092	0.219	a

Table A1.17. Results of pairwise comparisons of estimated marginal mean (emmean) relative abundance of exotic species using distance from the trail edge and burned status. Results are averaged over the levels of trail use. Intervals are back-transformed from the log scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean exotic species relative abundance between distance from the trail edge and burned status with the Tukey adjustments for multiple tests.

distance (m)	burned status	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
0	burned	0.111	0.025	Inf	0.071	0.174	a
	unburned	0.122	0.019	Inf	0.090	0.165	a
2	burned	0.081	0.021	Inf	0.048	0.135	a
	unburned	0.127	0.021	Inf	0.092	0.176	a
5	burned	0.055	0.016	Inf	0.032	0.096	a
	unburned	0.134	0.022	Inf	0.098	0.184	b
10	burned	0.066	0.022	Inf	0.034	0.126	a
	unburned	0.084	0.017	Inf	0.057	0.125	a
15	burned	0.055	0.016	Inf	0.031	0.096	a
	unburned	0.104	0.018	Inf	0.074	0.147	b

Table A1.18. Results of pairwise comparisons of estimated marginal mean (emmean) relative abundance of exotic species using vegetation type and burned status. Results are averaged over the levels of distance. Intervals are back-transformed from the log scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean exotic species relative abundance between vegetation type and burned status with the Tukey adjustments for multiple tests.

vegetation	burned status	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
coniferous	unburned	0.061	0.0290	Inf	0.024	0.049	a
	burned	0.081	0.0207	Inf	0.049	0.134	a
mixed	unburned	0.105	0.0221	Inf	0.070	0.159	a
	burned	0.112	0.0182	Inf	0.081	0.154	a
grassland	unburned	0.071	0.0235	Inf	0.037	0.135	a
	burned	0.247	0.0406	Inf	0.179	0.341	b

Table A1.19. Results of pairwise comparisons of estimated marginal mean (emmean) relative abundance of exotic species using vegetation type and trail use level. Results are set using predicators as elevation (-1.02), transect (t009) and distance (0m). Intervals are back-transformed from the log scale. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final column denote significant differences in mean exotic species relative abundance between vegetation and use level with the Tukey adjustments for multiple tests.

vegetation	use level	emmean	SE	df	lower	upper	diff. (Tukey adjusted)
coniferous	off-trail	0.063	0.0255	Inf	0.029	0.140	a
	low	0.106	0.0288	Inf	0.062	0.180	a
	medium	0.100	0.0405	Inf	0.043	0.220	a
	high	0.117	0.0527	Inf	0.048	0.283	a
mixed	off-trail	0.129	0.0381	Inf	0.072	0.230	a
	low	0.149	0.0268	Inf	0.104	0.211	a
	medium	0.190	0.0474	Inf	0.117	0.310	a
	high	0.128	0.0247	Inf	0.088	0.187	a
grassland	off-trail	0.145	0.0438	Inf	0.080	0.262	a
	low	0.463	0.1020	Inf	0.300	0.714	b
	medium	0.133	0.0266	Inf	0.089	0.196	a
	high	0.409	0.0784	Inf	0.281	0.596	b

Table A1.20. Results of ANOVA test comparison between the null (intercept and random effects only) and the final models for relative abundance of exotic species.

model	df	AIC	BIC	logLik	deviance	p
subset 1 – use level excluded						
null	3	-278.88	-270.21	142.44	-284.44	**<0.001**
final	13	-303.55	-265.98	164.78	-329.55	
subset 2 – vegetation type excluded						
null	3	-336.22	-327.11	171.11	-342.22	**<0.001**
final	28	-348.19	-263.16	202.10	-404.19	
subset 3 – burn status excluded						
null	3	-336.22	-327.11	171.11	-342.22	**<0.001**
final	19	-363.41	-305.71	200.71	-401.41	