## RECREATIONAL TRAIL IMPACTS ON THE PLANT COMMUNITIES OF CASTLE AND CASTLE WILDLAND PROVINCIAL PARKS IN SOUTHERN ALBERTA

## TRINITAS CHISHOLM Bachelor of Science, University of Lethbridge, 2018

A thesis submitted

in partial fulfillment of the requirements for the degree of

## **MASTER OF SCIENCE**

in

## **BIOLOGICAL SCIENCE**

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

© Trinitas Evette Chisholm, 2022

# RECREATIONAL TRAIL IMPACTS ON THE PLANT COMMUNITIES OF CASTLE AND CASTLE WILDLAND PROVINCIAL PARKS IN SOUTHERN ALBERTA

## TRINITAS CHISHOLM

## Date of Defense: November 1, 2022

Dr. J.L. McCune Thesis Supervisor	Assistant Professor	Ph.D.
Dr. J.F. Bain Thesis Examination Committee Member	Professor Emeritus	Ph.D.
Dr. J. Lee-Yaw Thesis Examination Committee Member	Assistant Professor	Ph.D.
Dr. R. Laird Thesis Examination Committee Member	Associate Professor	Ph.D.
Dr. C. Goater Chair, Thesis Examination Committee	Professor	Ph.D.

# **DEDICATION**

To anyone reading this. With seemingly insurmountable struggles comes undeniable success in pursuing your passion. Keep trudging up that mountain so you can enjoy the

view.

## ABSTRACT

I measured the effect of recreational trails on plant species richness, community composition, and the presence of exotic and rare species in the Castle Provincial Parks of Alberta, Canada, by surveying 142 transects adjacent to or far from trails. I also characterized the habitat of species from the rare genus *Botrychium* Swartz and tested a species distribution model (SDM) to identify suitable *Botrychium* habitat. Plant communities near trails had higher species richness, shifts in composition, and greater occurrence of exotic plant species. These effects extended farther from off-highway vehicle (OHV) trails than from footpaths, but only in mixed/broadleaf and shrubland vegetation. The SDM was not a strong predictor of *Botrychium* presence, but I found *Botrychium* in 29% of surveyed sites. To minimize trail effects such as colonization by exotic species, managers should prioritize closing trails to OHVs or limiting OHV traffic, particularly in mixed/broadleaf and shrubland vegetation.

### ACKNOWLEDGMENTS

To my family who have been patiently waiting for me to finish my degrees and are always there to give me helpful words of wisdom. To my partner, Kyle Bischke, who constructed the quadrats used in my project, adopted my dog during field season, and most importantly, provided me with the mental encouragement to keep pushing through those difficult moments. To my friends who, entertained my outspoken thoughts, passion for *Botrychium* and botanizing on camping and hiking trips, even though they still may not know exactly what my research entails. To my mentors: Jenny Burke, who inspired me to find that same passion for native plants that she does; her excitement and love for botany got me curious and wanting to know more about the fascinating world of plants and herbaria. Dr. John F. Bain, my favourite LEA Herbarium curator who can climb up steep scree slopes like no other in hopes of finding those rare plants! And to Joanne Golden who instilled confidence in my plant skills and encouraged me to pursue grad school. These three are all equally responsible for my botanical craze and have inspired me to continue this journey which has led me to climb many mountains and enjoy many views. To my funding partners, Alberta Conservation Association (ACA) who provided financial support for my research which helped enormously in making this project happen. To Alberta Environment & Parks (AEP) for allowing me to conduct my research in Castle. To Wonnita Andrus for providing location data of exotic plant control areas and the keys for accessing gated trails. To my committee members, Dr. John F. Bain, Dr. Julie Lee-Yaw, and Dr. Robert Laird, who provided constructive feedback on my proposal, presentations, and thesis. To my lab members who listened through practice presentations and provided me with feedback and advice on my project. To my field assistants, Kirsty McFadyen, David Musk, Dani Jakovljevic, and Cooper Hayward, who

v

endured long field hours, unpredictable mountain weather, and sometimes uncomfortable tenting trips. And last but certainly not least, a very special thank-you to my supervisor, Dr. Jenny McCune. Jenny provided advice during difficult moments and guided me in the statistical analyses world which allowed me to explore my ecological curiosities about the plant communities. She is always encouraging and supportive of her students along their journey, motivating us to put our best foot forward in everything we do. Throughout my entire project, Jenny has been patient from start to finish, and she inspires me to continue finding those little moments to still play the piano. Thank-you. Without any of you, this project would not have been possible!

DEDICATION	iii
ABSTRACT	iv
ACKNOWLEDGMENTS.	V
LIST OF TABLES	ix
LIST OF FIGURES	xiv
<b>CHAPTER 1: INTRODUC</b>	<b>TION</b> 1
1.1 Background	1
1.2 Objectives	5
1.3 Thesis Organiza	tion5
CHAPTER 2: RECREATI COMMUNITIES OF CAS PARKS (CCWPP)	ONAL TRAIL IMPACTS ON THE PLANT FLE AND CASTLE WILDLAND PROVINCIAL
2.1 Abstract	
2.2 Introduction	9
2.3 Methods	
2.3.1 Study an	ea18
2.3.2 Study D	esign22
2.3.3 Data Co	llection24
2.3.4 Statistic	al Analyses27
2.4 Results	
2.4.1 Species	richness
2.4.2 Commu	nity composition41
2.4.3 Presence	e of at least one exotic species44
2.4.4 Presence	e of at least one rare species48
2.5 Discussion	
2.5.1 Trail im	pacts on species richness51
2.5.2 Trail im	pacts on plant community composition55
2.5.3 Trail im	pacts on the presence of exotic species57

# **TABLE OF CONTENTS**

2.5.4 The effect of trails on the presence of exotic species at higher elevations	61
2.5.5 Trail impacts on the presence of rare species	63
2.6 Conclusion	65
CHAPTER 3: HABITAT CHARACTERISTICS OF KNOWN BOTRYCHIUM OCCURRENCES AND QUANTITATIVE ANALYSIS OF ITS ASSOCIATION WITH TRAILS	
<b>3.1</b> Abstract	66
3.2 Introduction	67
3.3 Methods	73
3.3.1 Assessing <i>Botrychium</i> habitat	.73
3.3.2 Testing a Species Distribution Model	74
3.3.3 Data Collection	79
3.3.4 Statistical Analyses	81
3.4 Results	82
3.4.1 Assessing factors associated with <i>Botrychium</i> occurrences in CCWPP	82
3.4.2 SDM as a predictor for off-trail <i>Botrychium</i> occurrences	.86
3.4.3 Quantifying differences in community composition of plots with without <i>Botrychium</i>	and 89
3.5 Discussion	91
<b>3.6</b> Conclusion	99
CHAPTER 4: CONCLUSION	100
4.1 Limitations and future directions	101
4.2 Concluding Statement	102
REFERENCES	104
APPENDICES1	116
1- Chapter 2 Supplementary Materials	116
2- Chapter 3 Supplementary Materials	134

# LIST OF TABLES

Table 1. Number of control and on-trail transects surveyed within each vegetation type in each watershed in CCWPP.    23
Table 2. Predictor variables used in mixed models for each response variable
Table 3. Results of the model for species richness
Table 4. Results of the model for species richness of footpaths and OHV trails   only
Table 5. Results of the model for shifts in community composition (Bray-Curtisdissimilarity) compared to the 10m quadrat
Table 6. Results of the model for the probability of at least one exotic species   present
Table 7. Results of the model for the probability of at least one rare species   present
Table 8. Results of the model for the probability of at least one rare species present forfootpaths and OHV trails only
Table 9. Environmental predictors used to build the <i>Botrychium</i> SDM
Table 10. Table of <i>Botrychium</i> species (rows) identified from photographed occurrences within each vegetation type (columns)
Table 11. Table of associated species identified in <i>Botrychium</i> photographs ( $n = 81$ ) and the number of times each species was listed as an associate
Table 12. Characteristics of the 24 off-trail plots surveyed in the summer of 2021, inorder of increasing predicted habitat suitability according to a species distributionmodel
Table 13. Predictor variables included in the model for <i>Botrychium</i> habitat   suitability
Table 14. Results of PERMANOVA pairwise tests comparing species composition in plots with <i>Botrychium</i> present and absent
Table 15. Significant indicator species of plots with or without <i>Botrychium</i> according to an indicator species analysis with 9,999 permutations
Table A1.1. Final locations of trailside and off-trail transects surveyed in June to Augustof 2020 and 2021
Table A1.2. Results of pairwise comparisons of estimated marginal mean maximumheight of vegetation of each trail type compared between distances from trail121

Table A1.3. Results of pairwise comparisons of estimated marginal mean soil compaction values at each distance compared between trail types
Table A1.4. Results of pairwise comparisons of estimated marginal mean (emmean) soilcompaction values for each trail type between distances from trail
Table A1.5. List of exotic species (n = 35) recorded during two survey seasons, fromJune to August of 2020 and 2021
Table A1.6. List of rare species (n = 15) recorded during two survey seasons, from Juneto August of 2020 and 2021125
Table A1.7. Results of pairwise comparisons of estimated marginal mean species richness at each distance for each vegetation type
Table A1.8. Results of pairwise comparisons of mean species richness (emmean) at eachdistance from trail for each trail type
Table A1.9. Results of pairwise comparisons of the slope of the relationship betweenspecies richness and distance from trail (emtrends) for the subset data of only footpathsand OHV trails within each vegetation type
Table A1.10. Results of pairwise comparisons of community dissimilarity within each vegetation type
Table A1.11. Results of pairwise comparisons of mean Bray-Curtis dissimilarity values(emmean) between each trail type at each distance from trail
Table A1.12. Results of pairwise comparisons of mean Bray-Curtis dissimilarity values(compared to the 10m quadrat) for footpaths and OHV trails (emmean) for eachvegetation type.129
Table A1.13. Results of pairwise comparisons of the probability of exotic speciespresence within each vegetation type
Table A1.14a. Results of pairwise comparisons of the probability of exotic speciespresent (emmean) at each distance from trail for each trail type
Table A1.14b. Results of pairwise comparisons of the probability of exotic speciespresent (emmean) for each trail type at each distance
Table A1.15. Results of estimated marginal means of linear trends comparing the slope of the relationship between the probability of at least one exotic species and distance from trail (trend) for the subset data of only footpaths and OHV trails within each vegetation type
Table A1.16. Results of pairwise comparisons (emmeans) of the mean probability of at least one exotic species per transect compared between each vegetation type

Table A1.17. Results of pairwise comparisons (emtrends) of the slope of the relationship
between the probability of at least one exotic species per transect and elevation compared
between each trail type
Table A1.18. Results of pairwise comparisons of the probability of rare species present

Table A2.1. Results of the indicator species analysis for plots with or without *Botrychium* according to an indicator species analysis with 9,999 permutations......134

# **LIST OF FIGURES**

Figure 13. The diversity of <i>Botrychium</i> species found along two popular hiking trails in CCWPP, Alberta, Canada	0
Figure 14. Inset: shows model extent (grey shaded) and location of Castle Provincial Par and Castle Wildland Provincial Park in the southwest corner of Alberta, Canada. Main map: CCWPP, coloured based on predicted habitat suitability for <i>Botrychium</i> according to a species distribution model (SDM)	8
Figure 15. A schematic diagram of a 50 m x 50 m plot80	)
Figure 16. The frequencies of a) moonwort species; and b) vegetation types of the 85 occurrence records	1
Figure 17. Histograms showing the frequency of occurrences of <i>Botrychium</i>	6
Figure 18. NMDS (non-metric multidimensional scaling) ordination of all 50 m x 50 m sites in species space	0

## **CHAPTER 1: INTRODUCTION**

#### 1.1 Background

Protected parks have been established in Canada since the 1800s, primarily to support the economy through recreational activities, and secondarily, to protect wildlife and the wilderness (Foster, 1998). As the popularity of parks and the human population continue to grow, both the number of recreational trails and the intensity of their use will increase, placing more impact on the surrounding ecosystem (Debarbieux et al., 2014). Globally, research on the impact of recreational trails on plant communities has increased (Sumanapala & Wolf, 2019); however, most studies focus on parks and wilderness reserves throughout the United States (e.g., Cole, 1978; Benninger-Truax et al., 1992; Gibson et al., 2000; Dickens et al., 2005) and Australia (e.g., Scherrer & Pickering, 2006; Ngugi et al., 2014; Pickering & Norman, 2017). Although some studies of trail impacts on plant communities have been done in Canada (Price, 1985; Parikesit et al., 1995; Thurston & Reader, 2001; Nepal & Way, 2007; Crisfield et al., 2012; Trip & Wiersma, 2015; Grenke et al., 2018), only a handful of published studies have been conducted in Alberta's Rocky Mountains (Price, 1985; Crisfield et al., 2012; Grenke et al., 2018) even though parks in this region (including Banff, Jasper, Yoho, and Waterton Lakes National Parks) have the highest attendance rates among Canada's National Parks (Parks Canada, 2021). Understanding the impact of recreational trails is an important consideration for all natural areas and protected parks in balancing recreation and conservation.

Many studies on trail impacts have focused on large mammals like bears (Kasworm & Manley, 1990; Benn & Herrero, 2002), wolves (Whittington et al., 2005; Naylor et al., 2009; Rogala et al., 2011), and elk (Naylor et al., 2009; Rogala et al., 2011). These animals tend to avoid high traffic trails and roads (e.g., Kasworm & Manley, 1990; Whittington et al., 2005; Rogala et al., 2011), and change their daily routine of resting, feeding, and travel to avoid high traffic trails (Rogala et al., 2011). Trails also affect birds, with increased nest predation (Miller et al., 1998), lower nest success (Yoo and Koper, 2017), and lower bird densities near roads and trails (Thompson, 2015). Trails can also positively impact some animals. For example, salamanders are associated with microhabitats found near low traffic trails (Davis, 2007; Smith et al., 2017).

The effect of recreational trails on vegetation has been studied since the 1930s, with studies noting how trailside conditions can favour certain growth forms. For example, Bates (1935) found that species with prostrate, low-growing lifeforms were more likely to survive trailside than species with upright, brittle-stems. Trails can also affect the species richness of a plant community. For example, some studies have reported higher plant species richness near trails than away from trails, likely due to higher light availability trailside (Bates, 1935; Dale & Weaver, 1974; Tyser & Worley, 1992). Others report that intermittent disturbance along trails prevents dominance by the strongest competitor (Larson, 2002; Dickens, 2005). Increased richness near trails is also facilitated by the introduction of seeds of exotic species and disturbance-adapted native species via animals (Campbell & Gibson, 2001), hikers' boots and clothing (Mount & Pickering, 2009), or vehicles (von der Lippe & Kowarik, 2007; Yang et al., 2021). Trails also alter environmental conditions, which in turn affects the kinds of species growing within a community. Therefore, the composition of plant communities near trails is often different than those away from trails (Müllerová et al., 2011; Benninger-Traux et al., 1992).

Finally, the presence or absence of rare plant species can be affected by nearby trails. Small populations of rare plant species in popular recreation areas are susceptible to trampling by hikers and OHVs (off-highway vehicles), especially when these activities stray from designated trails (e.g., Kerbiriou et al., 2008) or occur in sensitive alpine habitats (e.g., Rossi et al., 2009). However, the presence of trails can sometimes benefit rare plants, perhaps because intermittent disturbance reduces competition for light or nutrients (e.g., Catling & Kostuik, 2011; Wedegärtner et al., 2022).

In Canada, only a handful of recreational trail studies have focused on plant communities (Parikesit et al., 1995; Nepal & Way, 2007; Crisfield et al., 2012; Trip & Wiersma, 2015). In Ontario, plant species richness was highest along trails with intermediate use levels (Parikesit et al, 1995), consistent with the intermediate disturbance hypothesis (Connell, 1978). A study in Newfoundland found that dry boreal forests were less resistant to changes in species composition caused by trails compared to heath or bog sites (Trip & Wiersma, 2015). In British Columbia, Nepal & Way (2007) found that two backcountry trails had significantly higher species richness of herbaceous species trailside compared to off-trail. In contrast, alpine vegetation in the northern Rocky Mountains of Alberta had lower species richness along trails compared to the undisturbed or naturally disturbed tundra (Crisfield et al., 2012). Differences in trail impacts across Canada and between different vegetation types indicate a need for more studies assessing the effect of recreational trails on plant communities.

Castle Provincial Park and Castle Wildland Provincial Park (CCWPP) were established in 2017 (Alberta Environment & Parks, 2018). For over 10,000 years this region has been home to the Piikani nation, members of the Blackfoot confederacy, who hunt and fish the land (Alberta Wilderness Association, 2022). The Castle region, situated in the southwest Rocky Mountain range of Alberta, has 106 species of plants that are provincially tracked due to their rarity, more than twice as many as Banff or Jasper (Farr et al., 2017). The region is also a world centre of diversity for a small, cryptic fern genus called moonwort (*Botrychium* Sw.; Wagner et al., 1983; Williston, 2001).

CCWPP was originally part of Waterton Lakes Dominion Park (now Waterton Lakes National Park), established in 1895 as Canada's fourth National Park after Banff, Glacier, and Yoho National Parks (Lothian, 1987). However, with the enactment of the Dominion Forest Reserves and Parks Act in 1911, the Castle region was removed from the National Park (Doherty, 2012). This resulted in the Castle region's re-designation to forest reserve status, which limited public use, but still allowed for livestock grazing and timber harvest (Gillis & Roach, 1986). The CCWPP region was designated as a Provincial Game Reserve in 1921, providing extended areas of pasture for ranchers. However, this status was removed in 1954, reverting the region's status to Provincial Crown Land, which permitted managed cattle grazing, timber harvest, extraction of oil and gas, as well as unregulated recreational use (Castle-Crown Wilderness Coalition (CWCC), 2022). In 1974, a Government of Alberta study recommended that the area should be protected (CCWC, 2022), but the CCWPP were not established as provincial parks until 43 years later (Alberta Environment and Parks, 2018). After designation as provincial parks, many trails in the southern region of Castle Provincial Park were closed to OHV users; however, most trails in the northwest area of CCWPP remain open to OHV use. The provincial government planned to close 130 km of OHV trails by the end of 2021; however, strong pushback against the trail closures by local OHV users resulted

in the delay of this phase-out (Bellefontaine, 2019). Currently, there are an estimated 2,000 km of linear features, which include roads and recreational trails, in CCWPP (Farr et al. 2017). Although there have been studies on the trail impacts on animals such as bears (Lee & Hanneman, 2011; Proctor et al., 2020), and elk (Ciuti et al., 2012; Paton et al., 2017), how trails affect plant communities in this area has not yet been studied.

## **1.2 Objectives**

The overall goal of my research was to quantify the effects of recreational trails on plant communities in the Castle and Castle Wildland Provincial Parks and determine how these effects vary among different trail types and different vegetation types. My specific objectives were:

- To establish a set of plots along trails in CCWPP which can be resurveyed for future research.
- 2. To measure the effect of recreational trails on species richness and community composition, and to quantify how far this effect extends away from the trail.
- To measure the effect of recreational trails on the presence of exotic and rare species.
- To test how trail use type, vegetation type, or interactions between them, influence the effect of trails on species richness, composition, and the presence of exotic and rare species.
- 5. To characterize the habitats associated with *Botrychium* occurrences and test a habitat suitability model as a predictor of *Botrychium* occurrences away from trails in CCWPP.

## **1.3 Thesis Organization**

In Chapter 2, I test the effect of recreational trails on i) the species richness of vascular plants, ii) the composition of plant communities, iii) the presence of exotic plants, and iv) the presence of critically imperiled (S1) and imperiled (S2) provincially tracked rare plants in CCWPP. I surveyed 118 trail, and 24 off-trail transects throughout the two provincial parks, recording the abundance of all vascular plants within a 1 m x 1 m survey area directly adjacent to the trail edge (0 m), and 2 m, 5 m, and 10 m along the transect perpendicular to the trail or off-trail starting point. I then used these data to test the effects of trail type, distance from trail edge, and vegetation type on vascular plant richness, the shift in plant community composition, and the presence of exotic and rare species moving along the transect.

In Chapter 3, I focus on the genus *Botrychium* (moonwort), which includes 21 species found in Alberta, 15 of which are considered by NatureServe to be provincially rare (NatureServe, 2022). CCWPP is part of the region designated as the world's centre of *Botrychium* diversity (Wagner et al., 1983; Williston, 2001). *Botrychium* are small ferns that have an aboveground stem divided into two axes: one that is sterile and leaf-like, the other with small round clusters of fertile sporangia which house spores (Farrar, 2011). Observations that several species of moonwort are often found near trail edges support the idea that moonwort may benefit from trails (Müllerová et al., 2011). I assess habitat characteristics of *Botrychium* occurrences to determine potential predictors of species distribution. Then, using a species distribution model built using all known records of species in the *Botrychium* genus in Alberta, I visited 24 sites at least 100 m away from any recreational trail in CCWPP that varied in their predicted species distribution. I recorded all vascular plant species present, while carefully searching for

moonwort presence. I then used these data to test the species distribution model as a predictor for moonwort occurrences away from trails and to characterize the plant community composition of sites with versus without *Botrychium* present.

Chapter 4 summarizes the findings of Chapters 2 and 3 and highlights the implications for trail management in CCWPP.

The effects of trails on plants have been studied in many places, but we know very little about how trails affect the plant communities in CCWPP, a hotspot for plant diversity. My research provides the foundation for ongoing ecological research on the plant communities in the two parks, and their response to disturbance associated with trails. With potential for more and more visitors as the park gains popularity and interest, it is important to understand how plant communities are affected by trails. My research will help managers make decisions about trail closures by revealing which vegetation types are most sensitive to trail-use and identifying trail types that are most likely to serve as conduits for invasion by exotic plant species. In addition, my research contributes information on habitat preferences for understudied, rare species like moonwort. Understanding how roads and trails affect plant communities in CCWPP is integral to balancing recreational use and conservation.

## CHAPTER 2: RECREATIONAL TRAIL IMPACTS ON THE PLANT COMMUNITIES OF CASTLE AND CASTLE WILDLAND PROVINCIAL PARKS (CCWPP)

## 2.1 Abstract

In protected parks, whose mandates balance recreation and conservation, it is important to understand how trails affect plant communities. I investigated the impacts of recreational trails on plant communities in Castle Provincial and Castle Wildland Provincial Parks (CCWPP), a provincial hotspot of plant diversity, including many rare species. I surveyed plant communities in transects extending 11 m from trails that vary in trail use and vegetation type, and in control transects distant from any trail. I tested the effects of trails on species richness, community composition, and the presence of exotic and rare species. I predicted that communities adjacent to trail edges would have higher species richness, shifts in community composition, and greater occurrence of exotic species compared to communities several meters from a trail or control transects. I also predicted that the magnitude of these differences would vary for different trail types and different vegetation types. For example, I predicted that the effects of OHV (off-highway vehicle) trails would extend farther from the trail edge compared to footpaths and that the effect of trails would be stronger in coniferous forests, which have restricted light availability compared to other vegetation types. My results showed the predicted patterns in most cases, with increased species richness, shifts in community composition, and increased probability of finding exotic species within five metres of trails or roads. However, vegetation type and trail type influenced the magnitude and extent over which these changes occurred. In grasslands, there were no significant increases in species

richness or shifts in composition near trail edges, likely because light availability is similar whether near or far from the trail. Grasslands had nearly 100% probability of exotic species occurrence up to 10 m away from trails, whereas in coniferous forests the probability of exotic species occurrences decreased dramatically 10 m away from the trail. Exotic species had a higher likelihood of occurring beyond 2 m from OHV trails than from footpaths, but only in mixed/broadleaf or shrubland vegetation. Although rare species were slightly more likely to occur in control transects away from trails, we found 15 different species near trails with either a provincial conservation status of critically imperiled (S1) or imperiled (S2). As the first study to look at trail impacts on plant communities in CCWPP, results of this study highlight that the effect of recreational trails depends on the type of trail and the type of vegetation it goes through. Limiting OHV trails through shrubland and mixed forest vegetation could reduce spread of exotic species from the trailside into these vegetation types.

## **2.2 Introduction**

As the human population continues to increase, more habitat is converted to human land use, and the remaining protected areas face increased numbers of recreational visitors (Wittemyer et al., 2008; Debarbieux et al., 2014; Monz et al., 2021). Protected areas often have two goals: conserving ecosystems *and* providing a space for outdoor recreational activities. For example, under Alberta's *Protected Parks Act*, the purpose of establishing provincial parks is for preservation of natural heritage, and for the enjoyment of outdoor recreation (Government of Alberta, 2017). For this reason, it is important to understand how recreational activities affect ecological communities in protected areas. An important question is how roads and trails - which provide access for recreation -

affect plant communities. Parks are often criss-crossed by many kilometres of roads and trails (Figure 1). The construction, maintenance, and continued use of roads and trails increases soil compaction and erosion (Webb et al., 1978; Ballantyne & Pickering, 2015; Marion et al., 2016), decreases soil moisture (Webb et al., 1978; Ballantyne & Pickering, 2015), and increases light and disturbance levels (Watkins et al., 2003; Avon et al., 2010). It is important to quantify how these altered conditions affect plant community composition and diversity, how far these effects extend away from trails and roads, and whether impacts are greater for different types of trails or different vegetation types.

The species richness of a plant community can be affected by trails. Many studies have reported higher plant species richness near trails than away from trails, likely due to increased light availability trailside coupled with the fact that fewer species are able to tolerate the low light conditions below dense canopies of forest interiors (Bates, 1935; Dale & Weaver, 1974; Tyser & Worley, 1992). Others suggest that the intermittent disturbance along trails promotes species richness by preventing dominance by the strongest competitor (Larson, 2002; Dickens, 2005). Increased richness near trails could also be caused by the introduction of seeds of exotic species and disturbance-adapted native species via animals (Campbell & Gibson, 2001), hikers' boots and clothing (Mount & Pickering, 2009), or vehicles (von der Lippe & Kowarik, 2007; Yang et al., 2021). Plant species richness near trails also varies depending on the vegetation type that a trail traverses. For example, in the Rocky Mountain ranges of Colorado, USA, Wells et al. (2013) determined that native species richness along trails was significantly higher in aspen forests, riparian areas, and meadows compared to evergreen forests. Species richness near trails can also vary depending on the level of trail use. For example,

Benninger-Truax et al. (1992) determined that species richness was significantly higher along light and moderately used trails compared to heavily used trails. Similarly, Parikesit et al. (1995) found higher species richness along trails with intermediate disturbance compared to heavily used trails or undisturbed sites. Most studies have found that the effect of trails on plant species richness extends no more than 5m from roads or trails (Watkins et al., 2003; Godefroid & Koedam, 2004; Benninger-Truax et al., 1992). However, the extent of a trail effect on plant species richness could vary for different regions.



Figure 1. Photograph taken in the summer of 2021 from the summit of Table Mountain, showing the main gravel road traversing through coniferous and wetland habitats in Castle Provincial & Wildland Provincial Parks, heading towards Beaver Mines Lake in Alberta, Canada.

The composition of plant communities is also altered by the presence of nearby roads and trails. This follows from the fact that some species prefer trailside conditions, while others are sensitive to them. For example, one study in the alpine tundra of the Czech Republic found that highly competitive species tolerant of human disturbance were dominant close to roads whereas less competitive stress-tolerant species became dominant farther from the road (Müllerová et al., 2011). Another study in the coniferous forests of Rocky Mountain National Park, USA found that in addition to significantly higher species richness trailside, there was a shift in community composition towards higher abundance of species with disturbance tolerant traits, such as ground-level leaves, or below ground stems (Benninger-Traux et al., 1992). In contrast, undisturbed communities away from trails were dominated by shade-loving species. The degree to which plant community composition changes near trails can be affected by the vegetation type that a trail traverses. For example, Trip & Wiersma (2015) found that forested habitats had a sharper contrast in species composition moving from intact vegetation towards a trail compared to open bogs or heaths. The authors suggest that species of open habitats are adapted to high-light conditions and more resistant to disturbance because they include stoloniferous/rhizomatous grasses that are resistant to trampling, whereas many forest species are not (Trip & Wiersma, 2015). Therefore, the species composition moving towards a trail in open habitats is more similar to the composition far from the trail.

Roads and trails can also facilitate the introduction and sometimes invasion of exotic plants. The increased prevalence of exotic plants near roads and trails is often attributed to their ability to adapt to disturbances. For example, fast growth and large

production of easily dispersed seeds are traits associated with exotic plants found in disturbed areas (Baker, 1974; Lake & Leishman, 2004; Van Kleunen et al., 2015). Exotic plants are dispersed into native plant communities by vectors associated with roads and trails such as tires of vehicles (von der Lippe & Kowarik, 2007; Yang et al., 2021), boots and clothing (Campbell & Gibson, 2001; Mount & Pickering, 2009), and the hooves and fur of animals (Campbell & Gibson, 2001; Gower, 2008).

Many studies have focused on the impact of roads and trails on the presence of exotic species found trailside, however, the distance that exotic species can spread into intact vegetation away from different corridors varies. For example, a study from the Great Lakes area of Minnesota, USA, found that increased exotic species richness and cover did not extend more than 1 m from the trail edge (Dickens et al., 2005). However, in another region of the Great Lakes in Wisconsin, USA, Watkins et al. (2003) found that exotic species were prevalent up to 15 m from roads. Tyser & Worley (1992) found that although most exotic species were limited to within 1-2 m of grasslands along primary and secondary roads, common dandelion (*Taraxacum officinale* F.H. Wiggers) and two exotic grasses, timothy grass (*Phleum pratense* Linnaeus) and Kentucky bluegrass (*Poa pratensis* Linnaeus) occurred as far as 100 m from backcountry trails.

The type and intensity of trail use can also affect the presence and abundance of exotic species found along trails. For example, Benninger-Truax et al. (1992) found significantly higher richness of exotic plants along moderately used trails compared to lightly used trails. Potito & Beatty (2005) found significantly higher exotic species cover when comparing heavily used trails to newly established trails. Different vegetation types can also affect richness or frequency of exotic species trailside. Larson et al. (2001), for

example, found higher numbers and frequencies of exotic species near trails in mesic compared to drier mixed grass vegetation in North Dakota. Similarly, in the Central Grasslands and Colorado Rockies (USA), Stohlgren et al. (1999) found significantly higher exotic frequency in wetter aspen and meadow sites compared to drier coniferous forest sites. How far exotic species spread into the surrounding vegetation, and whether trail types or vegetation types are influencing this extent, should be studied in other natural areas impacted by roads and trails.

Most studies in montane regions report a steady decrease in exotic species richness with increasing elevation (Becker et al., 2005; Pauchard et al., 2009). Several authors have suggested that this pattern is a result of the harsher climate, and lower propagule pressure at high elevations: fewer exotic species are able to survive high elevation conditions, and fewer seeds are able to reach these areas (Becker et al., 2005; Averett et al., 2016). With changing climate and more visitors reaching higher elevations, exotic species invasions at higher elevations are becoming more frequent in many areas of the world (Becker et al., 2005; Pauchard et al., 2009; Averett et al., 2016; Medvecká et al., 2018, Liedtke et al., 2020); however, I know of no studies that have examined whether recreation is facilitating the spread of exotic plants to higher elevations within protected areas in Canada's montane regions.

Protected areas are often home to rare plant species, many of which require intact, relatively undisturbed ecosystems to thrive. Disturbance via human recreation is a leading threat to rare plants in Canada (McCune et al. 2013), and around the world (e.g., Ballantyne & Pickering, 2013; Hernandez-Yanez et al. 2016). For example, trampling, recreational activities, OHVs, and horse riding are all listed as reported threats to rare

plant species and communities in Australia (Kelly et al., 2003). Although rare plant species in popular recreation areas are susceptible to trampling by hikers and OHVs, especially when these activities stray from designated trails, the presence of trails can sometimes benefit rare plants. Taylor and Raney (2013) found increased abundance of the rare thread-leaved sundew (*Drosera filiformis* Rafinesque) near OHV trails, a result of micro-habitats created by the tire tracks that favour the thread-leaved sundew and decrease competition for resources with other bog species. Similarly, Catling & Kostuik (2011) found that a native orchid, *Calypso bulbosa* var. *americana* (R. Brown) Luer, was more abundant within 1 m of recreational trails compared to 1 m to 3 m beyond the trail, which the authors suggest is a result of reduced competition from trampling of neighboring disturbance intolerant species. Protected areas rich in plant diversity and popular for outdoor recreation must be studied at local scales to understand the impacts of roads and trails on rare plant species.

Castle Provincial Park (49.4314°N, 114.3933°W) and Castle Wildland Provincial Park (49.241°N, 114.244°W) in southwestern Alberta, Canada (CCWPP) are ideal study sites to test the effects of trails on plant communities in the Rocky Mountains. Together, these two parks encompass over 105,000 hectares of protected land (Alberta Environment and Parks, 2018). CCWPP has a long history of industrial and recreational use, including oil and gas extraction, community grazing, hunting, fishing, camping, and trail use by OHVs, equestrians, and hikers. As a result, it is estimated that approximately 2,000 km of linear features criss-cross the Parks (Farr et al., 2017). Nearly half of all Alberta's vascular plant species are found in the CCWPP region, with over 100 species that are provincially and/or nationally rare (Alberta Environment & Parks, 2018), making this

region a hotspot for plant diversity. In addition, CCWPP has long been a popular offhighway vehicle destination for many locals and people from surrounding communities such as the Crowsnest Pass (Alberta Environment & Parks, 2015). After designating CCWPP as provincial parks in 2017, the province moved to decommission over 130 km of OHV trails, but this was met with strong opposition from local OHV advocates (Bellefontaine, 2019). Without quantitative data on trail effects, managers do not have the evidence they need to make decisions about trail closures or expansions. Although a few studies have examined the effect of roads and trails on large mammals within CCWPP (Lee & Hanneman, 2011; Ciuti et al., 2012; Paton et al., 2017; Proctor et al., 2020), no study has quantified the effects of trails on plant communities. Indeed, only a handful of such studies have ever been done in Canada (Price, 1985; Parikesit et al., 1995; Thurston & Reader, 2001; Nepal & Way, 2007; Crisfield et al., 2012; Trip & Wiersma, 2015; Grenke et al., 2018).

In this study, I test the effect of recreational trails and roads on plant communities in CCWPP. Specifically, I investigate how trail use type, vegetation type, or interactions between them influence the effect of trails on plant species richness, community composition, and the presence of exotic and provincially rare species. My prediction are as follows:

(1) I predict that species richness will increase near trail edges as more exotic species and disturbance-tolerant native species are found trailside, increasing the number of species present. In addition, I predict that the strength of this effect will vary with vegetation and trail type. For example, I expect that the increase in species richness near trails will be smaller in open light habitats such as grasslands and higher in dense canopy

coniferous forests where high light availability is restricted to trail edges. I also expect the increase in species richness moving from intact vegetation towards trails to be greater near OHV trails compared to footpaths because of more propagule pressure from OHV tires, which likely carry more seeds compared to foot traffic. In addition, I predict that interactions between vegetation type and trail type could affect the degree of increased species richness near trails compared to farther away. For example, I predict that the greater impact from OHV trails compared to footpaths will be less drastic in grasslands and more pronounced in coniferous forests.

(2) I predict that community composition will shift near trails, as trailside disturbance and altered abiotic conditions favour a different suite of species. Coniferous forests with densely shaded understories often support few shade-tolerant species and so I predict that shifts in composition moving towards trails will be greater in coniferous forests compared to grasslands, where light levels near and far from trails are similar. I also predict shifts in composition with increasing proximity to footpaths will be less drastic compared to roads or OHV trails due to the increased disturbance frequency and intensity associated with wider trails and increased propagule pressure from vehicles bringing in more exotic seeds and dispersing them farther into the vegetation.

(3) I predict that exotic species will be found most frequently directly beside trails and that the probability of their presence will decline when moving away from trails; however, this effect will differ between vegetation types and trail types. I predict that the presence of exotic species will be higher and extend farther in more open vegetation types such as grasslands. Grasslands are more open habitats with a more even distribution of light, allowing shade-intolerant exotic species to grow farther out from trails compared

to coniferous forests with little light penetrating through the dense canopy of the forest interior. Therefore, the decline in occurrence of exotic species moving away from trails will be steeper in coniferous forests. I also predict that exotic species will have a higher likelihood of occurring near OHV trails and roads compared to footpaths, and that exotics will be more likely to occur farther away from OHV trails and roads because they have higher frequency of use and vehicle tires bring in more seeds than foot traffic (Pickering & Mount, 2010). If trails are facilitating exotic species spread to higher elevations, I predict that the probability of finding exotic species at higher elevations will be greater along OHV trails compared to footpaths, and lowest on control transects. However, if the occurrence of exotic species declines at higher elevations simply because of the harsh climatic conditions, I do not expect to see any differences between trail types in the relationship between exotic species presence and elevation.

(4) In this study, I define rare species as those ranked critically imperiled (S1) or imperiled (S2) in Alberta, as designated by NatureServe (NatureServe, 2022). It is unclear whether this group of species will be favoured by conditions near trails. If most rare species are somewhat disturbance tolerant, and benefit from increased light levels near trails, I predict that rare species will be more likely to occur closer to trails. However, if most rare species are sensitive to trail disturbance, I predict that rare plants will occur more frequently farther from trails.

### 2.3 Methods

## 2.3.1 Study area

The Rocky Mountain ecoregion of southwestern Alberta, which includes CCWPP, is a hotspot of vascular plant diversity in the province, with over half of all

Alberta's native plant species growing in the region (Kershaw, 2008). Bordered by British Columbia to the west, Crowsnest Pass in the North, and Waterton Lakes National Park to the South, CCWPP is part of the 'Crown of the Continent' ecosystem which houses important watersheds and habitats for many plants and animals, including species that are nationally and/or provincially rare (Alberta Parks, 2020; Figure 2).



Figure 2. Map of the study area, outlining Castle Provincial Park (light orange) and Castle Wildland Provincial Park (pink) and official trails (brown). Circles depict trail transect sites, coloured by vegetation type; black diamonds depict off-trail transect sites.

CCWPP is within the Rocky Mountain natural region, which includes the montane, subalpine, and alpine natural subregions of Alberta (Alberta Parks, 2020). These subregions have mean annual temperatures of 2.3°C, -0.1°C, and -2.4°C, mean frost-free periods of 64, 55, and 40 days, and growing season precipitation of 382 mm, 419 mm, and 472 mm, respectively (Natural Regions Committee, 2006). Although

CCWPP are two of the smaller protected parks in Alberta, they include a large elevation range, from 1,336 meters above sea level (a.s.l.) to 2,640 m a.s.l. on Loaf Mountain, the highest point in CCWPP. This large range in elevation results in a diversity of vegetation types.

The montane subregion (825 m to 1,850 m a.s.l.) includes montane grasslands dominated by species such as mountain rough fescue (Festuca campestris Rydberg), Idaho fescue (Festuca idahoensis Elmer), and Parry oatgrass (Danthonia parryi Scribner) (Willoughby et al., 2008). Pine reed grass (*Calamagrostis rubescens* Buckley), buffalo berry (Shepherdia canadensis (Linnaeus) Nuttall), and bearberry (Arctostaphylos uvaursi (Linnaeus) Sprengel) are understory species of well-drained open forest or mixed stand sites, whereas common understory species such as thimbleberry (Rubus parviflorus Nuttall) and white meadowsweet (Spiraea lucida Douglas ex Greene) are found in moister nutrient-rich coniferous forest sites (Natural Regions Committee, 2006). The subalpine subregion (1,300 m to 2,300 m a.s.l) is dominated by coniferous forests, with many young lodgepole pine (Pinus contorta Douglas ex Loudon) stands in low elevation post-fire sites, and subalpine fir (Abies lasiocarpa (Hooker) Nuttall) with occasional white-bark pine (*Pinus albicaulis* Engelmann) populations at higher elevations. Common understory species include buffalo berry, false azalea (Menziesia ferruginea J.E. Smith), and white-flowered rhododendron (Rhododendron albiflorum Hooker) shrubs (Natural Regions Committee, 2006). The alpine subregion vegetation (1,900 m to 3,650 m a.s.l.), includes alpine meadows and windswept barren tundra. Although vegetation is relatively sparse, some low-growing cushion species do occur, including white mountain avens

(*Dryas drummondii* Richardson ex Hooker) and moss campion (*Silene acaulis* (Linnaeus) Jacquin) in the ridgetops and shallow snow areas (Natural Regions Committee, 2006).

The natural disturbance regime of the Rocky Mountain ecoregion includes biotic, geomorphic, and hydrological processes such as wildfires, windfall, wildlife grazing, flooding, drought, avalanches, insect infestations, forest pathogens, and beaver activity (Alberta Environment and Parks, 2018). In CCWPP, the 2003 Lost Creek Fire burned nearly 19,000 hectares of the two parks, resulting in large stands of young lodgepole pine in the northern regions of the parks (Farr et al., 2017). Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks have been reported in areas north and east of CCWPP and are likely to impact CCWPP in the future (Powell, 1966; Robertson et al., 2009; Taylor et al., 2006). After the replacement of bison with cattle introduced by European settlers, much of the area was used for unregulated grazing, resulting in increased frequency of invasive and agronomic plant species in the grasslands (Willoughby et al., 2008; Alberta Environment and Parks, 2018).

CCWPP is part of the territory of the Blackfoot people. For over 10,000 years the Blackfoot people (Niitsitapi) have used the land for hunting, fishing, and sacred ceremonies (Alberta Wilderness Association, 2022). CWPP was originally included as part of Waterton Dominion Park (now Waterton Lakes National Park), which was established in 1895 as Canada's fourth National Park after Banff, Glacier, and Yoho National Parks (Lothian, 1987). In 1911 the Castle region was removed from the National Park designation and ten years later was designated as a Provincial Game Reserve, which provided extended areas of pasture for ranchers. In 1954, the area became Provincial Crown Land with unregulated recreational activities including hiking, hunting, and off-

highway vehicle use, as well as extractive resource industries including logging, gravel extraction, and oil and gas wells (Castle- Crown Wilderness Coalition, 2022). Currently, there are over 2,000 km of linear features – including roads and trails - in CWPP (Farr et al., 2017). Trail types include long-standing foot trails for hiking, biking, and equestrian use, heavy use off-highway vehicle trails (OHV), and industry size gravel roads used for access to oil and gas wells and some trailheads.

#### 2.3.2 Study Design

To measure the effects of trails on plant communities, from June to August of 2020 and 2021, my field assistants and I surveyed 118 transects near trails and 24 transects at least 100 m away from any recreational trail, to serve as controls (Figure 2, Table 1). To select trailside sites to survey, I first stratified by watershed and vegetation type to ensure representation of all vegetation types and all watersheds throughout the study area. I delineated the watershed boundaries from the Hydrologic Unit Code (HUC) Watersheds of Alberta vector data produced by the Government of Alberta (Alberta Environment and Parks, 2017). I used a 2010 map of Alberta's land cover produced by ABMI (Alberta Biodiversity Monitoring Institute) based on Landsat imagery to determine the vegetation types (coniferous forest, broadleaf forest, mixed forest, grassland, and shrubland; Castilla et al., 2014). Unfortunately, I was not able to obtain an official trail layer from Alberta Environment and Parks, or any information on usage levels of trails in the area. Therefore, I used a trail layer that was georeferenced and digitized by hand from the 2018 version of the Castle Provincial Park summer trails map and overlaid it on the watershed and vegetation layers using ArcMap version 10.2.1. I used the "Create Random Points" function in ArcMap to randomly select 20 points along

a trail within each watershed and vegetation type combination. I set the minimum

distance between points to 50 meters.

Table 1. Number of control and on-trail transects surveyed within each vegetation type in each watershed in CCWPP.

Watershed	Vegetation	Control	Trailside	Grand Total
	-	transects	transects	
Carbondale	broadleaf	0	3	3
River	coniferous	4	5	9
	grassland	0	3	3
	mixed	0	7	7
	shrubland	5	2	7
Drywood Creek	broadleaf	2	4	6
	coniferous	0	1	1
	grassland	0	6	6
	mixed	0	5	5
	shrubland	1	2	3
Middle Castle	broadleaf	0	3	3
River	coniferous	1	7	8
	grassland	1	2	3
	mixed	0	8	8
	shrubland	1	4	5
Mill Creek	broadleaf	0	0	0
	coniferous	1	6	7
	grassland	0	4	4
	mixed	0	3	3
	shrubland	0	2	2
Upper Castle	broadleaf	1	1	2
River	coniferous	0	4	4
	grassland	0	1	1
	mixed	1	3	4
	shrubland	1	4	5
Upper	broadleaf	0	0	0
Crowsnest River	coniferous	1	6	7
	grassland	0	0	0
	mixed	0	3	3
	shrubland	1	2	3
West Castle	broadleaf	0	1	1
River	coniferous	2	5	7
	grassland	0	2	2
	mixed	1	5	6
	shrubland	0	4	4
	Grand Total	24	118	142
Following this, I received spatial coordinates from Alberta Environment and Parks of trailside treatments of exotic species by Parks staff in 2018 and 2019 (hand pulling or herbicide application). I excluded any of the randomly chosen points within 100 m of these areas to avoid potential effects of weed treatments on the presence of exotic species.

I chose trailside transects to survey from the randomly selected survey points based on the goal of surveying a similar number of different vegetation types within the different watersheds represented in CCWPP. Logistical constraints related to the feasibility of hiking from access points limited the number of sites surveyed. I chose the sites of control transects based on sampling sites that I used to test a species distribution model for *Botrychium* (see Chapter 3). This allowed me to efficiently obtain a sample of transects located at least 100 m from any trail (mean distance =  $394 \text{ m} \pm 43 \text{ m}$ ) as a control for trailside transects, while also being able to collect data for Chapter 3. At each of the 24 50 m x 50 m plots that I surveyed to test the *Botrychium* model, I also set up a transect identical to the trailside transects running due north for consistency, and recorded the same data precisely as collected for the trailside transects. Because these 24 sites were chosen from a set of randomly selected plots with a range of predicted habitat suitability for *Botrychium*, they were not stratified by vegetation type or watershed. However, the surveyed control transects do represent all watersheds, and all vegetation types.

#### 2.3.3 Data Collection

I used a Garmin eTrex® 20 handheld GPS to navigate to each trailside and control transect site. Because I was unable to acquire an accurate shapefile of trails in CCWPP, the trail layer I used was subject to digitizing error, so the final locations of the

trailside transects occasionally had to be moved such that they began directly on a trail. Therefore, I took GPS coordinates of the final locations of all trailside transects so they can be precisely re-located and resurveyed for future comparisons (Appendix 1, Table A1).

At each trailside location, I placed a transect on the side of the trail closest to the GPS coordinates. I determined the start (0 meters) of the transect based on the point where vegetation was visibly more continuous in contrast to the trampled trail surface while looking down the length of the trail. I then laid out an 11m transect perpendicular to the trail (Figure 3). For control transects, I used the GPS coordinates of the center of the 50 m x 50 m survey area as the start of the transect (0 meters). I recorded elevation of each surveyed transect from the GPS unit and measured the aspect and slope using a compass and clinometer. For trailside transects, I measured trail width and depth (depth of deepest part of trail surface relative to ground directly beside the trail) using a measuring tape. I took soil compaction measurements (kg/cm<sup>2</sup>) in the center of the trail and any ruts located on the trail, using a pocket spring-operated soil penetrometer (5DPJ8 Humboldt). Wider trails with greater soil compaction and deeper ruts generally have higher frequency and/or intensity of use (Dale & Weaver 1974; Trip & Wiersma, 2015). I took photos from the 0 m point looking towards the end of each transect, as well as images of the trail from both directions for future reference and research.

For each trailside and control transect, I chose which side of the transect to lay the quadrats based on which side had the fewest obstructions (i.e., deadfall, boulders, or large standing trees which would skew the representation of the understory species present in that area) by visually looking down the transect line. I then used a 1 m x 1 m quadrat

(constructed of light-weight PVC pipe) to sample the plant community at 0 m (directly trailside), 2 m, 5 m, and 10 m along the transect, placing all quadrats on the same side. I selected 10 m as the most distant sampling point because most studies of trail effects on plant communities indicate no significant trail impact on species richness beyond 5 m from roads or trails (Watkins et al., 2003; Godefroid & Koedam, 2004; Dickens et al., 2005; Ngugi et al., 2014).





In each quadrat, I took measurements of maximum understory vegetation height (vegetation under 2 m tall) and soil compaction (using the same pocket penetrometer as above). I recorded the presence of each vascular plant understory species (less than 2 m tall) and following methods outlined in Stohlgren et al. (1999), I estimated the percent cover of each vascular plant species, bare ground, and moss or lichen in each of the quadrats by training myself and my field assistant to recognise 1% of a 1 m x 1 m area and estimate to the nearest percent. I took photographs of each quadrat from above. I also

collected plant samples and took photos of species not easily identifiable in the field for later identification in the lab.

I identified all vascular plant species (excluding sedges) using 'Vascular Flora of Alberta' (Kershaw & Allen, 2020) and 'Flora of Alberta' (Moss & Packer, 1983) and sedge species using 'Field guide to Intermountain sedges' (Hurd et al., 1998). Nomenclature of identified species is based on Canadensys' online Database of Vascular Plants of Canada (Brouillet et al. 2010+) and NatureServe explorer 2.0 (NatureServe, 2022). I determined the origin (exotic or native) and provincial conservation rank (Srank) of each species using Alberta Conservation Information Management System (September 2018 version: ACIMS, 2018). Exotic species, also referred to as non-native species, are defined by NatureServe as species found outside their native range, whose presence in a natural ecosystem is due to direct or indirect human intervention (Morse et al., 2004). The conservation ranking of each species is based on NatureServe's conservation status assessment methodology which focuses on the rarity, threats, and trends of a particular species (Faber-Langendoen et al., 2012). The S-rank refers to 'subnational' conservation ranks where S1 defines species as critically imperiled provincially with a very high risk of extirpation; S2 refers to imperiled, high risk of extirpation; S3 refers to vulnerable, moderate risk of extirpation; S4 refers to apparently secure; and S5 refers to species that are secure, with little to no risk of extirpation (NatureServe, 2022). For this study, I define provincially rare species as any S1- or S2ranked species.

#### 2.3.4 Statistical analyses

I used measurements of trail width to define trail type. I classified trails less than 1m wide as footpaths; trails observed to have tire ruts and ranging in width from 1.1 m to 3.9 m as OHV trails; and trails greater than 3.9 m as roads. Width requirements for single lane roads in Alberta are a minimum of 4 m (Alberta Infrastructure and Transportation, 1996). While I stratified site selection by a GIS layer of vegetation types provided by ABMI (Castilla et al., 2014), I found that the actual vegetation type at the selected transect sites sometimes differed from this layer. Therefore, I used my on-the-ground assessment of vegetation type in all analyses. After completing the surveys, I found that we were not able to survey any footpath transects in broadleaf vegetation; therefore, I lumped the vegetation types 'broadleaf' and 'mixed' into one category – called 'mixed' – for analyses. The 'mixed' vegetation type therefore included 'mixed' vegetation, where neither coniferous nor broadleaf trees are more than 75% dominant in the canopy, and 'broadleaf' vegetation, where broadleaf trees are more than 75% dominant.

To test the effect of trail proximity on vegetation height and soil compaction, I compared the mean maximum height of vegetation and mean soil compaction at each distance category using estimated marginal means. To determine whether different trail types had different effects on vegetation height and soil compaction, I conducted pairwise comparisons of the estimated marginal mean maximum vegetation height and mean soil compaction values, respectively, between trail types at each distance and between distances for each trail type using the Tukey adjustment for multiple tests (Wright, 1992).

I used mixed models with transect as the random effect to test the effects of distance from trail, trail use type, and vegetation type on species richness, community composition, the presence of at least one exotic species, and the presence of at least one

S1 or S2 provincially tracked species. I also tested the effects of interactions between distance from trail and trail type, and distance from trail and vegetation type. I built one model for each response variable: species richness, community composition, the presence of at least one exotic species, and the presence of at least one rare species. Species richness is the total number of vascular plant species recorded in each quadrat. As a measure of changes in community composition near the trail compared to away from the trail, I calculated the Bray-Curtis dissimilarity between the 10 m quadrat and each of the other three quadrats on the same transect. I calculated the Bray-Curtis dissimilarity using the square-root transformed abundance of each species in each quadrat. A Bray-Curtis dissimilarity value of 0 indicates identical community composition between quadrats, whereas a value of 1 indicates no species in common (Bray & Curtis, 1957). For example, if there was very little difference in community composition comparing the 10 m quadrat to the 0 m quadrat, the Bray-Curtis dissimilarity between these two quadrats would be close to zero. Quadrats with at least one exotic species received a '1' for exotic species presence, while those with no exotic species received a '0'. Similarly, quadrats with at least one rare species recorded received a '1' for rare species presence, while those with no rare species present received a '0'. All response and predictor variables are listed in Table 2.

In each model, I included covariates that might affect the response variable in addition to the predictors of interest. For the species richness model, I included elevation as a covariate because higher elevations tend to have fewer species due to harsh climatic conditions and because lower elevations tend to have more human disturbance which introduces more species compared to less disturbed, high elevation areas (Pauchard et al.,

2009). For exotic species presence, I included elevation because the occurrence of exotic species tends to decline with elevation (e.g., Becker et al., 2005; Pauchard et al., 2009; Medvecká et al., 2018).

Response	Predictor Variables	Variable type		
Variable				
Species	Elevation	Continuous (meters)		
richness	Northness	Continuous (index)		
	Vegetation type	Categorical (grassland, shrubland,		
		mixed, coniferous)		
	Distance from trail	Continuous (meters)		
	Trail type	Categorical (control, footpath, OHV,		
		road)		
	Distance from trail X Vegetation	Continuous X Categorical		
	type			
	Distance from trail X Trail type	Continuous X Categorical		
<b>Bray-Curtis</b>	Distance from trail	Continuous (meters)		
Dissimilarity	Trail type	Categorical (control, footpath, OHV,		
		road)		
	Vegetation type	Categorical (grassland, shrubland,		
		mixed, coniferous)		
	Distance from trail X Trail type	Continuous X Categorical		
	Distance from trail X Vegetation	Continuous X Categorical		
	type			
Probability	Elevation	Continuous (meters)		
of at least	Northness	Continuous (index)		
one exotic	Vegetation type	Categorical (grassland, shrubland,		
species		mixed, coniferous)		
	Distance from trail	Continuous (meters)		
	Trail type	Categorical (control, footpath, OHV,		
	Distance from the il V V set of in	road)		
	Distance from traff X vegetation	Continuous A Categorical		
	Distance from trail X Trail type	Continuous x Categorical		
Probability	Elevation	Continuous (meters)		
of at least	Distance from trail	Continuous (meters)		
one rare	Vegetation type	Categorical (grassland, shrubland,		
species	vegetation type	mixed, coniferous)		
	Trail type	Categorical (control, footpath, OHV, road)		
	Distance from trail X Vegetation type	Continuous X Categorical		
	Distance from trail X Trail type	Continuous X Categorical		

Table 2. Predictor variables used in mixed models for each response variable.

I also included aspect in both models because within plant communities studied in southern Alberta, species richness, regardless of species origin, is reported to be higher on north-facing slopes which tend to retain more moisture than south-facing slopes (Lieffers & Larkin-Lieffers, 1986). I transformed the predictor variable aspect to a linear variable, 'northness' index (Equation 1), where north-facing transects have a value of 1, south-facing transects have a value of 0, and east and west are equally counted as 0.5. I did not include elevation or aspect as covariates in the model for Bray-Curtis dissimilarity because the magnitudes of shifts in community composition over space is not expected to differ with elevation or aspect. I included only elevation as a covariate in the model for presence of rare species because some studies report increased presence of rare species at higher elevations due to reduced competition and less disturbance (Lomolino, 2001; Vetaas & Grytnes, 2002; Pauchard et al., 2009).

$$Northness = \frac{|(aspect in degrees - 180)|}{180}$$
 Equation 1

To determine trail effects on species richness and community composition, I used linear mixed-effects models (LMMs). I first confirmed that there were no strong correlations between any of the predictors using Pearson's correlation coefficients. The strongest correlation was a positive correlation between elevation and northness (r = 0.14). Then, for each response variable, I built a LMM with transect as a random factor to account for non-independence of quadrats from the same transect. I standardized the continuous predictors by subtracting the mean and dividing by two standard deviations. I used diagnostic plots to ensure that model assumptions were met for each model and constructed spatial correlograms to ensure no spatial autocorrelation in the residuals (Bjørnstad & Falck, 2001). 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 re-fit the model without them and re-ran the drop1 test. If distance from trail was a significant predictor, I re-fit the model with distance as a categorical predictor and used post-hoc pairwise Tukey tests to determine which pairs of distances differed significantly (Wright, 1992). As a measure of the variance explained by each model, I calculated the percent null deviance explained using Equation 2, where null deviance is the deviance of the intercept-only plus random effects model:

$$\frac{null \, deviance - residual \, deviance}{null \, deviance} \times 100 \qquad \qquad \text{Equation } 2$$

To determine trail effects on the presence of exotic species and provincially tracked species, I used the same approach as for species richness and community composition (above), except I used generalized linear mixed models (GLMMs) with a logit link because exotic species and rare species presence/absence are binomial responses. I checked for model specification errors and overdispersion using scaled residuals for each model (Hartig & Hartig, 2017) and again confirmed no spatial autocorrelation in model residuals using correlograms (Bjørnstad & Falck, 2001). When I included all the two-way interactions in the model for rare species presence/absence, the model failed to converge. Therefore, I included each interaction one at a time and used a drop1 test to determine if it was a significant predictor, then built the final model with only the significant interactions. As a measure of the variance explained by each model, I once again calculated the percent null deviance using Equation 2. For all response variables, I predicted that there could be an interaction between vegetation type and trail type, such that the effect of trail type could vary depending on the vegetation type. I also predicted that the effect of distance from trail on the response variables could vary depending on the trail type and vegetation type combination. However, my sampling did not achieve replication in all trail type by vegetation type combinations. Therefore, I used the subset of data including only OHV trails and footpaths – which were the most common trail types - to test for an interaction between vegetation type, and for a 3-way interaction between vegetation type, trail type, and distance from the trail. I followed the same approach above to determine whether any of these interactions were significant. If there was a significant 3-way interaction, I used estimated marginal means of linear trends to test for significant differences in the slope of the relationship between the response variable and distance from trail for different combinations of vegetation type and trail type.

To test whether trail use is facilitating the colonization of higher elevation sites by exotic species, I calculated the presence or absence of at least one exotic species on each transect by lumping the data for all four quadrats on each transect. I then built a generalized linear model (GLM) with a logit link to model presence/absence of at least one exotic plant per transect based on the predictors: elevation, vegetation type, trail type, and interactions between elevation and vegetation type as well as elevation and trail type. If the interaction between elevation and trail type is significant, it would suggest that some trail types are facilitating the colonization of higher elevation sites by exotic species more than others. As above, I ensured that there were no model specification issues and

no spatial autocorrelation in model residuals. Once again, I used a drop1 test to determine which predictors were significant, while accounting for all other predictors in the model.

I carried out all statistical analyses using the statistical software R version 4.0.3 (R Core Team, 2020). I used the packages 'lmer4' (Bates et al., 2015), and 'glmmTMB' (Magnusson et al., 2017) to build GLMMs, 'ncf' to build spatial correlograms (Bjørnstad & Falck, 2001), 'DHARMa' to test for model misspecification (Hartig & Hartig, 2017), 'arm' to standardize predictors (Gelman et al., 2013), 'emmeans' to carry out post-hoc pairwise tests (Lenth et al., 2019), 'vegan' to calculate Bray-Curtis dissimilarity (Oksanen et al., 2013), 'ggplot2' to create graphs of soil compaction and maximum vegetation height, and 'visreg' to create partial regression plots for visualizing significant effects in each model (Breheny and Burchett, 2017).

### 2.4 Results

The average on-trail soil compaction was  $3.9 \pm 1.7$  kg/cm<sup>2</sup> on footpaths,  $4.1 \pm 1.4$  kg/cm<sup>2</sup> on OHV trails, and  $4.9 \pm 0.4$  kg/cm<sup>2</sup> on roads. The maximum height of understory vegetation was higher at 10m compared to the trail edge for shrublands and mixed vegetation but declined with distance from trail in coniferous forests and did not change in grasslands (Figure 4A). Although vegetation height tended to increase moving away from trails, only for roads was the average maximum height of vegetation significantly higher at 10 m compared to 0 m (Figure 4B, Appendix 1, Table A1.2). Soil compaction declined moving away from trails in all vegetation types, with the lowest levels of soil compaction in coniferous forests (Figure 4C). The average soil compaction beside roads was higher at 0 m and 2 m compared to other trail types and control transects (Figure 4D). There was no significant difference in soil compaction between footpaths and OHV

trails within 0 m quadrats. At 2 m, soil compaction was significantly higher for roads than all other trails and control quadrats (Appendix 1, Table A1.3). There was no change in soil compaction moving from 0 m to 10 m on control transects. On footpaths, only the 0 m quadrat was significantly higher than the other distances. On OHV trails and roads, soil compaction was significantly elevated in the 0 m and 2 m quadrats compared to 5 m and 10 m (Appendix 1, Table A1.4)



Figure 4. The maximum height of understory vegetation (A-B) and soil compaction (C-D) with increasing distance from trails for (A & C) vegetation types and (B & D) trail use types. Control transects are excluded from A and C. Points represent mean values; error bars show  $\pm$  1 standard error.

We recorded 388 plant species in 568 quadrats within 142 transects. 35 species were exotic; one species was ranked S1, and 14 species were S2 provincially tracked rare species (see Appendix 1; Table A1.5 for a list of all exotic species, and Table A1.6 for a list of all rare species). I could not identify five specimens to species. The most frequent species were *Fragaria virginiana* Mill. (wild strawberry, 245 quadrats), *Taraxacum* 

*officinale* (221 quadrats), *Achillea millefolium* L. (Common yarrow, 217 quadrats) and *Phleum pratense* (202 quadrats). The most frequent native species found in quadrats were *Fragaria virginiana*, *Achillea millefolium*, *Spiraea lucida* (192 quadrats),

*Symphyotrichum laeve* (L.) Å. Löve & D. Löve (smooth blue aster, 180 quadrats), and *Galium boreale* (L.) (northern bedstraw, 164 quadrats). The most frequently recorded exotic species in trailside transects were *Taraxacum officinale*, *Phleum pratense*, and *Poa pratensis* (88 quadrats). These species were also recorded in 15, 9, and 15 of the 24 off-trail control quadrats, respectively. The exotic species *Plantago major* (L.) (Nipple-seed plantain), *Poa annua* (L.) (Annual bluegrass), *Alyssum alyssoides* (L.) L. (Pale alyssum), *Matricaria discoidea* DC. (Pineapple-weed chamomile), and *Echium vulgare* L. (Common viper's-bugloss) were only found directly trailside (0 m), and never occurred in quadrats 2 m or more from a trail or in any of the control transects. Although *Verbascum thapsus* L. (Common mullein) was found only at intermediate distances from a single trail (2 m and 5 m quadrat), it was also found in one control transect. I recorded exotic species at elevations ranging from 1,338 m a.s.l to 1,914 m a.s.l, with *Taraxacum officinale* having the widest range (1,338 m a.s.l to 1,914 m a.s.l).

I recorded one provincially tracked S1 species, *Microsteris gracilis* (Hook.) Greene (slender phlox) in two quadrats of different trail transects. The most frequently recorded provincially tracked S2 species was *Melica subulata* (Griseb.) Scribn. (Alaska oniongrass, 22 trail and 4 control quadrats), followed by *Festuca occidentalis* Hook. (Western fescue, 8 trail and 2 control quadrats), *Paxistima myrsinites* (Pursh) Raf. (Oregon boxleaf, 7 trail and 3 control quadrats), and *Carex geyeri* Boott. (Geyer's sedge, 6 trail and 4 control quadrats). Overall, I found at least one rare species in one quadrat on a roadside transect (at the 10 m distance; 2% of all road quadrats), 16 quadrats along footpaths (18% of all footpath quadrats), 22 control quadrats (23% of all control quadrats), and 41 OHV trail quadrats (13% of all OHV quadrats).

The number of species in a quadrat ranged from zero to 29. Two quadrats had no species present. Both were at the 10 m distance; one was a rocky, dried streambed, whereas the other was the interior of an old coniferous forest. The number of exotic species in a quadrat ranged from zero to nine, with a mean of 1.7 species. Only one quadrat had nine exotic species, and it was the 2 m quadrat of a transect located in the vicinity of a popular campsite where RVs (recreational vehicles) and OHVs were present. Most quadrats had zero or one rare species. However, I recorded three provincially tracked S2 species in a quadrat 5 m from a footpath trail in a mixed forest. Of all quadrats surveyed, 14% had at least one S1 or S2 provincially tracked rare species present.

### 2.4.1 Species richness

Significant predictors of species richness included elevation, the interaction between vegetation type and distance from trail, and the interaction between trail type and distance from trail (Table 3; Figure 5). Species richness declined significantly with increasing elevation (Figure 5a), whereas the effect of distance from trail on species richness depended on vegetation type (Figure 5c; Appendix 1, Table A1.7). In grassland and broadleaf/mixed forests, species richness did not change significantly with distance. In shrublands, species richness in the 2 m and 5 m quadrats was significantly higher than in the 10 m quadrat. In coniferous forests, species richness in the 0 m and 2 m quadrats

was significantly higher than in the 10 m quadrat. The effect of distance from trail on species richness also varied with trail type (Figure 5d; Appendix 1, Table A1.8). In control transects more than 100 m from any trail, there was no significant change in species richness from 0 m to 10 m. On footpath transects, species richness was significantly higher at 0 m and 2 m compared to 10 m. On OHV transects, species richness was significantly higher at 0 m, 2 m, and 5 m compared to 10 m. On roadside transects, the 0 m quadrat had significantly lower species richness than 2 m, 5 m, or 10 m away. The model for species richness explained only 3.4% of the null deviance.

Predictor	Coefficient	SE	AIC*	P-value**
(Intercept)	11.77	1.42	3379.5	n/a
elevation	-2.89	0.79	3391.3	<0.001
aspect (northness)	-0.63	0.76	3378.3	0.408
vegetation type (shrubland)	2.24	1.32	n/a	n/a
vegetation type (mixed)	1.17	1.23		
vegetation type (coniferous)	-0.83	1.25		
distance	3.41	1.21	n/a	n/a
trail type (footpath)	2.03	1.30	n/a	n/a
trail type (OHV)	1.31	1.04		
trail type (road)	-0.45	1.58		
vegetation type (shrubland) x	-3.91	1.16		
distance				
vegetation type (mixed) x distance	-2.68	1.03	3390.9	<0.001
vegetation type (coniferous) x	-4.30	1.08		
distance				
trail type (footpath) x distance	-4.38	1.14		
trail type (OHV trail) x distance	-2.93	0.90	3410.6	<0.001
trail type (road) x distance	2.34	1.34		

Table 3. Results of the model for species richness. I included transect as a random effect to account for non-independence of quadrats within the same transect.

\*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.

\*\* 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 the effect of a) elevation, b) northness, c) the interaction of distance from trail and vegetation type, and d) the interaction of distance from trail and trail type on the species richness within each quadrat. Northness was not a significant predictor according to the drop1 test. For all panels, all other variables are held at the median value (for continuous variables) or the most common category (for categorical variables).

For the subset including footpaths and OHV trails only, significant predictors of species richness were elevation and the three-way interaction between distance from trail, vegetation type, and trail type (Table 4). Species richness once again declined significantly with increasing elevation, as in the full dataset. The effect of distance from trail on species richness depended on both vegetation type and trail type (Figure 6). Results of estimated marginal means for linear trends (Appendix 1, Table A1.9) indicate significantly steeper change in species richness moving from 10 m to 0 m for footpaths compared to OHV trails in shrublands (p = 0.008) and mixed vegetation types (p = 0.025). In grasslands and coniferous forests, the slopes of species richness with distance from footpaths and OHV trails were not significantly different (p = 0.647 and p = 0.087, respectively). The model explained 4.3% of null deviance in species richness.

Table 4. Results of the model for species richness of footpaths and OHV trails only. I included transect as a random effect to account for non-independence of quadrats within the same transect.

Predictor	Coefficient	SE	AIC*	P-value**
(Intercept)	13.89	1.19	2469	n/a
elevation	-2.24	0.91	2473.4	0.016
aspect (northness)	0.03	0.86	2467	0.974
vegetation type (shrubland)	1.23	1.51	n/a	n/a
vegetation type (mixed)	0.91	1.44	n/a	n/a
vegetation type (coniferous)	-1.53	1.38	n/a	n/a
distance	0.69	1.06	n/a	n/a
trail type	1.40	2.33	n/a	n/a
vegetation type (shrubland) x distance	-3.50	1.38	n/a	n/a
vegetation type (mixed) x distance	-3.47	1.23	n/a	n/a
vegetation type (coniferous) x distance	-5.18	1.24	n/a	n/a
distance x trail type	0.97	2.11	n/a	n/a
vegetation type (shrubland) x trail type	-1.36	3.07	n/a	n/a
vegetation type (mixed) x trail type	-2.16	3.11	n/a	n/a
vegetation type (coniferous) x trail type	-4.43	3.00	n/a	n/a
vegetation type (shrubland) x distance x	4.03	2.81		
trail type				
vegetation type (mixed) x distance x trail	3.12	2.78	2175 1	0.007
type			2473.4	0.007
vegetation type (coniferous) x distance x	-3.90	2.71		
trail type				

\*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.

\*\* 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 the effect of distance from trail on species richness for footpaths versus OHV trails within each vegetation type. Asterisks indicate significant differences (p < 0.05) observed between slopes for footpath compared to OHV transects based on a test of the estimated marginal means for linear trends. For all panels, all other variables are held at the median value.

#### 2.4.2 Community composition

Significant predictors of the difference in community composition (as measured by Bray-Curtis dissimilarity values) of 0 m, 2 m, and 5 m quadrats compared to the 10 m quadrat included vegetation type and the interaction between distance from trail and trail type (Table 5). The mean community dissimilarity of all quadrats compared to the 10 m quadrat was significantly lower in grasslands compared to all other vegetation types (Figure 7a; Appendix 1, Table A1.10). The effect of trail type on community composition varied with distance from trail (Figure 7b; Appendix 1, Table A1.11). At 0 m, the shift in composition from 10 m was significantly greater for roads and OHV trails compared to control transects. At 2 m and at 5 m, the shift in composition was not significantly greater than the control transects for any type of trail transect. The model explained 45.1% of deviance in community composition shifts.

Predictor	Coefficient	SE	AIC*	P-value**
(Intercept)	0.42	0.05	-419.67	n/a
distance	0.00	0.01	n/a	n/a
trail type (footpath)	0.11	0.05		n/a
trail type (OHV)	0.18	0.04	n/a	
trail type (road)	0.24	0.06		
vegetation type (shrubland)	0.17	0.05		
vegetation type (mixed)	0.13	0.04	-409.53	<0.001
vegetation type (coniferous)	0.16	0.04		
distance x trail type (footpath)	-0.02	0.01		
distance x trail type (OHV)	-0.04	0.01	-395.87	<0.001
distance x trail type (road)	-0.05	0.01		

Table 5. Results of the model for shifts in community composition (Bray-Curtis dissimilarity) compared to the 10 m quadrat. I included transect as a random effect to account for non-independence of quadrats within the same transect.

\*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.

\*\* 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 the effect of a) vegetation type and b) the interaction of distance from trail and trail type on Bray-Curtis dissimilarity of each quadrat compared to the 10 m quadrat. For all panels, all other variables are held at the median (for continuous variables) or the most common category (for categorical variables).

For the data subset including footpaths and OHV trails only, significant predictors

of shifts in community composition included the interactions between distance from trail

and vegetation type, distance from trail and trail type, and vegetation type and trail type, but not the 3-way interaction. Shifts in community composition moving from 10 m quadrats towards trails were smallest in grassland plant communities, whereas shrublands had the steepest shift in community composition moving towards the trail (Figure 8a). There was a significantly greater shift in community composition moving from 10 m to 0 m for OHV trails compared to footpaths (Figure 8b). In grasslands, mixed forests, and coniferous forests, transects on OHV trails had greater shifts in community composition compared to footpaths (Figure 8c). Interestingly, in shrublands, this pattern was reversed (Figure 8c). However, pairwise tests comparing mean dissimilarity of plant communities on OHV transects compared to footpaths within each vegetation type indicate significant differences between footpaths and OHV trails only in grasslands (Appendix 1, Table A1.12).



Figure 8. Partial regression plots showing the effect of a) the interaction between distance from trail and vegetation type b) the interaction of distance from trail and trail type, and c) the interaction between vegetation type and trail type on Bray-Curtis dissimilarity of 0 m, 2 m, and 5 m quadrats compared to the 10 m quadrat in each transect, for footpath and OHV trail transects only. For all panels, all other variables are held at the median (for continuous variables) or the most common category (for categorical variables).

# 2.4.3 Presence of at least one exotic species

Significant predictors of the presence of at least one exotic species included elevation, vegetation type, and the interaction between distance from trail and trail type (Table 6). The probability of finding at least one exotic species in a quadrat declined with increasing elevation (Figure 9a). Grassland and shrubland quadrats had the highest probability of having at least one exotic species, at nearly 100%. Grasslands also had significantly higher probability of having exotic plants than mixed/broadleaf forests (Appendix 1, Table A1.13). Coniferous forests had significantly lower probability than all other vegetation types (Figure 9c). In control and on roadside transects, the probability of at least one exotic did not change significantly with distance (Figure 9d). Control transects had about 40% probability of supporting exotic species whereas transects near roads had a uniformly high probability of exotic species occurrence, with over 70% probability even at the 10 m quadrat. On footpath transects, the probability of at least one exotic was significantly higher at 0 m and 2 m quadrats compared to 10 m as well as at 0 m compared to 5 m. On OHV transects, exotic plants were more likely to occur at 0 m than 2 m, and at 2 m than 5 m, but there was no significant difference between 5 m and 10 m quadrats in the probability of at least one exotic plant being present (Appendix 1, Table A1.14a). At 10 m, no trail types had significantly higher probability of finding an exotic species than control transects, whereas at 0 m, OHV trails, roads and footpaths had a higher predicted probability of finding an exotic species compared to control transects, although pairwise tests suggest this difference was significant only for OHV trails and footpaths (Appendix 1, Table A1.14b). The model explained 29.4 % of the null deviance.

Predictor	Coefficient	SE	AIC*	P-value
(Intercept)	2.74	1.45	476.01	n/a
elevation	-4.10	0.90	505.9	<0.001
aspect (northness)	0.09	0.66	474.03	0.896
distance	-0.06	0.78	n/a	n/a
vegetation type (shrubland)	-2.70	1.33	512.42	<0.001
vegetation type (mixed)	-4.28	1.35		
vegetation type (coniferous)	-7.09	1.53		
trail type (footpath)	1.37	1.18	n/a	n/a
trail type (OHV)	3.11	1.03	n/a	n/a
trail type (road)	3.13	1.56	n/a	n/a
distance x trail type (footpath)	-4.87	1.41	488.06	<0.001
distance x trail type (OHV)	-3.42	0.96		
distance x trail type (road)	-2.00	1.38		

Table 6. Results of the model for the probability of at least one exotic species present. I included transect as a random effect to account for non-independence of quadrats within the same transect.

\*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.

\*\* 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 9. Partial regression plots showing the effect of a) elevation, b) northness, c) vegetation type, and d) the interaction between distance from trail and trail type on the probability of occurrence of one or more exotic species within each quadrat. Northness was not a significant predictor according to the drop1 test. For all panels, all other variables are held at the median (for continuous variables) or the most common category (for categorical variables).

For the subset including footpaths and OHV trails only, significant predictors for the probability of having at least one exotic species were elevation (as seen with the full data set) and the 3-way interaction. Pairwise tests of the mean probability at each distance indicate high probability of finding exotic species in grasslands regardless of distance with no significant differences between trail types (Figure 10a). In shrublands, OHV trails have significantly higher probability of supporting exotic species than footpaths at 10 m (Figure 10b), whereas in mixed/broadleaf vegetation, OHV trails have significantly higher probability of exotics at both 5 m and 10 m (Figure 10c). In coniferous forests, at 0 m, the probability of exotic species is higher for OHV trails, however, after 2 m, the probability of exotic species is higher for footpaths (Figure 10d). Results of estimated marginal means for linear trends (Appendix 1, Table A1.15) indicate that the probability of exotic occurrence with distance from the trail is significantly different for OHV trails compared to footpaths in shrublands, mixed forests, and coniferous forests.



Figure 10. Partial regression plots showing the 3-way interaction between distance from trail, vegetation type, and trail type on the presence of exotic species within each quadrat for footpaths (blue) and OHV trails (orange). For all panels, all other variables are held at the median.

The probability of having at least one exotic species present in a transect (all quadrats lumped) included vegetation type and the interaction between elevation and trail type. In line with the quadrat level results, there was higher probability of exotic presence in grassland transects than all other vegetation types (Figure 11a; Appendix 1, Table

A1.16). The probability of finding at least one exotic species in a transect declined with elevation, but the slope of this decline varied for different trail types (Figure 11b). The decline in the probability of finding exotic species with increasing elevation was significantly steeper for footpaths than OHV trails (Appendix 1, Table A1.17). The model explained 47.9% of null deviance.



Figure 11. Partial regression plots showing the effect of a) vegetation type, and b) the interaction between elevation and trail type on the presence of exotic species within each transect. Three outliers at high elevations were removed prior to building the model. For all panels, all other variables are held at the median (for continuous variables) or the most common category (for categorical variables).

#### 2.4.4 Presence of at least one rare species

The only significant predictor for the probability of at least one rare species was trail type (Table 7; Figure 12). The probability of finding at least one rare species was higher for control transects than for trailside transects, however, post-hoc pairwise tests showed no significant differences between the different trail types (Appendix 1, Table A1.18). The model explained 4.0% of null deviance.

For the subset including footpaths and OHV trails only, no individual variable

was a significant predictor of the probability of finding at least one rare species once all

the other predictors had been accounted for (Table 8). The model explained 1.8% of null

deviance.

Table 7. Results of the model for the probability of at least one rare species present. I included transect as a random effect to account for non-independence of quadrats within the same transect.

Predictor	Coefficient	SE	AIC*	P-value**
(Intercept)	-3.15	1.13	408.79	n/a
elevation	-0.61	0.56	407.99	0.275
distance	0.40	0.30	408.61	0.178
vegetation type (shrubland)	0.80	1.07		
vegetation type (mixed)	1.02	1.05	406.64	0.279
vegetation type (coniferous)	1.73	1.02		
trail type (footpath)	-0.51	0.87		
trail type (OHV)	-1.31 0.70 410.7		410.7	0.048
trail type (road)	-3.30	1.48		

\*AIC values include all factors in the model except the one being tested.

\*\* P-values indicate the significance of each predictor using a drop1 test. Predictors with p < 0.05 are indicated in bold text.



Figure 12. Partial regression plots showing the effect of a) elevation, b) distance from trail, c) vegetation type, and d) trail type on the probability of at least one rare species. Non-significant predictors are indicated by dashed lines; trail type was the only significant predictor in the model according to the drop1 tests. For all panels, all other variables are held at the median (for continuous variables) or the most common category (for categorical variables).

Table 8. Results of the model for the probability of at least one rare species present for
footpaths and OHV trails only. I included transect as a random effect to account for non-
independence of quadrats within the same transect.

Predictor	Coefficient	SE	AIC*	P-value**
(Intercept)	-4.11	1.35	303.33	n/a
elevation	-0.24	0.36	301.76	0.5133
distance	0.07	0.18	301.5	0.6815
vegetation type (shrubland)	0.91	1.35	300.38	0.3839
vegetation type (mixed)	1.62	1.33		
vegetation type (coniferous)	1.96	1.27		
trail type	-0.89	0.79	302.55	0.2691

\*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.

\*\* P-values indicate the significance of each predictor using a drop1 test.

## **2.5 Discussion**

My results show that trails are affecting plant communities in CCWPP. I found higher species richness, shifts in community composition, and increased probability of exotic species presence near trails. These patterns, although relatively consistent, varied in different vegetation types and with different trail types. The trail effect was less prominent in grasslands than in other vegetation types, suggesting that vegetation types are affected differently by trails. There were greater shifts in plant community composition near OHV trails than footpaths, and a higher probability of exotic presence 10 m away, suggesting that OHV trails facilitate the spread of exotics *out* from trails more than footpaths. Importantly, the magnitude and extent of the effect of trails on plant communities sometimes depended on interactions between vegetation type and trail type. For example, OHV trails are associated with elevated species richness and a higher probability than footpaths of exotic species presence 10 m away from the trail edge, but only in mixed/broadleaf and shrubland vegetation, not in grasslands or coniferous forests. These findings show that currently, grasslands are highly invaded even 11 m away from trails, regardless of the trail type. In contrast, the presence of exotic species in mixed/broadleaf vegetation and shrublands beyond 2 m seemed to be facilitated by OHV trails but not by footpaths. If management goals are to reduce the spread of exotic species, managers should prioritize limiting or prohibiting OHV traffic through mixed/broadleaf forests and shrubland vegetation.

# 2.5.1 Trail impacts on species richness

As predicted, I found that species richness generally increased moving toward trails. Across all trail types and vegetation types, on average there were significantly

more species at  $0m (14.7 \pm 5.8)$  compared to at  $10m (11.9 \pm 5.6)$ . This increase in species richness moving toward trails could be attributed to one or more factors including higher light levels near trails compared to far from trails (e.g., Bates ,1935; Dale & Weaver, 1974; Tyser & Worley, 1992), increased disturbance near trails preventing competitive dominance by a few species (Larson, 2002; Dickens, 2005), or increased seed supply near trails due to seed dispersal on clothing or fur (Campbell & Gibson, 2001; von der Lippe & Kowarik, 2007; Mount & Pickering, 2009). I did not directly measure trail use intensity or seed availability, however, significantly higher soil compaction levels directly beside all trails compared to control transects provides evidence of greater trail disturbance via trampling near trails. My results align with findings of Benninger-Truax et al. (1992) who found significantly higher species richness at the trail edge compared to their 'interior' plot at 5 m, attributing their findings to more disturbance tolerant species near trails. This is contrary to Crisfield et al. (2012) who found lower species richness near trails in alpine meadows, due to fewer alpine species tolerant of trampling. This suggests that an increase in species richness near trails occurs in some vegetation types but not others.

In my study, the change in species richness moving towards trails did in fact depend on the vegetation type. The increase in species richness moving from 10 m towards a trail was smaller for grasslands than for all other vegetation types. Different vegetation types have different gradients of light or water availability and consist of plants with traits adapted to such conditions (Dale & Weaver, 1974; Cole, 1978; Hall & Kuss, 1989; Stohlgren et al., 1999; Hill & Pickering, 2009; Meryem et al., 2009). For example, grasslands and meadows with no tree canopy consist mainly of rhizomatous

grasses and herbaceous species tolerant of full sun exposure and rainfall. Therefore, in grasslands, more species can establish far from trails where sun and water availability are comparable to conditions found directly beside trails. In contrast, coniferous forests are generally associated with less light and brittle, woody species that must compete for light and water which are limited below dense canopies. In my study, I found that grasslands had nearly no change in the number of species found near trails compared to 10 m away. Mixed/broadleaf vegetation also showed no statistically significant changes in species richness with distance from trails, likely because the canopy is much more open than in coniferous forests, and mottled sunlight can penetrate areas away from trails. The effect of trails on species richness also extended beyond 5 m in shrublands, whereas in coniferous forests, the effect on species richness extended no more than 2 m, suggesting the role of increased light availability near the more open trailside.

Patterns of species richness also varied depending on the trail type, indicating the importance of trail disturbance. I found that directly beside trails, species richness was significantly higher for OHV trails and footpaths compared to roads or controls. Additionally, relative to 10 m from trails, species richness increased closer to OHV trails and footpaths and declined closer to roadsides. These results suggest that directly roadside, conditions are too harsh for most species to survive (Wolf & Croft, 2014) likely because soil compaction reduces water availability for seeds (Marion et al., 2016) and hardens the soil surface making it too dense for seeds to penetrate and begin germinating (Alessa & Earnhart, 2000). In my study, soil compaction was highest directly beside roads where species richness was lowest, relative to footpaths and OHV trails where species richness was highest. This matches other studies which found significantly

greater species richness along light and moderate use trails compared to heavy use trails (Benninger-Truax et al., 1992), and lightly used or recently abandoned trails compared to high-use trails or undisturbed sites (Parikesit et al., 1995). My results support the idea of an intermediate disturbance effect suggested by Benninger-Truax et al. (1992) and Parikesit et al. (1995), whereby the highest species richness is observed beside footpaths and OHV trails compared to undisturbed or highly disturbed trails, and species richness is lowest directly beside roadsides, which have the highest disturbance levels. Together, these results provide evidence that too much disturbance or compaction negatively impacts species richness directly trailside. While many studies do not find a trail effect on species richness extending beyond 5 m from trails, in CCWPP this effect extends past 5 m from OHV trails but not from footpaths. Therefore, in addition to the effect of trails through different vegetation types on species richness, increased trailside disturbance can also influence the extent to which increased species richness can be found away from trails.

My study shows that vegetation type and trail type interact to influence the extent of trail impacts on species richness. For example, I found that in shrublands and mixed or broadleaf forests, the decline in species richness when moving away from footpaths towards intact vegetation is steeper compared to OHV trails. At 10 m, OHV transects had elevated species richness compared to footpaths, suggesting that the trail effect extends farther out from OHV trails in shrublands and mixed/broadleaf forests. In contrast, the slope of the decline in species richness with distance from the trail did not differ between footpaths and OHV trails in grasslands or coniferous forests. Myers & Harms (2009) suggest that disturbance can influence species richness by opening space, increasing the

success of propagules arriving to plant communities, and by providing opportunity for propagules from the soil seed bank to establish. Higher propagule pressure from OHVs compared to hikers, in addition to moderate light availability in shrublands and mixed/broadleaf vegetation may result in a larger zone of trail influence for OHV trails in these vegetation types. This is not evident in grasslands—where high light availability promotes more even distribution of all species—nor coniferous forests—where low light availability dramatically reduces the number of propagules able to establish in more shaded environments farther from the trail edge. Species able to colonize quickly and tolerate disturbance are likely the main contributors to the increased species richness observed trailside. Species richness does not reveal *which* species are contributing to species richness along trails. Therefore, it is important to consider measures of community composition to fully understand how trails affect plant communities.

#### 2.5.2 Trail impacts on plant community composition

In my study, recreational trails also affect plant community composition in CCWPP. I predicted that there would be shifts in community composition near trails compared to vegetation 10 m away from the trail edge and that shifts would be smaller in grasslands compared to other vegetation types due to grassland communities having more species adapted to disturbance and high light conditions (Dale & Weaver, 1974; Cole, 1978; Hall & Kuss, 1989; Hill & Pickering, 2009). I found that the change in species composition at 0 m, 2 m, or 5 m compared to 10 m away was lower in grasslands (mean Bray-Curtis dissimilarity of 0.53) than all other vegetation types. The shifts in composition moving towards trails in grasslands was no more than expected from natural variability that occurs in undisturbed vegetation, as measured in control transects. These

results suggest that shifts in community composition may be lower for trails in open habitats with high light availability such as grasslands compared to forested habitats. Alternatively, these results may suggest the compositional differences associated with trails have extended farther than 10 m in grasslands in CCWPP.

I found that the extent of trail impacts on community composition was also affected by trail type, as suggested by the significant interaction between distance from trail and trail type. Roads and OHV trails were associated with the greatest change in composition at 0 m; the mean community dissimilarity at 0m was 0.79 for roads and 0.74 for OHV trails, 0.66 for footpaths, and 0.55 for control transects more than 100 m from trails. Although roads and OHV trails exhibit a significantly greater shift in composition than expected just based on a shift in distance, this difference is only significant at 0 m. It seems increased disturbance associated with roads and OHV trails supports the establishment of disturbance tolerant species, however, the extent of compositional shifts varies with trail type. My results show that shifts in community composition extend a shorter distance from the trail edge along footpaths compared to OHV trails. For all trail types, the community dissimilarity at 5 m compared to 10 m was no different than control transects. For footpaths, the shift in composition was higher than 5 m only at 0 m, suggesting the trail effect does not extend much past the immediate trail edge. For OHV trails, the community dissimilarity at both 0 m and 2 m were significantly greater than dissimilarity at 5 m, suggesting that changes in composition extend to 2 m but not beyond 5 m from trails. Therefore, trail effects on community composition are not observed at 5 m, indicating that shifts in composition occur less than 5 m from trails. Other studies have noted similar patterns. Wolf & Croft (2014) found that shifts in community

composition extended a greater distance from high use trails than from low use trails. The authors attribute these findings to trailside disturbance and increased soil compaction which facilitates the spread of species tolerant of disturbance—a trait commonly associated with exotic species—farther away from higher use trails (Wolf & Croft, 2014). My results indicate that not only is the degree of compositional shifts greater near roads and OHV trails than footpaths, but they extend farther away. In CCWPP, to reduce the severity and extent of compositional shifts in vegetation along trails, managers should limit the number of roads and OHV trails.

I also found the interaction between vegetation type and trail type to be a significant predictor of shifts in community composition near trails. Of all vegetation types, grassland showed the lowest shifts in community composition near trails. However, OHV trails through grasslands are associated with significantly greater compositional shifts compared to footpaths. Perhaps this reflects increased dispersal and establishment of disturbance tolerant propagules associated with OHV use relative to footpaths. If Parks managers are concerned with changes to the composition of plant communities near trails, they should minimize OHV trails through grasslands.

# 2.5.3 Trail impacts on the presence of exotic species

As expected, in CCWPP, the probability of exotic species occurrence increases moving toward trails. This falls in line with most studies that have found significantly greater occurrence or abundance of exotics near trails compared to away (e.g., Tyser & Worley, 1992; Potito & Beatty, 2005; Dickens et al., 2005; Lake & Leishman, 2004). These studies associate increased exotic species occurrence near trails with the ability of this group to adapt to disturbance. In my study, I found that compared to trails and

undisturbed areas away from trails, roads showed a high likelihood of exotic species 10 m away, suggesting that for roads, I was unable to capture the trail effect threshold and that it likely extends some distance beyond 10 m.

Although most studies indicate the effects of park roads and trails on exotic occurrence are within 15 m (Tyser & Worley, 1992; Watkins et al., 2003; Dickens et al., 2005; Gower, 2008) some species can still be found far away from trails. For example, along high-traffic highways and railways near Banff National Park, Hansen & Clevenger (2005) found high frequency of exotics occurring up to 25 m away, suggesting that higher-use roads and trails promote invasion of exotic species well beyond trail edges. In my study, three exotic species also occurred with high frequencies in control transects at least 100 m from trails: Poa pratensis, Taraxacum officinale, and Phleum pratense. These are the same species identified by Tyser & Worley (1992) that occur more than 100 m from backcountry trails in Glacier National Park just south of the border from CCWPP. The authors note that seeds of *P. pratensis* and *P. pratense* were likely brought in the 1800s during road construction – giving them centuries to spread. Previous studies have found positive correlations between resident time of exotic species and their spread across the landscape (Castro et al., 2005; Harris et al., 2007; Ahern et al., 2010; Phillips et al., 2010). They are also preferred species among native grazers like deer or elk, who probably assisted the dispersal of their seeds via their dung or fur (Tyser & Worley 1992). The lower elevation grasslands in CCWPP are also subjected to community cattle grazing. Additionally, *Phleum pratense* and *Poa pratensis* are listed as good forage value in Alberta's rangelands (Tannas, 2003). As a result, unintentional spread by cattle may be an additional factor that has contributed to the spread of these two grass species away from trails in CCWPP.

I also found that the likelihood of finding at least one exotic species near trails depends on the type of vegetation. On average, grasslands had nearly a 100% probability of at least one exotic occurring, followed by shrublands (98%), mixed/broadleaf (92%), and then coniferous forests (42%). Environmental conditions such as light (McDougall et al., 2018), increased soil pH and decreased nitrates (Gilbert & Lechowicz, 2005) which are found to promote native species presence also promotes exotic species presence (Lonsdale, 1999; Stohlgren et al., 1999; Seabloom et al., 2003; Gilbert & Lechowicz, 2005; McDougall et al., 2018). This matches my results that show the likelihood of exotic species occurring 10 m away from trails is highest in grasslands, where light and water availability is also high, and lowest in coniferous forests, where environmental conditions limit plant growth. In CCWPP, grassland plant communities not only have the lowest compositional shifts regardless of distance from trails, but they also have the highest likelihood of exotic species present 10 m from trails, suggesting that the grasslands surveyed may already be highly invaded by exotic species. In protected parks, the increased presence of exotic species, which has been correlated to increased number of visitors (Lonsdale, 1999), has important implications for mitigating potential exotic species invasions, especially along higher use trails.

Trail type also influenced the probability of finding at least one exotic species away from trails. Road transects had the highest likelihood (about 78%) of exotic species occurring at 10 m, followed by OHV trails (40%), and then footpaths (3%). Interestingly, the probability of exotic presence in control sites 100 m away from any trail remained
relatively consistent at about 32% even at the 10 m distance which was significantly higher than the probability of exotics occurring 10 m away from footpaths. This supports the idea that a subset of the exotic species observed away from trails are likely dispersed by means other than trail-associated vectors or have been residents for a long time and therefore have had more time to disperse farther from trails than newly introduced species. As an example, both P. pratense and T. officinale have been recorded in Alberta more than 100 years ago and in conjunction with *P. pratensis* which was found in Alberta as early as 1856 (GBIF, 2022), these three species have the highest frequencies 10 m from trails compared to all other exotics surveyed in CCWPP. Although all trails had significantly higher likelihood of exotics 0 m from the edge than 10 m away, wide, or heavier-use trails may exert a greater disturbance effect on the surrounding vegetation and soils compared to narrow or lighter-use trails (Tyser & Worley, 1992; Potito & Beatty, 2005; Hochrein, 2008; Törn et al., 2009; Zhou et al., 2020), which promotes the establishment of more disturbance tolerant exotics. These patterns can be attributed to increased propagule pressure associated with wider or heavier use trails that can facilitate the wind-mediated dispersal of exotic propagules farther away from the trailside. In my study, additional evidence of a disturbance effect from trails can be seen with soil compaction values that decline with distance from trails. Compared to consistently low compaction values observed across distance at undisturbed (control) sites, all trail types had significantly greater soil compaction directly beside trails, with roads having the greatest compaction. Heavily used roads for example, are often devoid of any vegetation directly roadside, indicating extreme disturbance effects (Hansen & Clevenger, 2005). My results show that some exotic species can tolerate highly compact, disturbed habitats

that occur directly beside roads and OHV trails, and that higher use trail types can disperse exotic propagules farther than footpaths.

I also found that the extent of the trail effect on the likelihood of finding an exotic species depended on the interaction between vegetation type and trail type. Compared to footpaths, OHV trails had a greater likelihood of supporting exotic species farther from the trail edge, but this was significant only for shrublands and mixed/broadleaf vegetation. This result mirrors the result for species richness, where species richness was elevated farther out from OHV trails than footpaths, but only in these same two vegetation types. In shrublands and mixed/broadleaf vegetation, adequate light far from OHV trails combined with higher propagule pressure are facilitating the spread of exotic species farther than footpaths. Parendes & Jones (2000) found the greatest exotic species prevalence in areas of high light availability and high-use trails compared to sites that had lower light availability or were less disturbed. The authors suggest that in addition to characteristics associated with different vegetation types (e.g., light, water, nutrients), exotic invasions may also depend on characteristics associated with the propagules being dispersed (e.g., dispersal mechanisms, seed morphology, germination requirements; Parendes & Jones, 2000). While the closure of all OHV trails in shrubland or mixed/broadleaf vegetation may not be possible, managers could focus exotic species monitoring near trails through these vegetation types and encourage users to stay on trails. Additionally, managers should consider limiting OHV traffic to reduce the spread of exotic species.

2.5.4 The effect of trails on the presence of exotic species at higher elevations

I examined the probability of finding at least one exotic species at the transect level to determine whether trails are facilitating the spread of exotic species upwards in elevation. I found that the decline in probability of finding exotics with increasing elevation was less steep in transects near OHV trails relative to footpaths, which is consistent with the hypothesis that OHV trails are facilitating exotic species spread to higher elevations. Trails not only transport propagules, but they can also channel human disturbance to higher elevations (Barros & Pickering, 2014). Similarly, Pauchard et al. (2009) note that the rate of exotic invasions at higher elevations can be attributed to changes in climatic and nutrient regimes as well as increased propagule pressure from increased access and development of montane regions for recreational use. Seeds can attach to humans, and they can also cling to vehicles and vehicle tires, especially if weather permits muddy trail conditions causing additional seed retention on vehicles (Taylor et al., 2012) and facilitate long-distance dispersal of exotic species (von der Lippe & Kowarik, 2007). In my study, footpaths may not be exerting enough propagule pressure or disturbance to result in significant changes to exotic presence at higher elevations. The higher soil compaction farther out from OHV trails, and the fact that OHV trails have a higher probability of exotic species farther away from the trail support the idea that OHV trails are facilitating exotic spread to higher elevations, whereas footpaths may not exert enough disturbance or propagule pressure to facilitate the spread of exotics to higher elevations.

My study is the first in North America to show evidence that the spread of exotics to higher elevations is being facilitated by recreational trails, particularly OHV trails. If park management is concerned with exotic species spreading to higher elevations, exotic control efforts at higher elevations should be directed towards OHV trails. Prevention efforts of cleaning vehicles prior to trail use could also reduce the propagule pressure exerted by OHV traffic. Additionally, if closure of trails is not possible or is too unpopular, limiting the amount of traffic along OHV trails at higher elevations would help reduce the spread of exotics upward.

# 2.5.5 Trail impacts on the presence of rare species

The protection and conservation of rare species is crucial in regions where hotspots of biodiversity intersect with recreation. In CCWPP, 14% of quadrats and 23% of transects had at least one S1 or S2 provincially tracked rare species. The likelihood of rare species across vegetation types ranged from 1% in grasslands to 6% in coniferous forests, although vegetation type was not a significant predictor. Among the most frequent rare species in CCWPP, two are grasses (*Melica subulata* and *Festuca occidentalis*), one is a shrub (*Paxistima myrsinites*), and one is a sedge (*Carex geyeri*), all of which are upright, perennial species. Based on the habitat descriptions in Moss & Packer (1983) and Kuijt (1982), none of these species are associated with disturbance. *Festuca occidentalis* and *Carex geyeri* both exhibited higher frequencies at intermediate distances (2 m and 5 m), whereas *Melica subulata* and *Paxistima myrsintes* had increasing frequencies farther from the trail edge. These data suggest that the rare species surveyed occupy a diverse range of niches and vegetation types.

The only significant predictor in the likelihood of finding at least one rare species was trail type. Rare species occurred slightly more often in transects more than 100 m from trails (11%), followed by footpaths (7%), OHV trails (3%) then roads, with nearly 0% probability of rare species occurring. Catling & Kostiuk (2011) found higher density

of some orchids—Calypso bulbosa var. americana (R. Brown) Leur on trails in Waterton Lakes National Park as well as Epipactis hellborine (L.) Crantz and Goodvera oblongifolia Raf. on trails in Ontario—within 1.5 m of trails, suggesting that some rare plants can tolerate light trampling and compact soil. In CCWPP, I found that footpaths are nearly as likely as sites beyond 100 m from trails to have a rare species present, and they have lower compaction relative to roads but not OHV trails. These data suggest that the rare species I observed can tolerate some level of disturbance beyond the immediate trailside. Within trailside transects only, I did not find evidence of the effect of distance from trails influencing rare species presence; the 10 m quadrat was no more likely to have a rare species present than the 0 m quadrat. Although greater shifts in composition and greater probability of exotics occur at 0 m compared to 10 m for most trails, the likelihood of finding a rare species was the same, regardless of distance from trails. Of the rare species that were found along trails, 6 of 15 (40%) occurred at the trail edge (0 m) in frequencies equal to or greater than frequencies found at 2 m. McIntyre & Lavorel (1994) found a significant negative correlation between the number of rare species and the proportion of exotic species, which was independent of the contrasting effects of habitat factors, suggesting a competitive nature between the two groups of species. These vegetation responses imply that both can withstand some disturbance, and rare species can still establish in vegetation near trails where exotic species are present.

Along recreational trails in CCWPP, I found occurrences of both exotic and rare species. Although there is no evidence to suggest that rare species are being outcompeted near trail edges by exotic species, my analyses focused on occurrence rather than abundance. It could be that exotic species do outcompete rare native species, but only if the exotic species are high in abundance. To maintain occurrences of rare species, managers should reduce the level of disturbance associated with recreational trails and avoid implementing new roads. Future studies should consider the abundance of exotic species relative to the abundance of rare species near trails to determine whether higher abundances of exotic species negatively affect the presence or abundance of rare species.

## **2.6 Conclusion**

In CCWPP, recreational trails are indeed affecting plant communities. Not only are OHV trails shown to affect the number of species and the likelihood of finding exotic species in plant communities relative to footpaths, but these effects also become more pronounced, depending on the type of vegetation the trail traverses. Overall, for OHV trails compared to footpaths, the increased species richness and exotic species probability observed directly beside trails extends farther in mixed/broadleaf and shrubland vegetation, and community composition is more dissimilar in grasslands. Although the probability of finding at least one rare species was lower near all trails relative to sites 100 m away, it seems they are slightly more likely to occur near footpaths where less disturbance occurs compared to the other trail types. Together, my results indicate that if park management is concerned with recreational trail impacts on plant communities in CCWPP, the number of OHV trails should be reduced, particularly through shrubland and mixed/broadleaf vegetation and additionally, at higher elevations. To improve the likelihood of rare species occurrences and subsequently decrease the chances of exotic species presence, reduce the level of disturbance associated with trails and avoid implementing new roads.

# CHAPTER 3: Habitat characteristics of known *Botrychium* occurrences and quantitative analyses of its association with trails

## 3.1 Abstract

Moonwort (Botrychium Swartz) is a genus of ferns which can be found in high diversity in the Rocky Mountains of southwestern Alberta. Observation records of these small, cryptic species may be subject to bias towards well-travelled areas near trails. Castle Provincial Park and Castle Wildland Provincial Park (CCWPP) are two recently established protected areas within this global hotspot of *Botrychium* diversity. However, prior to 2018, provincial and international databases included fewer than 15 occurrence records of *Botrychium* throughout CCWPP. Therefore, their frequency in the parks and their habitat preferences were not well understood. I used the pre-2018 occurrence records plus 73 georeferenced photos of *Botrychium* occurrences noted as part of the Castle Flora project, and an additional 8 georeferenced photos from my own surveys conducted in 2021 to characterize habitat preferences of Botrychium species found throughout CCWPP. I also tested the ability of a species distribution model (SDM) to successfully predict the presence of *Botrychium* species in CCWPP. I visited 24 sites at least 100 m away from official trails that varied in their predicted habitat suitability and carried out full plant community surveys. I found that most *Botrychium* occurrences were on south-facing slopes, in grassland vegetation, 10 m-100 m away from trails. I discovered 7 new occurrences in the off-trail surveys. Although 6 of the 7 new off-trail occurrences were found at sites with greater than 40% suitability, the species distribution model was not a significant predictor of *Botrychium* occurrence. My results show that Botrychium occur across a wide range of vegetation types, topographic conditions, and proximity to trails and there are likely many undiscovered populations in CCWPP. To

maximize discoveries of new occurrences, surveys should focus on grassland areas. Additionally, SDMs built for individual species could prove more useful in finding new records of targeted species.

### **3.2 Introduction**

Species within the genus *Botrychium* Swartz (commonly, moonwort), are cryptic, inconspicuous ferns belonging to the family Ophioglossaceae. There are 50 species recognized globally, and over 30 of these occur in North America (Flora of North America (FNA) Ed. Comm., 1993; Farrar, 2011). Moonwort are small in stature, reaching no more than 15 cm tall and often only noticed after a thorough survey of the groundlevel vegetation (Wagner & Wagner, 1981; Figure 13d). They are distinguishable by their single, upright green leaf that is divided into two stalks, a sterile leaf-like 'trophophore' and a 'sporophore' that bears tiny clusters of spherical sporangia which release spores upon maturation (Farrar, 2011; Figure 13b, c). Moonwort spores require a dark environment (below ground) and mycorrhizal associations to germinate and produce individual gametophytes that have both male and female reproductive structures (Whittier, 1973). Once fertilization has occurred, the gametophytes provide nutrients for the below-ground sporophyte (Johnson-Groh et al., 2002b). Eventually, the sporophyte will create its own mycorrhizal associations, allowing moonwort to persist underground – sometimes for several years – until conditions are favourable for the sporophyte to emerge aboveground and photosynthesize (Johnson-Groh et al., 2002b). The diverse morphology and unpredictable belowground period of moonwort has prompted systematic and molecular analyses to investigate the various lineages of species belonging to this genus (Hauk, 1995; Farrar, 2011; Dauphin et al., 2014; Stensvold &

Farrar, 2011; Dauphin et al., 2017). Although much is known about the life history of *Botrychium* species, less is known about their precise geographic distributions and habitat requirements.

The geographic distribution of many *Botrychium* species may be severely underestimated due to lack of observations (Williston, 2001). Limited ranges of some Botrychium species in North America have resulted in them being listed as species of conservation concern. Currently, there are 34 species found in North America with 18 listed as globally vulnerable (G3), imperiled (G2), or critically imperiled (G1) and one (B. subbifoliatum Brack. from Hawaii) as possibly extinct (NatureServe, 2022). In Alberta, 20 of these species occur, 5 which are ranked provincially as vulnerable (S3), 2 as imperiled (S2), and 7 as critically imperiled (S1) (NatureServe, 2022). B. pseudopinnatum W.H. Wagner (false northwestern moonwort) for example, is globally (G1) and provincially critically imperiled (S1) in Ontario, endemic to the northern shore of Lake Superior (NatureServe, 2022). B. x watertonense W.H. Wagner (GNA S1, Waterton moonwort) is endemic to Waterton Lakes National Park, and has greater than expected abundance for a sterile hybrid species – as most hybrid species occur in low abundances (Farrar, 2011). Species distribution maps can help identify gaps in the distribution which may be a factor of geographical barriers (e.g., mountains, dry flat plains) rather than lack of survey effort. However, more observations are needed to determine accurate distributions of Botrychium species.

Because of the large morphological variation within single species and their tendency to hybridize, taxonomic differentiation of moonwort species is difficult. Taxonomists rely on a combination of morphological characteristics, chromosome

number, and spore size to differentiate species belonging to *Botrychium* (Hauk, 1995; Farrar, 2011). *B. paradoxum* W.H. Wagner (G3 S1, peculiar moonwort) for example, is morphologically identified by a stalk that is divided into two identical sporophores (Figure 13a). *B. x watertonense* - a hybrid between *B. hesperium* (Maxon & R.T. Clausen) W.H. Wagner & Lellinger (G4 S3, western moonwort) and *B. paradoxum* – has a trophophore that also bears sporangia, a characteristic unique among moonwort (FNA Ed. Comm., 1993; Hauk, 1995; Lesica & Ahlenslager, 1996; Farrar, 2011). More observations of *Botrychium* occurrences are needed to fully understand how their morphological complexity is related to genetic diversity, and to correctly differentiate between members of *Botrychium* and determine species distribution ranges.

The habitats of *Botrychium* are diverse, ranging from open meadows to moist shaded woods at low elevations to alpine meadows at high elevations (Moss & Packer, 1983; FNA Ed. Comm., 1993; Fryer et al., 2022). Although all known species of *Botrychium* have been described in floras, the precise habitat requirements are often vague and limited to conditions at local occurrences which may not necessarily reflect conditions throughout the species' entire range. Most species of *Botrychium* are usually described as preferring some level of disturbance. For example, nearly all descriptions of rare *Botrychium* species in Alberta refer to 'roadside', 'ditches', or 'trailside' habitats (Fryer et al., 2022). However, these descriptions of habitats could be reflecting the fact that these small statured plants are easier to spot in more open habitats like trail edges, as well as bias due to opportunistic collecting or botanizing near roads or trails. It is uncertain if some *Botrychium* species indeed require such disturbances, or whether sampling bias is at play.



Figure 13. The diversity of *Botrychium* species found along two popular hiking trails in CCWPP, Alberta, Canada: a) *B. paradoxum* (S1) showing two fertile sporophores; b) *B. lunaria* (S5) showing one leafy trophophore growing behind the tall sporophore; c) *B. lanceolatum* (S4) showing mature yellow sporangia on the sporophore and dentate margins of the trophophore - a, b, and c were all found along South Drywood Creek in the same day- and d) a small *B. lunaria* no higher than 2 cm in height found along North Drywood Creek.

Globally, there are three areas of high moonwort diversity: the Alps in Europe

(Dauphin et al., 2014 as cited in Dauphin et al., 2017), the Great Lakes region in Ontario,

Canada, and the Rocky Mountains of southern Alberta, Canada (Hauk et al., 2012 as

cited in Dauphin et al., 2017). Of these locations, the world's centre of moonwort

diversity is in Alberta's southern Rocky Mountains (Wagner et al., 1983 as cited in Williston, 2001; Wagner & Wagner, 1994). Two recently established parks are located within this *Botrychium* hotspot: Castle Provincial Park and Castle Wildland Provincial Park (CCWPP). There are over 2,000 km of roads and trails traversing the Castle region, an area that has a long history of public land use for recreational activities, logging, industrial extraction of oil and gas, and community grazing (Farr et al., 2017). As a popular off-highway vehicle (OHV) destination that will likely see more visitors, and a provincial biodiversity hotspot, it is important to study the effects of trails on the many rare plant species within CCWPP. Despite CCWPP being part of a global hotspot of *Botrychium* species diversity, a systematic analysis of the habitat preferences of these species in CCWPP has yet to be conducted.

Until recently, there was very little floristic work done within CCWPP. In the summers of 2018 and 2019, Dr. John Bain designed and led a vascular plant inventory project for the newly designated parks. His team surveyed sites from all 9 watersheds throughout the two parks, collecting plant specimens from each surveyed site, and taking photos of all *Botrychium* plants observed during the surveys. As a member of the inventory team, I photographed 73 different occurrences of more than seven *Botrychium* species found in 5 different watersheds within CCWPP or just outside the official park boundaries (Upper Crowsnest River, Carbondale River, West Castle River, Pincher Creek, and Drywood Creek). I collected 12 different specimens for vouchers that were deposited as part of the CCWPP collection within the University of Lethbridge (LEA) Herbarium. Prior to this inventory project, known occurrences of *Botrychium* in CCWPP were limited to fewer than 15 localities total from GBIF (Global Biodiversity Information

Facility) and ACIMS (Alberta Conservation Information Management System), all in the southwest and southeast corner of the parks. During surveys conducted in 2021 as part of a trail impact analysis on plant communities in CCWPP (Chapter 2), I found an additional 8 occurrences (1 near trails and 7 off-trail) of *Botrychium*. In total, these 81 records provide a much larger sample of occurrences and allow for a more accurate characterization of *Botrychium* habitat preferences in CCWPP.

My research aims to improve the current limited knowledge of *Botrychium* species in this biodiverse area by characterizing the environmental conditions and plant communities in CCWPP associated with *Botrychium* occurrences. In addition, I test the efficacy of a species distribution model (SDM) to target sites with a high likelihood of suitable habitat for *Botrychium* occurrences. SDMs are predictive models that use occurrence data of target species and associated environmental variables to predict species distributions (habitat suitability or probability of occurrence of target species) within a specified region (Guisan & Zimmerman, 2000). SDMs have been used effectively to target rare plant surveys in other regions (Williams et al., 2009; Gogol-Prokurat, 2011; McCune, 2016). By investigating the habitat preferences of *Botrychium* occurrences in CCWPP, we can improve our understanding of their potential distribution across different habitats.

The specific objectives of my research are:

1) To assess factors associated with *Botrychium* occurrences in CCWPP, including associated species, vegetation type, presence of disturbance, proximity to trails, and environmental variables such as elevation, aspect, and slope.

2) To test a species distribution model as a predictor of *Botrychium* occurrences away from recreational trails in CCWPP and, if any species of *Botrychium* is found, to quantify differences in plant communities at sites with and without *Botrychium* present.

I expect that the species associated with *Botrychium* occurrences will consist mainly of other species that prefer open vegetation with some disturbance, including for example *Fragaria virginiana*, *Achillea millefolium*, and *Taraxacum officinale*. If *Botrychium* species do prefer disturbed habitats, I expect that most of the 81 occurrences will be near trails with some disturbance. If *Botrychium* species are less frequent away from human trails, I expect to rarely find them at sites 10 m or more from trails. If SDMs can efficiently predict habitat preferences, then I expect *Botrychium* occurrences to be found more often at sites with higher predicted suitability than lower suitability sites.

#### **3.3 Methods**

#### 3.3.1 Assessing Botrychium habitat

To characterize habitat characteristics of *Botrychium* species in CCWPP, I used the 73 georeferenced photographs I took from 2017-2020, 8 georeferenced photographs of new occurrences from 2021 (1 of the 8 was from a trailside survey as part of Chapter 2; 7 were from off-trail surveys), and 4 georeferenced records without photographs for a total of 85 different occurrences. First, I compiled information on associated species (except for the 4 records without photographs), proximity of trails, vegetation type, elevation, aspect, slope, evidence of disturbance noted (if any), and their dates of observation.

I developed a list of all associated species by examining each photograph and identifying any vascular plant species growing near the *Botrychium* species. To classify occurrences based on the vegetation type they were found in, I used a Geographic Information System (GIS) to determine the land class within which each occurrence is located based on the 2010 Wall-to-Wall Land Cover Inventory layer from the Alberta Biodiversity Monitoring Institute (ABMI; Castilla et al., 2014). I then calculated the total number of occurrences of each *Botrychium* species within each vegetation type. I used a GIS to measure the distance to the nearest trail from each Botrychium occurrence record to (1) official trails in CCWPP as of 2018, or (2) a layer with all southern Alberta trails as of 2021 which included updated CCWPP trails based on new usage regulations. I used a raster of a digital elevation model with 25 m resolution to determine the elevation, aspect, and slope of each georeferenced point. If occurrences had site descriptions, I noted whether disturbance was mentioned, and the type of disturbance. Only 23 of the 85 occurrence records had site descriptions associated with them. I also recorded the date of each occurrence record. Using these data, I compiled the top 10 most common associated species of all photographed *Botrychium* occurrences, developed a list of species and the vegetation types they were found in, assessed the range of proximity to trails, median elevation, elevation range for each species and for the genus, the mean slope and aspect, and date of observation for each occurrence.

## 3.3.2 Testing a Species Distribution Model

To test the ability of a species distribution model (SDM) to predict habitat suitability for *Botrychium* at the generic (genus-only) level, I used an SDM that was built using a total of 148 previous georeferenced occurrences of any *Botrychium* species throughout the province of Alberta. These records were gathered from the Alberta Conservation Information Management System (ACIMS; n = 39), herbarium records of the area harvested from Global Biodiversity Information Management System (GBIF; n =13), records of *Botrychium* species from the University of Lethbridge herbarium prior to 2018 (LEA; n = 7), observations by Jed Lloren during his research in Waterton Lakes National Park (Lloren, 2021; n = 3), observations from Parks Canada ecologist, Robert Sissons (n = 17), observations from the Castle inventory project (n = 69), and 5 occurrences noted during my trailside transects in the summer of 2020 (Chapter 2). Our research technician, Olivia Gauthier, built the SDM using the program MaxEnt (Phillips et al., 2006). This SDM was built as part of a larger project to build SDMs for 42 plant species ranked S1, S2, or S3 in Alberta by NatureServe. MaxEnt is a machine learning program that predicts habitat suitability of individual cells across a region using presenceonly data and environmental features (Phillips et al., 2006; Elith et al., 2011).

We used 13 environmental predictors (Table 9) and occurrence records with 100 m or less accuracy to build two models for predicting *Botrychium* habitat suitability. The predictors represent climatic, topographic, soil, and land cover conditions often used to predict plant species distributions. We built two SDM versions: one with the regularization setting at the default of 1, and one with regularization set at 0.5. The regularization parameter determines how strict models are with respect to overfitting; the first model, with a regularization parameter of 1 allowed for a more inclusive fit, whereas the second model with a regularization parameter of 0.5 was more conservative (Phillips et al., 2006). The model resolution was 50 m by 50 m grid cells, which we chose because this is an area that can be thoroughly surveyed in one day of fieldwork. Because some of

the 148 *Botrychium* records occurred within the same 50 m grid cell, this resulted in 111 unique records used by MaxEnt. The model extent included only the province of Alberta, and in addition was restricted to the natural subregions in which *Botrychium* is known to occur. These include Athabasca plain, upper boreal highlands, alpine, subalpine, montane, upper foothills, foothills parkland, dry mixed grass, foothills fescue, northern fescue, and mixed grass (Figure 14, inset map). For each model, we excluded 25% of the observations to use as test data. We set MaxEnt to repeat this procedure 10 times and take the average prediction from these 10 replicates. We used the cumulative model output, which avoids assumptions about the species' prevalence (Phillips et al., 2006). This resulted in a raster layer in which each 50 m x 50 m grid cell receives a value ranging from zero to 100, with 100 indicating the highest predicted relative habitat suitability (Figure 14).

Predictor	redictor Source			
		Туре		
Aspect	Alberta Provincial 25m Raster Digital	raster		
	Elevation Model (2017)			
Elevation	Alberta Provincial 25m Raster Digital	raster		
	Elevation Model (2017)			
Slope	Alberta Provincial 25m Raster Digital	raster		
	Elevation Model (2017)			
Land Use/Land	ABMI Wall-to-wall Land Cover Map 2010	polygon		
Cover	Version 1.0 (ABMIw2wLCV2010v1.0)			
Surficial	Surficial Geology of Alberta, 1:1,000,000 scale	polygon		
Geology	(Alberta Geological Survey)			
NDVI in	Alberta W2W Normalized Difference	raster		
October 2016	Vegetation Index (NDVI) (Alberta Biodiversity			
(an index of	Monitoring Institute, 2014)			
'greenness')				
Climate	Climate Data For Alberta (monthly climate	raster		
Moisture Deficit	normals from 1961-1990; ABMI)			
Mean Annual	Climate Data For Alberta (ABMI)	raster		
Precipitation				
Mean Annual	Climate Data For Alberta (ABMI)	raster		
Temperature				
Mean Summer	Climate Data For Alberta (ABMI)	raster		
Precipitation				
Mean Warm	Climate Data For Alberta (ABMI)	raster		
Month				
Temperature				
Number of	Climate Data For Alberta (ABMI)	raster		
Frost-free Days				
Precipitation as	Climate Data For Alberta (ABMI)	raster		
Snow				

Table 9. Environmental predictors used to build the *Botrychium* SDM.



Figure 14. Inset: shows model extent (grey shaded) and location of Castle Provincial Park and Castle Wildland Provincial Park in the southwest corner of Alberta, Canada. Main map: CCWPP, coloured based on predicted habitat suitability for *Botrychium* according to a species distribution model (SDM). Brown lines indicate official trails. Dark grey circles indicate *Botrychium* occurrences used to build the SDM that were found within the park boundaries (n = 69) or just beyond them (n = 8). The 24 50 m x 50 m off-trail plots are indicated by stars, including plots with no *Botrychium* species found (white, n = 17), and plots where a *Botrychium* species was found (red, n = 7). The yellow triangle indicates a new on-trail occurrence found during 2021 trailside surveys.

Using ArcMap, I imported the habitat suitability raster for Botrychium from the

SDM with regularization set to 0.5. I decided to use this SDM as it provides a more conservative estimate of the extent of suitable habitat throughout CCWPP. I then clipped this raster to include only cells more than 100 m but less than 1,000 m from official trails. I then stratified grid cells into 10 categories of relative suitability (0-10%, 10-20%, etc.). I used the sampling package in R to randomly select 10 cells from each of the first 7 strata and 20 from each of the highest 3 strata for a total of 130 potential survey sites. I chose

sites to survey from these 130 randomly chosen cells with the goal of ensuring replication within each stratum and across both park areas, as well as avoiding surveying two sites in the same suitability stratum that were near each other. I successfully surveyed 24 of these off-trail 50 m x 50 m sites with at least two sites in each stratum of predicted suitability (Figure 14).

## 3.3.3 Data Collection

My field assistants and I surveyed the 24 off-trail 50 m x 50 m plots, which also served as a control for trail transects (see Chapter 2). I used a Garmin eTrex® 20 handheld GPS to navigate to the coordinates for the centre of each plot. Logistical constraints based on our ability to hike to distant sites nowhere near trails limited the number of sites I surveyed. At the GPS coordinates, I ran a transect 25 m in each cardinal direction to delineate 4 quadrants within the plot (Figure 15). My field assistant and I then carefully searched each quadrant in turn by using a compass to walk parallel transects approximately 3 m from each other. We looked carefully for *Botrychium* while also recording all vascular plants observed and estimating their abundance based on a coarse abundance scale with 5 classes: 'very rare' (1-2 individuals present), 'rare' (2-10 individuals), 'infrequent' (>10 individuals but not common throughout entirety of plot), 'common' (seen throughout plot but not a dominant species) or 'dominant' (dominant species throughout the plot) in each 50 m x 50 m survey site. We also determined the vegetation type of each plot based on our observation of the entire 50 m x 50 m area. If the plot seemed to us a mixture of vegetation types, we assessed it according to the ABMI land class in which it was located. Each survey took two people 2 to 4 hours, depending on the terrain and diversity of species present. I took photographs from each GPS point

facing in each cardinal direction. I also photographed difficult to identify species and each *Botrychium* encountered, noting any species growing in the direct vicinity of the plant. I also took samples of grasses and sedges for identification in the lab.



Figure 15. A schematic diagram of a 50 m x 50 m plot. The red dashed lines delineate four quadrants originating from the target coordinates (black circle). In each quadrant, we systematically searched for *Botrychium* and all other vascular plant species.

I identified *Botrychium* species from both the 50 m x 50 m plots and the floral inventory project by first using a synthesized key specifically for the Botrychiaceae (now Ophioglossaceae) of Alberta (Williston, 2001). I then confirmed all identifications using a more recent dichotomous key '*Vascular Flora of Alberta*' (Kershaw & Allen, 2020). I also used this key as well as '*Flora of Alberta*' (Moss & Packer, 1983) to identify all other identifiable vascular plant species from the plots, except for sedges. I identified all sedge species using the '*Field guide to Intermountain sedges*' (Hurd et al., 1998). I used Canadensys' online Database of Vascular Plants of Canada (Brouillet et al. 2010+) and NatureServe explorer 2.0 (NatureServe, 2022) for currently accepted nomenclature of identified species.

## 3.3.4 Statistical Analyses

To determine whether the species distribution model is a reliable method of predicting *Botrychium* species occurrences using the 24 surveyed plots, I built a binomial generalized linear model (GLM) with *Botrychium* presence (1) or *Botrychium* absence (0) as the response variable and habitat suitability as the predictor variable. I then tested whether predicted habitat suitability was a significant predictor using a drop1 test. As a measure of the variance explained, I calculated the percent null deviance explained using Equation 1, where null deviance is considered the deviance of the intercept-only model:

$$\frac{null \, deviance - residual \, deviance}{null \, deviance} \times 100 \qquad \qquad \text{Equation 1}$$

To test whether the plant community composition differed between plots with versus without *Botrychium* present, I first created a NMDS (non-metric multidimensional scaling) ordination to visualize the distribution of all 24 50 m x 50 m plots in species space. I set the maximum number of starts for finding a stable solution to 999 and the number of dimensions to three. I ran the NMDS using the Bray-Curtis dissimilarity values between each pair of plots, based on the raw abundance class of each species in each plot. A Bray-Curtis dissimilarity value of 0 indicates identical community composition between plots, whereas a value of 1 indicates complete difference in species found between plots (Bray & Curtis, 1957). The ordination represents these differences in two dimensions, such that more similar plots are closer together in the ordination graph, whereas more dissimilar plots are far apart in the ordination graph.

I then used PERMANOVA (permutational multivariate analysis of variance) with 9,999 permutations to test for significant differences in community composition between plots with *Botrychium* present and with *Botrychium* absent. I also used PERMDISP (multivariate homogeneity of group dispersions) with 9,999 permutations to test whether beta diversity (degree of compositional variation) within the group with *Botrychium* present was significantly different than beta diversity within the group with *Botrychium* absent.

To determine whether any of the recorded species in the 24 surveyed plots were significant indicators of the presence of *Botrychium*, I used an indicator species analysis (ISA). Indicator species analysis uses permutation to determine which species are significantly more frequent and/or abundant in one group of sites compared to another (Dufrêne & Legendre, 1997; McCune & Grace, 2002). I first defined groups based on *Botrychium* presence or absence and then conducted an ISA with 9,999 permutations to determine whether any species were indicators of plots with *Botrychium* or plots without *Botrychium*.

I carried out all statistical analyses using the statistical software R version 4.0.3 (R Core Team, 2020). I used the package 'vegan' to construct the NMDS and conduct PERMANOVA and PERMDISP analyses (Oksanen et al., 2020), and 'labdsv version 2.0-1' for the ISA (Roberts, 2019).

## **3.4 Results**

3.4.1 Assessing factors associated with Botrychium occurrences in CCWPP

Of the 85 georeferenced occurrences of Botrychium, 77 are within CCWPP boundaries – 4 of which had no photo for identification to species – whereas 8 are just outside the boundary along an access trail. I identified 12 different Botrychium species in the 81 georeferenced photographs (Figure 16a, Table 10). Most *Botrychium* records occurred in grasslands or coniferous forests: 35% of all occurrences were in grasslands, followed by 22% in shrublands and coniferous forests, 7% in developed sites as well as rock/talus sites, 4% in mixed forests, and 2% in broadleaf vegetation (Figure 16b, Table 10). It should be noted that 'developed' sites, based on ABMI documentation, may be overestimated based on exaggerated minimum road widths of 60 m (Castilla et al., 2014) and as such, I found that the Botrychium species found within these sites coincided with well used OHV trails or were in the vicinity of Sartoris road, an access point for OHV users entering CCWPP from Crowsnest Pass. Among the 23 records with site descriptions, most mentioned some form of disturbance, for example either being near 'roads' or 'trailside' or in 'rocky exposure', 'burned', or 'weedy' areas. Observation dates ranged from as early as June 7<sup>th</sup> to as late as August 12<sup>th</sup>. The median occurrence date was July 18th. The most frequently occurring species was *Botrychium lanceolatum* (S.G. Gmel.) Ångstr. (23 occurrences), closely followed by *B. lunaria* (L.) Sw. (22 occurrences). The least frequent species were B. pallidum W.H. Wagner, B. paradoxum, B. michiganense W.H. Wagner ex A.V. Gilman, Farrar, & Zika (2 occurrences each) and B. spathulatum W.H. Wagner (1 occurrence; Table 10). Based on the nearby species identifiable from photo records, 67 different species were noted to grow in the vicinity of Botrychium species. The most common associated species were Achillea millefolium (identified near 22 different *Botrychium* occurrences), followed by *Fragaria virginiana* 

and *Taraxacum officinale* (each identified near 21 different *Botrychium* occurrences; Table 11). One of the least frequent species, *B. pallidum* had no identifiable associated species; both occurrences appear to be in dense duff of forest understories. The single occurrence of *B. spathulatum* was also growing in dense duff near a trail and had one associate that is likely *Osmorhiza* sp., although the individual was too young to confirm. The elevation of occurrences ranged from 1,430 m to 2,245 m above sea level (a.s.l; Figure 17a). 41% of occurrences were found on east to southeast-facing slopes, as 35 occurrences had an aspect around 100 degrees (Figure 17b). The highest frequency of *Botrychium* occurrences were in areas where the slope was just above 10 degrees (Figure 17c). The highest frequencies of *Botrychium* occurrences were found greater than 10m from trails (Figure 17d).



Figure 16. The frequencies of a) moonwort species; and b) vegetation types of the 85 occurrence records. Note: 'sp.' refers to the 4 records where no photograph was available for species identification. The 'developed' vegetation type includes industrial sites and roads, although based on ABMI documentation, this category is greatly overestimated (Castilla et al., 2014).

Vegetation type Specific	Droaulear	coniterous	developed	grassland	mixed	shrubland	talus	Total
epithet	0	2	0	0	0	0	0	2
ascenaens	0	3	0	0	0	0	0	3
campestre	0	1	3	3	0	2	1	10
crenulatum	1	5	0	0	1	0	0	7
lanceolatum	0	2	0	15	0	4	2	23
lunaria	0	3	0	8	0	8	3	22
michiganense	0	0	1	1	0	0	0	2
minganense	1	4	0	0	0	0	0	5
pallidum	0	0	0	0	2	0	0	2
paradoxum	0	0	0	0	0	2	0	2
pinnatum	0	0	1	0	0	2	0	3
sp.*	0	1	0	2	0	1	0	4
spathulatum	0	0	1	0	0	0	0	1
virginianum**	0	0	0	1	0	0	0	1
Total	2	19	6	30	3	19	6	85

Table 10. Table of *Botrychium* species (rows) identified from photographed occurrences within each vegetation type (columns).

\* 'sp.' refers to the 4 records where no photograph was available for species identification.

\*\* *Botrychium virginianum* now taxonomically accepted as *Botrypus virginianus* (L.) Michx. (Hauk et al., 2003).

Table 11. Table of associated species identified in *Botrychium* photographs (n = 81) and the number of times each species was listed as an associate. Note: *Antennaria* sp. is total count of all *Antennaria* species combined as identification to species is difficult without all flowering components.

Associated Species	Count
Achillea millefolium	22
Anaphalis margaritacea	7
Antennaria sp.	8
Fragaria virginiana	21
Galium boreale	6
Medicago lupulina *	8
Packera indecora	8
Penstemon confertus	10
Symphyotrichum leave	9
Taraxacum officinale *	21

\* Indicates species exotic to Alberta.



Figure 17. Histograms showing the frequency of occurrences of *Botrychium* (n = 85) across a) elevation (m); b) aspect (degrees); c) slope (degrees); and d) the proximity (m) to any trail recognized under new usage regulations in CCWPP as of 2021.

3.4.2 SDM as a predictor for off- trail Botrychium occurrences

In total I documented 350 vascular plant species in the 24 off-trail plots surveyed between June 7<sup>th</sup> and July 22<sup>nd</sup> of 2021. I also documented 4 different species of

*Botrychium* in 7 plots ranging in elevation from 1,430 m to 2,000 m a.s.l (Table 12). *Botrychium lunaria* (common moonwort, S5), was the most often observed (3 plots), followed by *B. campestre* (prairie moonwort, S3, 2 plots). I observed *B. minganense* (Mingan moonwort, S4), and *B. pallidum* (pale moonwort, S2) each only once. The mean percent suitability of sites where *Botrychium* was present was 53.48  $\pm$  25.97 %, whereas for sites where *Botrychium* was absent, the mean percent suitability was 41.88  $\pm$  31.45 %. *B. pallidum* was unexpectedly observed at a low suitability site (habitat suitability = 8.25%). All but two of the off-trail occurrences were in shrubland vegetation. Habitat suitability according to the SDM was not a significant predictor for the presence of *Botrychium* (Table 13). The explained deviance of the model including SDM predicted suitability was only 2.7%.

Plot	Suitability	Elevation	Watershed	Vegetation	Present?	Species
	(%)	(m)				
03	2.78	1492	Middle	grassland	no	n/a
			Castle			
o4	3.45	1429	Middle	shrubland	no	n/a
			Castle			
o10	8.25	1430	Upper	mixed	yes	B. pallidum
			Castle			
o13	12.38	1374	Carbondale	coniferous	no	n/a
o18	18.56	1513	Middle	coniferous	no	n/a
			Castle			
o19	19.04	1649	West Castle	coniferous	no	n/a
o21	24.58	1773	Upper	broadleaf	no	n/a
			Castle			
o23	25.31	1492	Mill Creek	coniferous	no	n/a
o25	27.91	1703	Carbondale	coniferous	no	n/a
o31	32.54	1632	West Castle	coniferous	no	n/a
033	34.58	1745	Carbondale	coniferous	no	n/a
o37	37.07	1591	Upper	shrubland	no	n/a
			Castle			
o42	42.78	1479	Drywood	broadleaf	yes	B.minganense
			Creek			
o45	43.15	1834	Carbondale	shrubland	yes	B. campestre
o54	53.00	1612	Carbondale	shrubland	yes	B. lunaria
057	54.76	1559	West Castle	mixed	no	n/a
068	63.26	1801	Carbondale	shrubland	no	n/a
o70	64.27	2000	Drywood	shrubland	yes	B. lunaria
			Creek			
o73	71.40	1646	Upper	shrubland	no	n/a
			Crowsnest			
o82	74.53	1891	Carbondale	shrubland	yes	B. lunaria
o105	88.40	1522	Carbondale	shrubland	yes	B. campestre
o106	88.41	1844	Upper	coniferous	no	n/a
			Crowsnest			
0123	96.72	1720	Drywood	broadleaf	no	n/a
			Creek			
0126	99.19	1762	Carbondale	coniferous	no	n/a

Table 12. Characteristics of the 24 off-trail plots surveyed in the summer of 2021, in order of increasing predicted habitat suitability according to a species distribution model. Plots in bold are those in which *Botrychium* was found ('Present?').

Predictor	Coefficient	SE	AIC*	P-value**
(Intercept)	-1.53	0.90	32.199	n/a
suitability	0.01	0.02	30.975	0.379

Table 13. Predictor variables included in the model for *Botrychium* habitat suitability.

\*AIC values include all factors in the model except the one being tested. \*\* P-values refer to the significance of SDM suitability based on a drop1 test.

3.4.3 Quantifying differences in community composition of plots with and without

Botrychium

In the NMDS ordination, plots with *Botrychium* present appear less clustered together in species space compared to plots with *Botrychium* absent (Figure 18). Results of the PERMANOVA indicate that plots with *Botrychium* present do not have significantly different community composition than plots where *Botrychium* was absent (Table 14). The average dispersion of plots with *Botrychium* present was  $0.497 \pm 0.022$ , whereas for the group of plots with *Botrychium* absent it was  $0.447 \pm 0.019$ . However, results of the PERMDISP analysis indicate that the variance (dispersion) within the group (beta diversity) of plots with *Botrychium* absent (p = 0.139).



Figure 18. NMDS (non-metric multidimensional scaling) ordination of all 50 m x 50 m sites in species space. Sites are coloured based on groupings of any species of *Botrychium* present (yes; red) or absent (no; black). Ellipses indicate ordination confidence intervals (90%).

Table 14. Results of PERMANOVA pairwise tests comparing species composition in plots with *Botrychium* present and absent. F.model indicates the pseudo-*F* ratio of between group variance to within group variance.  $R^2$  refers to the proportion of variance observed in species composition for the presence/absence of *Botrychium* that is explained by the model. P-value is based on 9,999 permutational tests using the pseudo-*F* ratios.

Pairs	F.Model	<b>R</b> <sup>2</sup>	P-value
Absent vs. Present	1.53607	0.065265	0.092

The results of the ISA indicate 4 significant indicator species. One species,

Agoseris glauca (pale agoseris), was a significant indicator of plots with Botrychium.

Three species, Acer glabrum (Rocky Mountain maple), Lonicera utahensis (Utah

honeysuckle), and Maianthemum racemosum (large false Solomon's seal) were

significant indicators of plots without Botrychium (Table 15). Indicator values for all

species are tabulated in Table 2B (Appendix 2).

Table 15. Significant indicator species of plots with or without *Botrychium* according to an indicator species analysis with 9,999 permutations. Values include the relative frequency and average relative abundance of species occurring in plots with *Botrychium* absent or present as well as the group each species has maximum indicator value for *Botrychium* (Occurrence- present or absent).

Scientific Name	Relative frequency (absent)	Relative frequency (present)	Relative abundance (absent)	Relative abundance (present)	Occurrence	p- value
Agoseris glauca	0.118	0.571	0.171	0.829	present	0.029
Acer glabrum	0.588	0.143	0.908	0.092	absent	0.049
Lonicera utahensis	0.588	0	1	0	absent	0.019
Maianthemum racemosum	0.882	0.286	0.753	0.247	absent	0.019

#### 3.5 Discussion

My results show that within CCWPP - two recently established parks in an area that has been dubbed the world's centre for moonwort diversity - at least 13 of the 20 species of *Botrychium* known in Alberta (NatureServe, 2022) occur. This study contributes more occurrences than were recorded prior to 2018. *Botrychium pallidum* (S2- imperiled) for example, has only been recorded in 2 areas of the park; my study adds one more occurrence to these previous observations in addition to several more occurrences of other *Botrychium* species. Because these species are often no larger than 15 cm tall with no showy flowers, being able to find them often relies on going to areas where they have been found previously. Additionally, surveys from this study found *Botrychium* species in the central and northwest areas of the two parks where there were no previous occurrence records. This suggests that greater survey effort is needed to better understand *Botrychium* species distribution and frequency in the parks.

The habitat assessment shows that in CCWPP, most occurrences of *Botrychium* are found in grasslands. However, as a genus they do not appear to be negatively impacted by shade, as suggested by the high frequency of *Botrychium* occurrences in coniferous forests. The high number of occurrences in grasslands matches habitat descriptions of the two most common species (B. lanceolatum and B. lunaria) which are noted as being found in 'open fields' (FNA Ed. Comm., 1993). In addition, Achillea millefolium, Fragaria virginiana, and Taraxacum officinale are not only common, weedy species in open habitats such as grasslands and the among the most frequent species found near trails in CCWPP (Chapter 2), as expected, they are the three most common species associated with species of *Botrychium*. Others have similarly found *Fragaria* virginiana commonly growing alongside B. paradoxum (Zika, 1992; Vanderhorst, 1993), suggesting that these associations in open grassland sites may be linked to mycorrhizal interactions between the two plants (Vanderhorst, 1997). Although my study did not consider the variation in composition of soil biota in different vegetation types, disturbance associated with soil compaction and exotic species presence could be impacting mycorrhizae in the soil, subsequently affecting *Botrychium* species presence.

In disturbed habitats, the presence of exotic species can cause shifts in the composition of mycorrhizal communities (Hawkes et al., 2006; Jordan et al., 2012; Sielaff et al., 2019), an important factor in growth for all members of *Botrychium*. If exotic species are shifting mycorrhizal communities to more non-mycorrhizal species (Hawkes et al., 2006) or have higher colonization rates of mycorrhizal fungi than native species (Sielaff et al., 2019), then it is likely that the presence of exotic species can negatively influence *Botrychium* presence. Interactions with non-mycorrhizal fungi have

been shown to reduce plant growth in contrast to the positive effects observed in the presence of mycorrhizal fungi (Klironomos, 2002). Such effects on the composition of soil biota may be more important in rare native plants such as those belonging to *Botrychium*, which rely on mycorrhizal associations for normal plant growth. Interestingly, in CCWPP, grasslands have the highest likelihood of exotic species occurring (Chapter 2) and they have the highest number of *Botrychium* occurrences. This suggests that more common *Botrychium* species can tolerate open, disturbed habitats where exotic species are highly likely to occur. However, the prevalence of *Botrychium* relative to exotic prevalence and abundance of mycorrhizal communities present in these grasslands has yet to be studied.

Most *Botrychium* occurrences were located on south-facing slopes with a relatively flat incline, suggesting that most *Botrychium* occurrences are associated with lower soil moisture levels (Lieffers & Larkin-Lieffers, 1987). This may also be related to availability of mycorrhizal fungi. *Botrychium* sporophyte growth requires mycorrhizal associations, and a study comparing differences in north and south-facing slopes found increased arbuscular mycorrhizal species richness associated with south-facing slopes (Chai et al., 2018). I also found that most *Botrychium* occurrences were beyond the immediate vicinity of trails. In addition to impacts on vegetation (Chapter 2), soil disturbance associated with trails can impact mycorrhizal communities by decreasing diversity and changing community composition (Amalia et al., 1968). Although *Botrychium* species are often noted to be found near trails, this is likely due to bias towards occurrences being recorded only from well-travelled areas (Ingegno, 2015). Rather, it seems that in CCWPP, most *Botrychium* occurrences are away from trails, and

this may reflect their close association with mycorrhizal communities which are negatively impacted by trail presence. To obtain a better understanding of *Botrychium* distribution throughout CCWPP, more field surveys targeting *Botrychium* species should be conducted in grasslands and coniferous forests in regions away from trails and other known occurrences.

Thorough field searches for single species are costly. Therefore, finding a more efficient method of locating rare species is often sought out. SDMs have been used successfully to increase the efficiency of surveys for rare plants (Boetsch et al., 2003; Bourg et al., 2005; McCune, 2016). Our generic SDM for *Botrychium* presence was not a good predictor of *Botrychium* occurrences, likely because species belonging to the same genus often have different specific habitat requirements. However, there was evidence of a trend towards higher predicted suitability at sites where species of *Botrychium* were found. It is possible that a larger sample of plots would have shown significant results. Unexpectedly, one of the 7 sites with *Botrychium* present was predicted to have less than 10% suitability. All other sites with *Botrychium* present ranged from 43% to 88%. A larger sample size could help determine whether the unexpected occurrence is an outlier or whether *Botrychium* occur more often than expected at sites with low predicted suitability, which would confirm that the SDM was not useful in this case.

The failure of the SDM to predict *Botrychium* occurrences could be because the model was built at the generic level – not for each species. *Botrychium* species are known to occur in very different habitats. For example, of the species present in both grasslands and coniferous forests, species with more occurrences in grasslands (*B. campestre, B. lanceolatum, B. lunaria*, and *B. michiganense*) or coniferous forests (*B. ascendens, B.* 

*crenulatum*, and *B. minganense*) had lower frequencies in the other habitat, suggesting some species occur at higher rates in certain habitats. Because of this, SDMs built using occurrences from the entire genus may not accurately predict suitable habitat for rare *Botrychium* species only found in a particular habitat. For example, Johnson-Groh et al. (2002a) found that a prairie species (*B. gallicomontanum*) must overcome more risks associated with open, exposed prairies by emerging much earlier than a forest species (*B. mormo*) which is less exposed to extreme changes in temperature and moisture. Future studies should use SDMs which are species-specific rather than generic to test whether some species of *Botrychium* occur in certain habitats over others.

It is possible that the SDM could be a good indicator of suitable habitat, but survey efforts missed occurrences in some high suitability plots. Although I was able to detect occurrences in coniferous forests, later emergence rates and other barriers such as dense leaf litter (Johnson-Groh et al., 2002a) could contribute to missed occurrences of more sporadic or difficult to detect *Botrychium* species such as *B. pallidum* or *B. paradoxum* (FNA Ed. Comm., 1993) in these habitats. Wagner & Wagner (1981) note open meadows are particularly subject to similar looking or dense herbaceous cover that make it difficult to see *Botrychium* individuals. Repeating surveys at different times of the growing season would ensure true absence of *Botrychium* from plots.

It is also possible that the SDM was not a good predictor of suitable habitat because it did not include important environmental predictors. *Botrychium* require mycorrhizal associations for successful establishment and as such, soil characteristics such as soil pH and nutrient levels - that are associated with mycorrhizal communities may be necessary to accurately predict *Botrychium* occurrences (Lilleskov & Parrent,
2007). In addition to topography, climate, geology, and soil factors, the landscape context may also be playing a role in accurately predicting suitable habitat. For example, in testing SDMs for 8 rare species in Ontario, McCune (2016) found that proximity to the nearest known occurrence of a rare species also influenced the likelihood of finding a new occurrence, in addition to predicted habitat suitability. One other study has used SDMs to predict habitat for *Botrychium* (Ingengo, 2015). In this study, elevation, aspect, slope, soils, geology, mean May precipitation, mean June temperature, and land cover were the predictor variables, however, the predictions of this SDM were not tested with independent surveys (Ingengo, 2015). SDMs predicting suitable habitat for *Botrychium* in Alberta should be re-built, provided data are available regarding these other potential predictors.

I did not find any significant differences in the plant community composition within 50 m x 50 m plots with versus without detections of *Botrychium*. In contrast, McCune (2016) found that regardless of the breadth of habitat for a target species, sites where the target species was found were more clustered in terms of plant community composition compared to all other suitable plots. This again could be due to lumping all *Botrychium* species together. The different *Botrychium* species we surveyed have different habitat preferences, and members of the genus occupy a diverse range of plant communities even within the same vegetation type. Although *Botrychium* as a genus was not found to be limited to a restricted subset of plant communities, more records of individual species may produce results that support specific plant community associations for individual species.

Although community composition did not differ significantly between sites with and without Botrychium present, there were significant indicator species of Botrychium presence or absence. The indicator species of *Botrychium* absent sites were *Lonicera* utahensis S.Watson (Rocky Mountain honeysuckle, S3), Maianthemum racemosum (L.) Link (Solomon's plume, S5), and *Acer glabrum* Torr. (Rocky Mountain maple, S3) which are characteristic species of shaded, often shrubby habitats of mixed or broadleaf forest understories (FNA Ed. Comm., 1993). This aligns with the assessment of the vegetation types of the 85 georeferenced occurrences of *Botrychium*: a total of only 4% of those records occurred in mixed and broadleaf forests, the fewest of any vegetation type. Agoseris glauca (Pursh) Raf. (Pale agoseris, S5) was significantly more frequent and abundant in the seven plots with Botrychium present. Agoseris glauca is a perennial species that produces a rosette of pubescent basal, pale green leaves from a thick taproot and a single showy, yellow flower at the tips of flowering stems (FNA Ed. Comm., 1993) making it much more conspicuous than *Botrychium*. Interestingly, *Agoseris glauca* was not noted as an associated species for any of the 81 photo records, or for any documented occurrences of *Botrychium* deposited at the University of Lethbridge (LEA) herbarium. This could be attributed to the fact that associated species in photographs were limited to the direct vicinity of the specimen, whereas the ISA considered a much larger 50 m x 50 m area. Agoseris glauca and Botrychium lunaria have been described together in plant communities in Alberta's northern Rocky Mountains (Russel & Roi, 1986), and they both occur in similar vegetation types—including moist to dry habitats, alpine meadows, montane forests, as well as gravelly or rocky soils-and elevation ranges (FNA Ed. Comm., 1993). Although both species are found in a wide variety of habitats, the more

conspicuous flowers of *Agoseris glauca* could be useful in pinpointing sites where smaller *Botrychium* plants are also found.

The habitats of *Botrychium* in CCWPP range from disturbed sites such as rocky talus or sites near roads and trails to coniferous forests, with grasslands being the most frequent vegetation type. Botrychium species are known to occur in very diverse habitats (Wagner & Wagner, 1981; FNA Ed. Comm., 1993; Williston, 2002). Of all the species identified from the 85 CCWPP records, Botrychium lanceolatum was the most common species, and it also occurred most frequently in grasslands. Although I expected to see more Botrychium directly beside trails compared to areas distant from trails, most occurrences (22) of moonwort recorded in CCWPP are found greater than 10 m but less than 100 m from trails, and there were 21 occurrences more than 1,000 m away from the nearest trail, which does not provide evidence that Botrychium species prefer disturbed habitats directly beside trails (less than 10 m) compared to off-trail habitats. The tendency for Botrychium to occur at least 10 m from trails follows what Amalia et al. (1968) found regarding negative trail impacts on mycorrhizal communities. Especially given the fact that *Botrychium* require mycorrhizal interactions to complete their life cycle (Rayner, 1927; Whittier, 1973; Winther & Friedman, 2007), abiotic or biotic factors affecting the mycorrhizae microbiome could influence the success of the host *Botrychium* species (Sandoz et al., 2020). Although my assessment of the georeferenced photos indicates that Botrychium was not very frequent beside recreational trails, they nonetheless were found near other linear disturbances such as deer trails and scree slopes. To maximize efficiency, surveys to find new occurrences of *Botrychium* should target grassland and

coniferous forest communities away from trails, particularly in the Middle and West Castle watersheds – where no occurrences have been recorded prior to this project.

## **3.6 Conclusion**

Altogether, these results indicate that *Botrychium* is relatively frequent throughout CCWPP. Although *Botrychium* species are often associated with trails, they also occur frequently away from trails. Surveys for additional Botrychium occurrences should focus on grassland and coniferous forests away from trails at elevations around 1,800 m a.s.l, along more southerly slopes, and avoid shaded mixed or broadleaf forest sites. Areas with Agoseris glauca may also be a good indicator of *Botrychium* habitat. Additionally, more extensive surveys should be conducted in areas where my study has uncovered new occurrences not previously recorded, including the Middle Castle River and West Castle River watersheds. Areas which have been under-surveyed that could also prove insightful in terms of Botrychium occurrences include the Mill Creek and Upper (South) Castle River watersheds, where no occurrences have been recorded in the parks. Although our SDM was not a great predictor of *Botrychium* at the genus level, new occurrences from this project provide better representation of *Botrychium* species distribution throughout CCWPP. These data could be used to build species-level SDMs to predict habitat suitability for individual species, allowing targeted searches for species that are thought to be rare.

### **CHAPTER 4: CONCLUSION**

As more people visit protected areas for recreation, understanding the impacts that trail users have on the plant communities is vital for maintaining sustainable use of recreational trails. In parks that have been recently established such as CCWPP, assessing trail impacts within different vegetation types and along different trail types could help mitigate unwanted changes to the native plant communities, especially at higher elevations. My study shows that the effects of recreational trails have already impacted grasslands in this region and shrublands and mixed/broadleaf vegetation are showing trends that may lead to similarly greater impacts over time. Although coniferous forests do not seem to be impacted by exotic species, this vegetation type could see similar trends in the future as more people visit the parks. Additionally, relative to footpaths, OHV trails were found to impact not only the number of species present, but the likelihood of exotic species presence, an effect that was also found at higher elevations. Barros et al. (2020) indicated exotic species favoured by off-trail disturbances can negatively impact alpine vegetation, calling for limited off-trail use at higher elevations. My results have important implications for CCWPP. In particular, the number of OHV trails (and roads) should be reduced, particularly through shrubland and mixed/broadleaf vegetation. Additionally, although it may not be feasible to close OHV trails at higher elevations, my results suggest that implementing tactics to reduce the spread of exotic species and limiting the amount of OHV traffic that reaches higher elevations is key to sustainable trail use within montane parks.

CCWPP is a hotspot for rare plants in Alberta, especially *Botrychium*. Prior to the recent floral inventory project and my present research, the distribution and habitat

preferences of *Botrychium* in CCWPP were poorly understood. My study shows that *Botrychium* is not limited to trailside vegetation as was previously assumed. *Botrychim* occur in many areas nowhere near trails, in various vegetation types—grasslands and coniferous forests in particular—and across a wide elevational range. Surveys should be conducted in areas where I found new occurrences, as well as areas which are currently still under-surveyed. The small stature and cryptic presence of these species make searches difficult and time consuming. More common species such as *Agoseris glauca* may be a good indicator of *Botrychium* habitat which could be used to improve the efficiency of field searches for these tiny ferns. Additionally, SDMs built for individual *Botrychium* species may prove useful in targeting specific species distributions throughout the parks. As suggested by my results of the likelihood of rare species presence (Chapter 2), park management should limit the amount of disturbance associated with trails to promote the presence of rare species such as *Botrychium*.

### 4.1 Limitations and future directions

My study has some limitations. In Chapter 2, I categorized trail types based on trail widths alone and used soil compaction as a proxy for trailside disturbance. As a result of the new Trails Act recently put in place by the government of Alberta (Government of Alberta, 2022), updated trail use maps have been constructed for the Castle region, which may not reflect the trail types I categorized as 'OHV trail'. Although the measures I used are likely accurate indicators of trail use intensity over the past few decades, future studies should assess these trail types accordingly to determine their impact on plant communities and provide further insight into the sustainability of current trail use in CCWPP.

Measures of trail use intensity were also not available for my study. Although the government of Alberta has attempted to capture visitor rates of most provincial parks, data are either unavailable or incomplete for some parks (Alberta Tourism, 2006) including Castle Provincial and Castle Wildland Provincial Parks. Future studies could additionally use camera traps or trail counters to measure actual trail use intensity of different trails. Some studies have used such methods to monitor and quantify wildlife and human-based activities along trails (Kays et al., 2009; Miller et al., 2017; Abildso et al., 2021). Similar approaches could be used in CCWPP which already utilizes camera traps for wildlife monitoring.

In Chapter 3, the sample size of off-trail *Botrychium* surveys was limited to 24 plots. Provided more time and resources, surveying more plots could provide a more precise indication of the utility of the SDM used. In addition, the SDM used in this study was built at the generic level, which may not reflect specific habitat preferences for all *Botrychium* species. Additional occurrence records from my study could be used to develop species-level analyses to improve our understanding of specific *Botrychium* species and their distributions throughout CCWPP.

#### **4.2 Concluding Statement**

Dozens of studies have investigated the impacts of recreations trails on plant communities throughout the world. However, very few have been carried out in Canada's Rocky Mountain Parks, where the number of visitors and recreational trail use is continuing to increase. I showed that the effect of trails on plant communities varies with different vegetation types and different trail types. I also showed that the presence of some rare species like *Botrychium* are more prevalent than previously recorded. More

studies of recreational trail impacts on plant communities and more field surveys of species whose distribution is poorly understood are needed, especially in southern Alberta's Rocky Mountains.

## REFERENCES

Abildso, C. G., V. Haas, S. M. Daily, and T. K. Bias. 2021. Field Test of a Passive Infrared Camera for Measuring Trail-Based Physical Activity. Frontiers in Public Health **9**:584740.

Ahern, R. G., D. A. Landis, A. A. Reznicek, and D. W. Schemske. 2010. Spread of exotic plants in the landscape: the role of time, growth habit, and history of invasiveness. Biological Invasions **12**:3157-3169.

Alberta Biodiversity Monitoring Institute (ABMI). [website]. Climate Data for Alberta. Accessed: August 31, 2022. https://www.abmi.ca/home/data-analytics/da-top/da-productoverview/Other-Geospatial-Land-Surface-Data/Climate-Variables.html

Alberta Biodiversity Monitoring Institute (ABMI). 2014. Alberta W2W Normalized Difference Vegetation Index (NDVI). Alberta Biodiversity Monitoring Institute, Edmonton, Alberta.

Alberta Environment and Parks. 2018. Castle Management Plan: Castle Provincial Park and Castle Wildland Provincial Park. Alberta Environment and Parks, Edmonton.

Alberta Parks. [website]. Park Research & Management 2020. Accessed: March 28, 2022. <u>https://www.albertaparks.ca/parks/south/castle-pp/park-research-management/</u>

Alberta Wilderness Association. [website]. Castle. Accessed: March 28, 2022. <u>https://albertawilderness.ca/issues/wildlands/areas-of-</u> concern/castle/#parentHorizontalTab4

Amalia, A., N. Dewi, A. Heriyanti, F. Daeni, and R. Atunnisa. 2021. A review on arbuscular mycorrhizal fungal communities in response to disturbance. Page 012001 *in* Journal of Physics: Conference Series. IOP Publishing.

Averett, J. P., B. McCune, C. G. Parks, B. J. Naylor, T. DelCurto, and R. Mata-Gonzalez. 2016. Non-native plant invasion along elevation and canopy closure gradients in a middle Rocky Mountain ecosystem. PloS one **11**:e0147826.

Avon, C., L. Bergès, Y. Dumas, and J.-L. Dupouey. 2010. Does the effect of forest roads extend a few meters or more into the adjacent forest? A study on understory plant diversity in managed oak stands. Forest Ecology and Management **259**:1546-1555.

Ballantyne, M., and C. M. Pickering. 2015. The impacts of trail infrastructure on vegetation and soils: Current literature and future directions. J Environ Manage **164**:53-64.

Barros, A., and C. M. Pickering. 2014. Non-native plant invasion in relation to tourism use of Aconcagua Park, Argentina, the highest protected area in the Southern Hemisphere. Mountain Research and Development **34**:13-26.

Barros, A., V. Aschero, A. Mazzolari, L. A. Cavieres, and C. M. Pickering. 2020. Going off trails: How dispersed visitor use affects alpine vegetation. J Environ Manage **267**:110546.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software **67**:1 - 48.

Bates, G. H. 1935. The Vegetation of Footpaths, Sidewalks, Cart-Tracks and Gateways. Journal of Ecology **23**:470-487.

Becker, T., H. Dietz, R. Billeter, H. Buschmann, and P. J. Edwards. 2005. Altitudinal distribution of alien plant species in the Swiss Alps. Perspectives in Plant Ecology, Evolution and Systematics **7**:173-183.

Bellefontaine, M. August 4, 2019. *Government puts hold on Castle Parks trail closure plan*. Retrieved from: <u>https://www.cbc.ca/news/canada/edmonton/government-puts-hold-on-castle-parks-trail-closure-plan-1.5234811</u>

Benn, B., and S. Herrero. 2002. Grizzly bear mortality and human access in Banff and Yoho National Parks, 1971-98. Ursus:213-221.

Benninger-Truax, M., J. L. Vankat, and R. L. Schaefer. 1992. Trail corridors as habitat and conduits for movement of plant species in Rocky Mountain National Park, Colorado, USA. Landscape ecology **6**:269-278.

Bjørnstad, O. N., and W. Falck. 2001. Nonparametric spatial covariance functions: estimation and testing. Environmental and Ecological Statistics **8**:53-70.

Boetsch, J. R., F. K. Van Manen, and J. D. Clark. 2003. Predicting Rare Plant Occurrence in Great Smoky Mountains National Park, USA. Natural Areas Journal **23**:229-237.

Bourg, N. A., W. J. McShea, and D. E. Gill. 2005. Putting a CART before the search: successful habitat prediction for a rare forest herb. Ecology **86**:2793-2804.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs **27**:326-349.

Breheny, P., and W. Burchett. 2017. Visualization of regression models using visreg. R J. **9**:56.

Brouillet, L., F. Coursol, S.J. Meades, M. Favreau, M. Anions, P. Bélisle & P. Desmet. 2010+. VASCAN, the Database of Vascular Plants of Canada. http://data.canadensys.net/vascan/(consulted on 2022-03-15)

Castilla, G., J. Hird, R. J. Hall, J. Schieck, and G. J. McDermid. 2014. Completion and updating of a landsat-based land cover polygon layer for Alberta, Canada. Canadian Journal of Remote Sensing **40**:92-109.

Castle- Crown Wilderness Coalition. [website]. History of the Castle. Accessed: March 28, 2022. http://ccwc.ab.ca/the-castle/history/

Castro, S. A., J. A. Figueroa, M. Muñoz-Schick, and F. M. Jaksic. 2005. Minimum residence time, biogeographical origin, and life cycle as determinants of the geographical extent of naturalized plants in continental Chile. Diversity and Distributions **11**:183-191.

Catling, P. M., and B. Kostiuk. 2011. Some Wild Canadian Orchids Benefit from Woodland Hiking Trails – and the Implications.

Chai, Y., S. Jiang, W. Guo, M. Qin, J. Pan, A. Bahadur, G. Shi, J. Luo, Z. Jin, Y. Liu, Q. Zhang, L. An, and H. Feng. 2018. The effect of slope aspect on the phylogenetic structure of arbuscular mycorrhizal fungal communities in an alpine ecosystem. Soil Biology and Biochemistry **126**:103-113.

Cole, D. N. 1978. Estimating the Susceptibility of Wildland Vegetation to Trailside Alteration. The Journal of applied ecology **15**:281-286.

Connell, J. H. 1978. Diversity in Tropical Rain Forests and Coral Reefs. Science (American Association for the Advancement of Science) **199**:1302-1310.

Crisfield, V. E., S. E. Macdonald, and A. J. Gould. 2012. Effects of Recreational Traffic on Alpine Plant Communities in the Northern Canadian Rockies. Arctic, Antarctic, and Alpine Research **44**:277-287.

Ciuti, S., J. M. Northrup, T. B. Muhly, S. Simi, M. Musiani, J. A. Pitt, and M. S. Boyce. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. PloS one 7:e50611.

Dauphin, B., D. R.Farrar, A. Maccagni, and J. R. Grant. 2017. A Worldwide Molecular Phylogeny Provides New Insight on Cryptic Diversity Within the Moonworts (Botrychium s. s., Ophioglossaceae). Systematic Botany **42**:620-639.

Dauphin, B., J. Vieu, and J. R. Grant. 2014. Molecular phylogenetics supports widespread cryptic species in moonworts (Botrychium ss, Ophioglossaceae). American Journal of Botany **101**:128-140.

Davis, A. K. 2007. Walking trails in a nature preserve alter terrestrial salamander distributions. Natural Areas Journal **27**:385-389.

Debarbieux, B., M. Varacca, and G. Rudaz. 2014. Challenges and opportunities for tourism development in mountain regions. Tourism in Mountain Regions. Department of Geography and Environment. University of Geneva Search in.

Dickens, S. J. M., F. Gerhardt, and S. K. Collinge. 2005. Recreational Portage Trails as Corridors Facilitating Non-Native Plant Invasions of the Boundary Waters Canoe Area Wilderness (USA). Conservation Biology **19**:1653-1657.

Doherty, J. 2012. American conservation and the expansion of Waterton Lakes Park 1910-1914. Alberta History **60**:17+.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological monographs **67**:345-366.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17:43-57.

Faber-Langendoen, D., J. Nichols, L. Master, K. Snow, A. Tomaino, R. Bittman, G. Hammerson, B. Heidel, L. Ramsay, and A. Teucher. 2012. NatureServe conservation status assessments: methodology for assigning ranks. NatureServe, Arlington, VA.

Farr, D., A. Braid, A. Janz, B. Sarchuk, S. Slater, A. Sztaba, D. Barrett, G. Stenhouse, A. Morehouse, and M. Wheatley. 2017. Ecological Response to Human Activities in Southwestern Alberta: Scientific Assessment and Synthesis. Government of Alberta.

Farrar, D. 2011. Systematics and taxonomy of genus Botrychium. Website [accessed 15 December 2011] http://www.public.iastate.edu/~herbarium/botrychium/Moonwort-Systematics.pdf.

Flora of North America Editorial Committee. 1993. Botrychium. In: Flora of North America North of Mexico [Online]. **2**: Pteridophytes and Gymnosperms. Oxford University Press on Demand. <u>Botrychium in Flora of North America @ efloras.org</u> (consulted on 2022-04-13).

Foster, J. 1998. Working for Wildlife: The Beginning of Preservation in Canada. University of Toronto Press.

Fryer, G. L., Jane; Ottenbreit, Kimberly; Metke, Christina; Cherniawsky, Donna; Griffiths, Amy; Foreman, Kristen; Mischkolz, Jenalee. 2022. Rare vascular plants of Alberta, 2nd Edition. 2 edition. The Alberta Native Plant Council, Edmonton, Alberta.

GBIF. 2022. GBIF Occurrence Download- *Poa pratensis* L. GBIF.org, <u>https://doi.org/10.15468/dl.acg54n</u>.

GBIF. 2022. GBIF Occurrence Download- *Phleum pratense* L. GBIF.org, <u>https://doi.org/10.15468/dl.p343t6</u>.

GBIF. 2022. GBIF Occurrence Download- *Taraxacum officinale* Weber ex Wiggins. GBIF.org, <u>https://doi.org/10.15468/dl.7mgygy</u>.

Gelman, A., Y.-S. Su, M. Yajima, J. Hill, M. G. Pittau, J. Kerman, T. Zheng, V. Dorie, and M. Y.-S. Su. 2013. Package 'arm'. Data Analysis Using Regression and Multilevel/Hierarchical Models.

Gibson, D. J., E. D. Adams, J. S. Ely, D. J. Gustafson, D. McEwen, and T. R. Evans. 2000. Eighteen years of herbaceous layer recovery of a recreation area in a mesic forest. Journal of the Torrey Botanical Society:230-239.

Gilbert, B., and M. J. Lechowicz. 2005. Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. Ecology **86**:1848-1855.

Gilman, A. V., and V. Marshfield. 2003. Botrychium lunaria (L.) Sw. Moonwort. Conservation and Research Plan for New England. Approved, Regional Advisory Council:19.

Godefroid, S., and N. Koedam. 2004. The impact of forest paths upon adjacent vegetation: effects of the path surfacing material on the species composition and soil compaction. Biological conservation **119**:405-419.

Gogol-Prokurat, M. 2011. Predicting habitat suitability for rare plants at local spatial scales using a species distribution model. Ecological Applications **21**:33-47.

Gower, S. T. 2008. Are horses responsible for introducing non-native plants along forest trails in the eastern United States? Forest Ecology and Management **256**:997-1003.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological modelling **135**:147-186.

Harris, C. J., B. R. Murray, G. C. Hose, and M. A. Hamilton. 2007. Introduction history and invasion success in exotic vines introduced to Australia. Diversity and Distributions **13**:467-475.

Hartig, F., and M. F. Hartig. 2017. Package 'DHARMa'. R package.

Hauk, W. D. 1995. A molecular assessment of relationships among cryptic species of Botrychium subgenus Botrychium (Ophioglossaceae). American Fern Journal:375-394.

Hauk, W. D., C. R. Parks, and M. W. Chase. 2003. Phylogenetic studies of Ophioglossaceae: evidence from rbcL and trnL-F plastid DNA sequences and morphology. Molecular phylogenetics and evolution **28**:131-151.

Hauk, W. D., L. Kennedy, and H. M. Hawke. 2012. A phylogenetic investigation of Botrychium ss (Ophioglossaceae): evidence from three plastid DNA sequence datasets. Systematic Botany **37**:320-330.

Hawkes, C. V., J. Belnap, C. D'Antonio, and M. K. Firestone. 2006. Arbuscular Mycorrhizal Assemblages in Native Plant Roots Change in the Presence of Invasive Exotic Grasses. Plant and Soil **281**:369-380.

Hochrein, H. 2008. Corridors and plant invasions: a comparative study of the role of roadsides and hiking trails on plant invasions in Moorea, French Polynesia.

Hurd, E. G., N. L. Shaw, J. Mastrogiuseppe, L. C. Smithman, and S. Goodrich. 1998. Field guide to Intermountain sedges. Gen. Tech. Rep. RMRS-GTR-10. Ogden, UT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 282 p. **10**.

Ingegno, A. 2015. Acknowledging Sampling Bias in Species Distribution Modelling: Predicting Botrychium sp. Habitat in Lincoln County, Montana.

Johnson-Groh, C. L., and J. M. Lee. 2002a. Phenology and demography of two species of Botrychium (Ophioglossaceae). American Journal of Botany **89**:1624-1633.

Johnson-Groh, C., C. Riedel, L. Schoessler, and K. Skogen. 2002b. Belowground distribution and abundance of Botrychium gametophytes and juvenile sporophytes. American Fern Journal **92**:80-92.

Kasworm, W. F., and T. L. Manley. 1990. Road and trail influences on grizzly bears and black bears in northwest Montana. Bears: Their Biology and Management:79-84.

Kays, R., B. Kranstauber, P. Jansen, C. Carbone, M. Rowcliffe, T. Fountain, and S. Tilak. 2009. Camera traps as sensor networks for monitoring animal communities. Pages 811-818 *in* 2009 IEEE 34th Conference on Local Computer Networks. IEEE.

Kelly, C. L., C. M. Pickering, and R. C. Buckley. 2003. Impacts of tourism on threatened plant taxa and communities in Australia. Ecological management & restoration 4:37-44.

Kershaw, L. J., and L. Allen. 2020. Vascular flora of Alberta: an illustrated guide. Linda Kershaw and Lorna Allen.

Kershaw, R. 2008. Exploring the Castle: discovering the backbone of the world in southern Alberta. Rocky Mountain Books, Surrey, B.C.

Kerbiriou, C., I. Leviol, F. Jiguet, and R. Julliard. 2008. The impact of human frequentation on coastal vegetation in a biosphere reserve. Journal of environmental management **88**:715-728.

Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature **417**:67-70.

Kuijt, J. 1982. A flora of Waterton Lakes National Park. University of Alberta Press, Edmonton.

Lake, J. C., and M. R. Leishman. 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. Biological conservation **117**:215-226.

Lee, P., and M. Hanneman. 2011. Castle Area Forest Land Use Zone (Alberta)–Linear disturbances, access densities, and grizzly bear habitat security areas. Edmonton, Alberta: Global Forest Watch Canada 1st Publication for International Year of Forests:5-6.

Lenth, R., H. Singmann, J. Love, P. Buerkner, and M. Herve. 2019. Estimated marginal means, aka least-squares means. R package version 1.3. 2.

Lesica, P., and K. Ahlenslager. 1996. Demography and life history of three sympatric species of Botrychium subg. Botrychium in Waterton Lakes National Park, Alberta. Canadian Journal of Botany **74**:538-543.

Liedtke, R., A. Barros, F. Essl, J. J. Lembrechts, R. E. M. Wedegärtner, A. Pauchard, and S. Dullinger. 2020. Hiking trails as conduits for the spread of non-native species in mountain areas. Biological Invasions **22**:1121-1134.

Lieffers, V. J., and P. Larkin-Lieffers. 1987. Slope, aspect, and slope position as factors controlling grassland communities in the coulees of the Oldman River, Alberta. Canadian Journal of Botany **65**:1371-1378.

Lilleskov, E. A., and J. L. Parrent. 2007. Can We Develop General Predictive Models of Mycorrhizal Fungal Community-Environment Relationships? The New Phytologist **174**:250-256.

Lloren, J. I. 2021. Quantifying plant community change at Waterton Lakes National Park over the past 25 years. University of Lethbridge (Canada).

Lomolino, M. V. 2001. Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography **10**:3-13.

Magnusson, A., H. Skaug, A. Nielsen, C. Berg, K. Kristensen, M. Maechler, K. van Bentham, B. Bolker, M. Brooks, and M. M. Brooks. 2017. Package 'glmmtmb'. R Package Version 0.2. 0.

Marion, J. L., Y.-F. Leung, H. Eagleston, and K. Burroughs. 2016. A Review and Synthesis of Recreation Ecology Research Findings on Visitor Impacts to Wilderness and Protected Natural Areas. Journal of Forestry **114**:352-362.

McCune, B., and J. Grace. 2002. Indicator species analysis. Analysis of ecological communities:198-204.

McCune, J. 2016. Species distribution models predict rare species occurrences despite significant effects of landscape context. Journal of Applied Ecology **53**:1871-1879.

Medvecká, J., M. Zaliberová, J. Májeková, D. Senko, and I. Jarolímek. 2018. Role of infrastructure and other environmental factors affecting the distribution of alien plants in the Tatra Mts. Folia Geobotanica **53**:349-364.

Miller, A. B., Y.F. Leung, and R. Kays. 2017. Coupling visitor and wildlife monitoring in protected areas using camera traps. Journal of outdoor recreation and tourism **17**:44-53.

Miller, S. G., R. L. Knight, and C. K. Miller. 1998. Influence of recreational trails on breeding bird communities. Ecological Applications **8**:162-169.

Morse, L. E., J. M. Randall, N. Benton, R. Hiebert, and S. Lu. 2004. An invasive species assessment protocol: Evaluating non-native plants for their impact on biodiversity, Version 1.

Moss, E. H., and J. G. Packer. 1983. Flora of Alberta: a manual of flowering plants, conifers, ferns and fern allies found growing without cultivation in the province of Alberta, Canada. 2nd edition. University of Toronto Press, Toronto.

Mount, A., and C. M. Pickering. 2009. Testing the capacity of clothing to act as a vector for non-native seed in protected areas. Journal of environmental management **91**:168-179.

Müllerová, J., M. Vítková, and O. Vítek. 2011. The impacts of road and walking trails upon adjacent vegetation: Effects of road building materials on species composition in a nutrient poor environment. Science of The Total Environment **409**:3839-3849.

Natural Regions Committee. 2006. Natural regions and subregions of Alberta. Compiled by D.J. Downing and W.W. Pettepiece. Government of Alberta, Edmonton, Alberta

NatureServe. 2022. NatureServe Explorer [Microsoft Edge]. NatureServe, Arlington, Virginia. Available https://explorer.natureserve.org/. (Accessed: February 4, 2022).

Naylor, L. M., M. J. Wisdom, and R. G. Anthony. 2009. Behavioral responses of North American elk to recreational activity. The Journal of Wildlife Management **73**:328-338.

Nepal, S. K., and P. Way. 2007. Comparison of vegetation conditions along two backcountry trails in Mount Robson Provincial Park, British Columbia (Canada). J Environ Manage **82**:240-249.

Ngugi, M. R., V. J. Neldner, and R. Dowling. 2014. Non-native plant species richness adjacent to a horse trail network in seven National Parks in southeast Queensland, Australia. Australasian Journal of Environmental Management **21**:413-428.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.M., Szoecs, E., and Wagner, H. 2020. vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Parendes, L. A., and J. A. Jones. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the HJ Andrews Experimental Forest, Oregon. Conservation Biology **14**:64-75.

Parikesit, P., D. W. Larson, and U. Matthes-Sears. 1995. Impacts of trails on cliff-edge forest structure. Canadian Journal of Botany **73**:943-953.

Paton, D. G., S. Ciuti, M. Quinn, and M. S. Boyce. 2017. Hunting exacerbates the response to human disturbance in large herbivores while migrating through a road network. Ecosphere **8**:e01841.

Pauchard, A., C. Kueffer, H. Dietz, C. C. Daehler, J. Alexander, P. J. Edwards, J. R. Arévalo, L. A. Cavieres, A. Guisan, and S. Haider. 2009. Ain't no mountain high enough: plant invasions reaching new elevations. Frontiers in Ecology and the Environment **7**:479-486.

Peck, J. H., C. J. Peck, and D. R. Farrar. 1990. Influences of life history attributes on formation of local and distant fern populations. American Fern Journal **80**:126-142.

Phillips, M. L., B. R. Murray, M. R. Leishman, and R. Ingram. 2010. The naturalization to invasion transition: Are there introduction-history correlates of invasiveness in exotic plants of Australia? Austral ecology **35**:695-703.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological modelling **190**:231-259.

Pickering, C., and A. Mount. 2010. Do tourists disperse weed seed? A global review of unintentional human-mediated terrestrial seed dispersal on clothing, vehicles and horses. Journal of Sustainable Tourism **18**:239-256.

Pickering, C., and P. Norman. 2017. Comparing impacts between formal and informal recreational trails. J Environ Manage **193**:270-279.

Powell, J. 1966. Distribution and outbreaks of Dendroctonus ponderosae in forests of Western Canada. Information Report AX-2, Forestry Research Laboratory, Canadian Department of Forestry, Calgary, Alberta.

Proctor, M. F., B. N. McLellan, G. B. Stenhouse, G. Mowat, C. T. Lamb, and M. S. Boyce. 2020. Effects of roads and motorized human access on grizzly bear populations in British Columbia and Alberta, Canada. Ursus **2019**:16-39.

Rayner, M. C. 1927. Mycorrhiza (continued). The New Phytologist 26:22-45.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <u>https://www.R-project.org/</u>.

Roberts, D. 2019. labdsv 2.0-1: ordination and multivariate analysis for ecology.

Robertson, C., T. A. Nelson, D. E. Jelinski, M. A. Wulder, and B. Boots. 2009. Spatialtemporal analysis of species range expansion: the case of the mountain pine beetle, Dendroctonus ponderosae. Journal of biogeography **36**:1446-1458.

Rogala, J. K., M. Hebblewhite, J. Whittington, C. A. White, J. Coleshill, and M. Musiani. 2011. Human activity differentially redistributes large mammals in the Canadian Rockies National Parks. Ecology and Society **16**.

Rossi, G., G. Parolo, and T. Ulian. 2009. Human trampling as a threat factor for the conservation of peripheral plant populations. Plant Biosystems **143**:104-113.

Sandoz, F. A., S. Bindschedler, B. Dauphin, L. Farinelli, J. R. Grant, and V. Hervé. 2020. Biotic and abiotic factors shape arbuscular mycorrhizal fungal communities associated with the roots of the widespread fern Botrychium lunaria (Ophioglossaceae). Environmental Microbiology Reports **12**:342-354.

Scherrer, P., and C. M. Pickering. 2006. Recovery of Alpine Herbfield on a Closed Walking Track in the Kosciuszko Alpine Zone, Australia. Arctic, Antarctic, and Alpine Research **38**:239-248.

Sielaff, A. C., H. W. Polley, A. Fuentes-Ramirez, K. Hofmockel, and B. J. Wilsey. 2019. Mycorrhizal colonization and its relationship with plant performance differs between exotic and native grassland plant species. Biological Invasions **21**:1981-1991. Smith, G. R., A. C. Burger, B. W. Marlowe, E. P. Tristano, and J. E. Rettig. 2017. Effect of recreational trail traffic level on eastern red-backed salamander (*Plethodon cinereus*) relative abundance. Journal of North American Herpetology:1-4.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic Plant Species Invade Hot Spots of Native Plant Diversity. Ecological Monographs **69**:25-46.

Sumanapala, and Wolf. 2019. Recreational Ecology: A Review of Research and Gap Analysis. Environments **6**.

Taylor, B. R., and S. Raney. 2013. Correlation Between ATV Tracks and Density of a Rare Plant (Drosera filiformis) in a Nova Scotia Bog. Rhodora **115**:158-169.

Taylor, K., T. Brummer, M. L. Taper, A. Wing, and L. J. Rew. 2012. Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. Diversity and Distributions **18**:942-951.

Taylor, S. W., A. L. Carroll, R. I. Alfaro, and L. Safranyik. 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. The mountain pine beetle: A synthesis of biology, management, and impacts on lodgepole pine:67-94.

Thompson, B. 2015. Recreational trails reduce the density of ground-dwelling birds in protected areas. Environmental Management **55**:1181-1190.

Thurston, E., and R. J. Reader. 2001. Impacts of experimentally applied mountain biking and hiking on vegetation and soil of a deciduous forest. Environmental Management **27**:397-409.

Törn, A., A. Tolvanen, Y. Norokorpi, R. Tervo, and P. Siikamäki. 2009. Comparing the impacts of hiking, skiing and horse riding on trail and vegetation in different types of forest. Journal of environmental management **90**:1427-1434.

Trip, N. v. V., and Y. F. Wiersma. 2015. A Comparison of All-Terrain Vehicle (ATV) Trail Impacts on Boreal Habitats Across Scales. Natural Areas Journal **35**:266-278, 213.

Tyser, R. W., and C. A. Worley. 1992. Alien Flora in Grasslands Adjacent to Road and Trail Corridors in Glacier National Park, Montana (U.S.A.). Conservation Biology **6**:253-262.

Vanderhorst, J. P. 1997. Conservation Assessment of Sensitive Moonworts (Ophioglossaceae; Botrychium Subgenus Botrychium) on the Kootenai National Forest. Montana Natural Heritage Program.

Vetaas, O. R., and J. A. Grytnes. 2002. Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. Global Ecology and Biogeography **11**:291-301.

von der Lippe, M., and I. Kowarik. 2007. Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conserv Biol **21**:986-996.

Wagner, W., and F. S. Wagner. 1981. New species of moonworts, Botrychium subg. Botrychium (Ophioglossaceae), from North America. American Fern Journal **71**:20-30.

Wagner, W., and F. S. Wagner. 1983. Two moonworts of the Rocky Mountains; Botrychium hesperium and a new species formerly confused with it. American Fern Journal **73**:53-62.

Wagner, W., and F. S. Wagner. 1994. Another widely disjunct, rare and local North American moonwort (Ophioglossaceae: Botrychium subg. Botrychium). American Fern Journal **84**:5-10.

Watkins, R. Z., J. Chen, J. Pickens, and K. D. Brosofske. 2003. Effects of forest roads on understory plants in a managed hardwood landscape. Conservation Biology **17**:411-419.

Webb, R. H., H. C. Ragland, W. H. Godwin, and O. Jenkins. 1978. Environmental effects of soil property changes with off-road vehicle use. Environmental Management **2**:219-233.

Wells, F. H., Lauenroth, William K., Bradford, John B. 2013. Recreational trails as corridors for alien plants in the Rocky Mountains, USA. Western North American Naturalist **72**.

Whittier, D.P. 1973. The effect of light and other factors on spore germination in *Botrychium dissectum*. Can. J. Bot. **51**: 1791-1794.

Whittington, J., C. C. St. Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications **15**:543-553.

Williams, J. N., C. Seo, J. Thorne, J. K. Nelson, S. Erwin, J. M. O'Brien, and M. W. Schwartz. 2009. Using species distribution models to predict new occurrences for rare plants. Diversity and Distributions **15**:565-576.

Williston, P. 2001. The Botrychiaceae of Alberta. Smithers, BC: Mnium Ecological Research.

Williston, P. 2002. The botrychiaceae of Alberta : a survey of element occurrences of the genera Botrychium and Sceptridium in Alberta. Edmonton.

Willoughby, M. G., Alexander, M. J., & Adams, B. W. (2008). Range plant community types and carrying capacity for the montane subregion. Alberta Sustainable Resource Development, and Agriculture and Agri-Food Canada. Edmonton, Alberta, Canada.

Winther, J. L., and W. E. Friedman. 2007. Arbuscular mycorrhizal symbionts in Botrychium (Ophioglossaceae). American Journal of Botany **94**:1248-1255.

Wittemyer, G., P. Elsen, W. T. Bean, A. C. O. Burton, and J. S. Brashares. 2008. Accelerated human population growth at protected area edges. Science **321**:123-126.

Wright, S. P. 1992. Adjusted p-values for simultaneous inference. Biometrics:1005-1013.

Yoo, J., and N. Koper. 2017. Effects of shallow natural gas well structures and associated roads on grassland songbird reproductive success in Alberta, Canada. PloS one **12**:e0174243.

Zhou, T., X. Luo, Y. Hou, Y. Xiang, and S. Peng. 2020. Quantifying the effects of road width on roadside vegetation and soil conditions in forests. Landscape ecology **35**:69-81.

Zika, P. 1992. Draft management guide for rare Botrychium species (moonworts and grape ferns) for the Mount Hood National Forest. Unpublished report. Oregon Natural Heritage Program, Portland, OR.

# **APPENDIX 1:** Chapter 2 Supplementary Materials

Note: All my data has been archived in the Federated Research Data Repository, DOI: 10.20383/103.0665

Table A1.1. Final locations of trailside and off-trail transects surveyed in June to August of 2020 and 2021. Columns include the specific watershed each site was in, the date the transect was surveyed (D-M-Y), latitude and longitude of the transect site, elevation (meters above sea level), aspect (degrees), slope steepness (+ indicates East declination; - indicates West declination), soil compaction taken at the middle of the trail (kg/cm<sup>2</sup>), and the type of vegetation (Veg.) determined at each site (S = shrubland; G = grassland; B = broadleaf; C = coniferous; M = mixed).

Site	Watershed	Date	Lat.	Long.	Elev. (m)	Aspect (°)	Slope (°)	Comp. (kg/cm <sup>2</sup> )	Veg.
t1	Carbondale	5-8-21	49.42	-114.55	1819	105	+ 20	5	S
t2	Carbondale	5-8-21	49.42	-114.55	1799	75	- 2	5	G
t4	Carbondale	28-7-20	49.49	-114.41	1900	48	- 32	4	G
t5	Carbondale	28-7-20	49.49	-114.42	1828	132	- 45	1.5	В
t9	Carbondale	18-8-20	49.40	-114.38	1619	310	- 8	3.5	С
t14	Carbondale	29-7-20	49.42	-114.43	1457	237	- 28	2.25	С
t15	Carbondale	25-6-20	49.44	-114.39	1484	260	+ 8	0.75	С
t16	Carbondale	25-6-20	49.43	-114.38	1575	60	- 2	2.5	С
t20	Carbondale	25-6-20	49.44	-114.39	1404	110	- 2	1.4	G
t21	Carbondale	25-6-20	49.44	-114.41	1441	240	+ 2	2.75	В
t22	Carbondale	8-7-21	49.44	-114.5	1503	348	+ 14	5	В
t24	Carbondale	30-7-20	49.50	-114.5	1510	204	+4	5	С
t25	Carbondale	30-7-20	49.50	-114.51	1531	91	- 6	5	М
t26	Carbondale	30-7-20	49.41	-114.49	1465	11	- 12	5	М
t27	Carbondale	30-7-20	49.42	-114.48	1456	349	+ 10	4.5	М
t28	Carbondale	2-7-20	49.42	-114.45	1451	120	- 6	0.75	М
t30	Carbondale	29-7-20	49.43	-114.45	1421	117	- 10	5	М
t33	Carbondale	29-7-20	49.43	-114.44	1432	333	- 18	5	М
t36	Carbondale	24-6-20	49.48	-114.45	1694	45	+ 11	4.5	М
t38	Carbondale	24-6-20	49.49	-114.46	1812	248	- 50	5	S
t47	Drywood Creek	21-7-20	49.23	-114.11	1907	122	- 40	5	С
t48	Drywood Creek	21-7-20	49.24	-114.08	1697	95	- 4	1.5	G
t49	Drywood Creek	22-7-20	49.26	-114.05	1585	154	- 24	5	М
t50	Drywood Creek	22-7-20	49.26	-114.04	1539	357	- 10	5	G
t51	Drywood Creek	25-8-20	49.27	-114.1	1688	128	- 28	5	G

t54	Drywood Creek	25-8-20	49.27	-114.08	1612	110	- 32	5	М
t55	Drywood Creek	26-8-20	49.27	-114.08	1603	79	- 42	5	М
t56	Drywood Creek	26-8-20	49.28	-114.08	1586	29	- 2	5	М
t57	Drywood Creek	29-6-21	49.28	-114.07	1510	234	- 8	5	G
t59	Drywood Creek	23-7-20	49.27	-114.02	1509	10	- 12	5	В
t60	Drywood Creek	23-7-20	49.27	-114.02	1510	344	- 12	5	В
t62	Drywood Creek	23-7-20	49.27	-114.02	1506	33	- 20	5	В
t63	Drywood Creek	25-8-20	49.27	-114.1	1683	186	- 30	5	М
t65	Drywood Creek	22-7-20	49.26	-114.04	1540	74	- 16	5	G
t66	Drywood Creek	22-7-20	49.27	-114.03	1523	56	- 22	5	G
t67	Drywood Creek	22-7-20	49.27	-114.03	1515	62	- 10	5	S
t68	Drywood Creek	25-8-20	49.27	-114.11	1707	200	- 36	5	S
t70	Drywood Creek	26-8-20	49.29	-114.07	1547	15	- 18	5	В
t71	Middle Castle	3-7-20	49.36	-114.26	2193	140	- 10	5	G
t72	Middle Castle	7-8-20	49.39	-114.34	1349	214	- 2	5	G
t73	Middle Castle	7-8-20	49.39	-114.34	1350	240	- 4	5	S
t74	Middle Castle	6-8-20	49.37	-114.26	1657	325	- 26	5	С
t75	Middle Castle	18-8-20	49.39	-114.38	1592	192	- 17	5	S
t76	Middle Castle	18-8-20	49.39	-114.38	1608	154	- 23	5	С
t78	Middle Castle	5-8-20	49.40	-114.31	1541	18	- 24	3.25	С
t79	Middle Castle	18-8-20	49.40	-114.38	1633	182	- 10	5	С
t80	Middle Castle	20-8-20	49.41	-114.36	1558	176	- 6	5	С
t81	Middle Castle	19-8-20	49.41	-114.36	1530	48	- 20	5	С
t82	Middle Castle	5-8-20	49.39	-114.29	1565	80	- 15	4.5	В
t83	Middle Castle	20-8-20	49.41	-114.36	1473	180	- 36	5	М
t84	Middle Castle	2-7-20	49.41	-114.34	1347	120	- 14	0.8	В
t85	Middle Castle	2-7-20	49.43	-114.33	1338	130	- 20	1.5	В

t87	Middle Castle	6-8-20	49.38	-114.27	1479	121	- 16	5	М
t88	Middle Castle	19-8-20	49.39	-114.37	1494	176	+ 16	5	М
t89	Middle Castle	5-8-20	49.40	-114.33	1378	280	- 22	5	М
t90	Middle	20-8-20	49.40	-114.36	1496	164	- 34	5	М
t91	Middle	25-6-20	49.40	-114.35	1368	130	- 12	3	М
t92	Middle Castle	2-7-20	49.43	-114.33	1344	163	- 8	1.75	С
t93	Middle Castle	2-7-20	49.44	-114.33	1375	130	- 2	0	М
t94	Middle Castle	6-8-20	49.38	-114.27	1538	50	- 11	5	S
t95	Middle Castle	6-8-20	49.38	-114.28	1471	352	- 10	5	S
t96	Middle Castle	7-8-20	49.38	-114.28	1483	258	- 2	5	М
t99	Mill Creek	16-7-20	49.36	-114.18	1530	296	- 10	5	G
t100	Mill Creek	15-7-20	49.36	-114.18	1491	270	- 8	2.5	G
t101	Mill Creek	16-7-20	49.36	-114.19	1438	40	+ 2	1.75	М
t103	Mill Creek	16-7-20	49.36	-114.19	1462	172	- 14	3.25	S
t104	Mill Creek	16-7-20	49.36	-114.2	1476	90	- 10	5	С
t105	Mill Creek	15-7-20	49.32	-114.19	1511	338	- 12	5	С
t106	Mill Creek	15-7-20	49.32	-114.19	1513	112	- 2	5	С
t107	Mill Creek	14-7-20	49.34	-114.2	1505	17	- 20	1.8	С
t108	Mill Creek	14-7-20	49.35	-114.2	1470	69	- 10	4	С
t111	Mill Creek	6-8-20	49.37	-114.25	1687	58	- 12	0	G
t112	Mill Creek	22-6-21	49.36	-114.23	1518	70	- 4	5	М
t114	Mill Creek	22-6-21	49.36	-114.23	1514	125	+ 3	3	М
t115	Mill Creek	14-7-20	49.35	-114.2	1469	120	- 10	5	S
t116	Mill Creek	14-7-20	49.35	-114.2	1477	275	- 12	2.5	С
t118	Mill Creek	16-7-20	49.36	-114.17	1544	128	- 2	5	G
t125	Upper Castle	21-6-21	49.36	-114.28	2137	169	+ 8	5	G
t125x	Upper Castle	3-7-20	49.36	-114.29	1618	327	- 8	5	С
t126	Upper Castle	13-7-21	49.23	-114.23	1544	275	+ 16	5	С
t128	Upper Castle	4-8-21	49.32	-114.33	1427	342	+ 3	2	М
t131	Upper Castle	26-6-20	49.37	-114.35	1401	240	- 27	1.3	S
t134	Upper Castle	13-7-21	49.29	-114.28	1461	242	- 8	4	В
t137	Upper Castle	13-7-21	49.26	-114.25	1518	280	- 4	5	М
t139	Upper Castle	4-8-21	49.28	-114.33	1719	293	+ 11	5	С
t140	Upper Castle	4-8-21	49.30	-114.33	1586	242	+ 26	5	М
t142	Upper Castle	7-8-20	49.38	-114.29	1463	267	- 3	5	S

t145	Upper Castle	4-8-21	49.29	-114.33	1661	273	- 19	3.25	S
t147	Upper Castle	3-7-20	49.36	-114.28	1764	125	- 52	5	С
t149	Upper Castle	3-7-20	49.36	-114.31	1436	341	- 2	1.5	S
t150	Upper Crowsnest	12-8-20	49.57	-114.63	1657	25	- 21	5	C
t152	Upper Crowsnest	12-8-20	49.58	-114.63	1664	320	- 2	5	C
t155	Upper Crowsnest	12-8-20	49.58	-114.64	1617	266	+ 12	5	С
t156	Upper Crowsnest	12-8-20	49.59	-114.66	1498	244	+ 1	5	М
t157	Upper Crowsnest	13-8-20	49.57	-114.57	1840	133	- 48	5	C
t158	Upper Crowsnest	13-8-20	49.57	-114.57	1847	150	- 51	5	S
t159	Upper Crowsnest	13-8-20	49.57	-114.57	1862	106	- 32	3	C
t160	Upper Crowsnest	12-8-20	49.59	-114.65	1523	248	+ 14	5	М
t161	Upper Crowsnest	12-8-20	49.59	-114.65	1541	230	+ 6	4	М
t162	Upper Crowsnest	13-8-20	49.57	-114.57	1910	20	- 1	5	С
t163	Upper Crowsnest	13-8-20	49.57	-114.57	1914	141	- 26	5	S
t166	West Castle	9-7-20	49.37	-114.43	1794	163	- 12	5	G
t167	West Castle	26-6-20	49.38	-114.35	1406	158	- 12	1.6	G
t169	West Castle	8-7-20	49.29	-114.4	1521	334	- 24	4.25	С
t170	West Castle	3-6-21	49.29	-114.4	1460	248	- 17	5	С
t171	West Castle	9-7-20	49.37	-114.43	1775	107	- 20	5	С
t172	West Castle	15-6-20	49.38	-114.36	1380	340	- 10	1.25	С
t174	West Castle	19-8-20	49.38	-114.39	1544	112	+ 3	5	S
t175	West Castle	8-7-20	49.28	-114.4	1639	87	- 28	5	В
t176	West Castle	8-7-20	49.27	-114.4	1686	67	- 38	3.5	М
t177	West Castle	8-7-20	49.27	-114.41	1784	344	- 42	5	S
t182	West Castle	10-7-20	49.34	-114.42	1405	241	- 12	5	М
t183	West Castle	10-7-20	49.35	-114.41	1409	120	- 22	3.5	М
t184	West Castle	9-7-20	49.37	-114.42	1751	138	+ 10	5	С
t185	West Castle	26-6-20	49.38	-114.35	1394	22	- 8	2.3	М
t186	West Castle	19-8-20	49.38	-114.38	1417	112	- 4	3.75	М
t189	West Castle	9-7-20	49.37	-114.42	1734	104	- 59	5	S
t190	West Castle	9-7-20	49.37	-114.42	1686	115	- 48	5	S
03	Middle Castle	29-7-21	49.38	-114.37	1492	200	+ 10	NA	G
04	Middle Castle	8-6-21	49.41	-114.35	1429	173	- 27	NA	S
o10	Upper Castle	7-6-21	49.39	-114.33	1430	320	- 3	NA	М

o13	Carbondale	28-6-21	49.42	-114.44	1374	276	- 13	NA	С
018	Middle Castle	30-6-21	49.40	-114.37	1513	82	- 2	NA	С
o19	West Castle	3-6-21	49.29	-114.39	1649	250	- 20	NA	С
o21	Upper Castle	26-7-21	49.30	-114.33	1773	255	+ 15	NA	В
o23	Mill Creek	24-6-21	49.35	-114.16	1492	224	+ 1	NA	С
o25	Carbondale	3-8-21	49.41	-114.43	1703	170	+ 19	NA	С
o31	West Castle	15-6-21	49.34	-114.43	1632	105	- 30	NA	С
o33	Carbondale	28-7-21	49.47	-114.5	1745	201	+ 13	NA	С
o37	Upper Castle	12-7-21	49.31	-114.29	1591	200	+ 11	NA	S
o42	Drywood Creek	29-6-21	49.29	-114.06	1479	78	- 1	NA	В
o45	Carbondale	17-6-21	49.54	-114.5	1834	222	+ 32	NA	S
o54	Carbondale	23-6-21	49.42	-114.49	1612	102	+ 2	NA	S
o57	West Castle	20-7-21	49.28	-114.38	1559	13	- 21	NA	М
068	Carbondale	14-7-21	49.53	-114.55	1801	204	+ 25	NA	S
o70	Drywood Creek	22-7-21	49.27	-114.1	2000	150	+ 40	NA	S
073	Upper Crowsnest	15-7-21	49.60	-114.66	1646	215	+ 41	NA	S
082	Carbondale	7-7-21	49.38	-114.53	1891	336	- 31	NA	S
o105	Carbondale	16-6-21	49.51	-114.51	1522	7	- 2	NA	S
o106	Upper Crowsnest	27-7-21	49.58	-114.56	1844	102	- 6	NA	С
o123	Drywood Creek	21-7-21	49.24	-114.08	1720	160	+ 17	NA	В
o126	Carbondale	23-7-21	49.51	-114.55	1762	15	- 13	NA	С

Table A1.2. Results of pairwise comparisons of estimated marginal mean maximum height of vegetation of each trail type compared between distances from trail. Results are averaged over the most common vegetation type (mixed/broadleaf). 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 two columns denote significant differences in mean maximum height of vegetation between quadrats at different distances, without adjustments or with the Tukey adjustment for multiple tests.

Trail use	Distance	emmean	SE	df	lower	upper	Difference	Difference
type	(m)						(not adjusted)	(Tukey adjusted)
Control	0	70.5	7.46	411	55.8	85.1	а	а
	2	64.4	7.46	411	49.7	79	а	а
	5	67.9	7.46	411	53.3	82.6	а	а
	10	61.2	7.46	411	46.5	75.9	а	а
Footpath	0	68.7	7.49	411	53.9	83.4	а	а
	2	71.4	7.49	411	56.7	86.1	а	а
	5	68.1	7.49	411	53.4	82.8	а	а
	10	78.7	7.49	411	63.9	93.4	а	а
OHV	0	68	4.18	411	59.7	76.2	а	а
	2	78.9	4.18	411	70.7	87.2	b	а
	5	72.2	4.18	411	64	80.4	ab	а
	10	71.4	4.18	411	63.2	79.6	ab	а
Road	0	53.7	9.66	411	34.7	72.7	а	а
	2	60.5	9.66	411	41.6	79.5	а	ab
	5	63.1	9.66	411	44.1	82.1	ab	ab
	10	83.7	9.66	411	64.7	102.7	b	b

Table A1.3. Results of pairwise comparisons of estimated marginal mean soil compaction values at each distance compared between trail types. Results are averaged over the most common vegetation type (mixed/broadleaf). Degrees of freedom (df) are determined using the Kenward-Roger method. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final two columns denote significant differences in mean soil compaction values between quadrats without adjustments or with the Tukey adjustment for multiple tests.

Distance	Trail use type	emmean	SE	df	lower	upper	Difference (not adjusted)	Difference (Tukey adjusted)
0m	Control	0.837	0.225	315	0.3939	1.279	a	a
	Footpath	1.581	0.229	329	1.1294	2.032	b	ab
	OHV	1.795	0.124	303	1.5501	2.04	b	b
	Road	2.668	0.293	319	2.0926	3.244	c	с
2m	Control	0.847	0.225	315	0.4043	1.29	a	a
	Footpath	0.966	0.229	329	0.5144	1.417	a	a
	OHV	1.121	0.124	303	0.8763	1.366	a	a
	Road	2.16	0.293	319	1.584	2.736	b	b
5m	Control	1.035	0.225	315	0.5918	1.477	a	a
	Footpath	0.965	0.229	329	0.5135	1.416	a	a
	OHV	0.704	0.124	303	0.4586	0.949	a	a
	Road	1.176	0.293	319	0.5997	1.751	a	a
10m	Control	0.92	0.225	315	0.4773	1.363	a	a
	Footpath	0.776	0.229	329	0.3249	1.228	a	a
	OHV	0.753	0.124	303	0.508	0.998	a	a
	Road	0.676	0.293	319	0.0997	1.251	a	a

Table A1.4. Results of pairwise comparisons of estimated marginal mean (emmean) soil compaction values for each trail type between distances from trail. Results are averaged over the most common vegetation type (mixed/broadleaf). Degrees of freedom (df) are determined using the Kenward-Roger method. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final two columns denote significant differences in mean soil compaction values between quadrats at different distances, without adjustments or with the Tukey adjustment for multiple tests.

Trail use	Distance	emmean	SE	df	lower	upper	Difference	Difference
type	(m)						(not adjusted)	(Tukey adjusted)
Control	0	1.00	0.06	291	0.876	1.13	а	а
	2	1.01	0.06	291	0.879	1.13	а	а
	5	1.06	0.06	291	0.929	1.18	а	а
	10	1.02	0.06	291	0.888	1.14	а	а
Footpath	0	1.223	0.07	303	1.094	1.35	а	а
	2	1.044	0.07	303	0.915	1.17	b	b
	5	1.026	0.07	303	0.897	1.15	b	b
	10	0.960	0.07	303	0.831	1.09	b	b
OHV	0	1.27	0.04	280	1.200	1.34	а	a
	2	1.09	0.04	280	1.019	1.16	b	b
	5	0.96	0.04	280	0.889	1.03	с	с
	10	0.97	0.04	280	0.903	1.04	с	с
Road	0	1.44	0.08	294	1.277	1.61	а	а
	2	1.35	0.08	294	1.187	1.52	а	а
	5	1.09	0.08	294	0.928	1.26	b	b
	10	0.94	0.08	294	0.780	1.11	b	b

Table A1.5. List of exotic species (n = 35) recorded during two survey seasons, from June to August of 2020 and 2021. Last four columns report the minimum, mean, median, and maximum elevation (meters above sea level) of each species surveyed.

Scientific name	Lifeform	Lifecycle	Min.	Mean	Med.	Max.
			Elev	Elev.	Elev.	Elev.
			(m)	(m)	(m)	(m)
Agrostis gigantea	grass	perennial	1378	1455	1456	1530
Agrostis stolonifera	grass	perennial	1432	1494	1491	1559
Alyssum alyssoides	herb	annual	1436	1436	1436	1436
Bromus inermis	grass	perennial	1350	1577	1572	1847
Capsella bursa-pastoris	herb	annual	1421	1421	1421	1421
Carum carvi	herb	biennial	1469	1469	1469	1469
Cerastium fontanum	herb	perennial	1457	1512	1513	1586
Cirsium arvense	herb	perennial	1368	1492	1467	1799
Dactylis glomerata	grass	perennial	1544	1544	1544	1544
Echium vulgare	herb	perennial	1812	1812	1812	1812
Festuca ovina	grass	perennial	1378	1421	1406	1479
Festuca trachyphylla	grass	perennial	1503	1503	1503	1503
Leucanthemum vulgare	herb	perennial	1349	1487	1477	1799
Linaria vulgaris	herb	perennial	1344	1485	1505	1617
Lolium pratense	grass	perennial	1421	1421	1421	1421
Matricaria discoidea	herb	annual	1510	1510	1510	1510
Medicago lupulina	herb	perennial	1349	1503	1510	1688
Melilotus alba	herb	annual	1683	1683	1683	1683
Melilotus officinalis	herb	annual	1585	1634	1634	1683
Phleum pratense	grass	perennial	1338	1524	1508	1900
Pilosella aurantiacum	herb	perennial	1694	1750	1745	1812
Plantago major	herb	perennial	1338	1490	1483	1657
Poa annua	grass	annual	1409	1537	1537	1664
Poa compressa	grass	perennial	1349	1529	1499	1900
Poa pratensis ssp. Pratensis	grass	perennial	1338	1499	1479	1828
Ranunculus acris	herb	perennial	1350	1520	1522	1794
Rumex acetosella	herb	perennial	1462	1462	1462	1462
Taraxacum officinale	herb	perennial	1338	1541	1510	1914
Thlaspi arvense	herb	annual	1421	1421	1421	1421
Tragopogon dubius	herb	perennial	1349	1444	1449	1506
Trifolium aureum	herb	perennial	1456	1459	1457	1465
Trifolium hybridum	herb	perennial	1338	1499	1494	1799
Trifolium pratense	herb	perennial	1349	1530	1478	1847
Trifolium repens	herb	perennial	1338	1500	1483	1799
Verbascum thapsus	herb	annual	1522	1608	1608	1694

Table A1.6. List of rare species (n = 15) recorded during two survey seasons, from June to August of 2020 and 2021. The last column indicates conservation status rank for Alberta (S1 = critically imperiled; S2 = imperiled).

Scientific name	Lifeform	Lifecycle	<b>Provincial Status</b>
Adenocaulon bicolor	herb	perennial	S2
Artemisia tridentata	subshrub	perennial	S2
Carex geyeri	sedge	perennial	S2
Draba reptans	herb	annual	S2
Elymus scribneri	grass	perennial	S2
Epilobium leptocarpum	herb	perennial	S2
Festuca occidentalis	grass	perennial	S2
Lupinus lepidus	herb	perennial	S2
Melica spectabilis	herb	perennial	S2
Melica subulata	grass	perennial	S2
Microsteris gracilis	herb	annual	S1
Paxistima myrsinites	shrub	perennial	S2
Platanthera unalascensis	herb	perennial	S2
Trisetum canescens	grass	perennial	S2
Viola glabella	herb	perennial	S2

Table A1.7. Results of pairwise comparisons of estimated marginal mean species richness at each distance for each vegetation type. Results are averaged over the most common trail type (OHV). 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 two columns denote significant differences in mean species richness between quadrats at different distances, without adjustments or with the Tukey adjustment for multiple tests.

Vegetation	Distance	mean	SE	df	lower	upper	Diff. (not	Diff.
	(m)						adjusted)	(Tukey adjusted)
Grassland	0	11.3	1.28	289	8.77	13.8	a	а
	2	11.3	1.28	289	8.81	13.9	а	а
	5	13.5	1.28	289	10.96	16	a	а
	10	13.9	1.28	289	11.33	16.4	а	а
Shrubland	0	14.6	1.07	291	12.51	16.7	ab	ab
	2	16	1.07	291	13.87	18.1	a	а
	5	15.6	1.07	291	13.45	17.7	a	а
	10	12.8	1.07	291	10.64	14.9	b	b
Mixed	0	13.1	0.86	285	11.42	14.8	a	а
	2	14.5	0.86	285	12.84	16.2	a	а
	5	14.1	0.86	285	12.42	15.8	a	а
	10	12.9	0.86	285	11.18	14.6	а	а
Coniferous	0	12.7	0.94	291	10.82	14.5	a	а
	2	12.7	0.94	291	10.83	14.5	a	а
	5	11.2	0.94	291	9.37	13.1	ab	ab
	10	10.1	0.94	291	8.22	11.9	b	b

Table A1.8. Results of pairwise comparisons of mean species richness (emmean) at each distance from trail for each trail type. Results are averaged over the most common vegetation type (mixed/broadleaf). Degrees of freedom (df) 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 two columns denote significant differences in mean species richness between quadrats, without adjustments or with the Tukey adjustment for multiple tests.

Trail use	Distance	emmean	SE	df	lower	upper	Difference	Difference
type	(m)						(not	(Tukey
							adjusted)	adjusted)
Control	0	12.16	1.17	288	9.87	14.5	a	а
	2	12.14	1.17	288	9.85	14.4	а	а
	5	12.31	1.17	288	10.01	14.6	а	а
	10	13.04	1.17	288	10.74	15.3	а	а
Footpath	0	16.43	1.16	293	14.16	18.7	а	а
	2	15.85	1.16	293	13.57	18.1	а	а
	5	13.75	1.16	293	11.47	16	ab	ab
	10	11.73	1.16	293	9.45	14	b	b
OHV	0	15.21	0.65	293	13.94	16.5	а	а
	2	13.99	0.65	293	12.72	15.3	ab	а
	5	13.7	0.65	293	12.43	15	b	а
	10	11.99	0.65	293	10.72	13.3	с	b
Road	0	7.89	1.51	287	4.92	10.9	а	а
	2	12.54	1.51	287	9.57	15.5	b	b
	5	14.62	1.51	287	11.64	17.6	b	b
	10	12.79	1.51	287	9.82	15.8	b	b

Table A1.9. Results of estimated marginal means of linear trends comparing the slope of the relationship between species richness and distance from trail (trend) for the subset data of only footpaths and OHV trails within each vegetation type. Degrees of freedom (df) determined using the Kenward-Roger method. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Bolded 'p-value' indicates significant differences between slopes.

Vegetation type	Trail type	trend	SE	df	lower	upper	p-value
Grassland	footpath	-0.010	0.224	304	-0.45	0.431	0.647
	OHV	0.118	0.167	304	-0.21	0.447	
Shrubland	footpath	-0.895	0.205	304	-1.297	-0.493	0.008
	OHV	-0.232	0.139	304	-0.506	0.041	
Mixed	footpath	-0.796	0.224	304	-1.237	-0.356	0.025
	OHV	-0.254	0.087	304	-0.426	-0.083	
Coniferous	footpath	-0.289	0.205	304	-0.691	0.114	0.087
	OHV	-0.677	0.096	304	-0.867	-0.487	

Table A1.10. Results of pairwise comparisons of mean community dissimilarity (emmean) within each vegetation type. Results are averaged over the most common trail type (OHV). Degrees of freedom (df) determined using the Kenward-Roger method. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in final two columns denote significant differences in mean Bray-Curtis dissimilarity values between quadrats, without adjustments or with the Tukey adjustment for multiple tests.

Vegetation	emmean	SE	df	lower	upper	Differences	Differences
						(not	(Tukey
						adjusted)	adjusted)
Grassland	0.496	0.0367	132	0.423	0.569	а	а
Shrubland	0.664	0.0293	132	0.606	0.722	b	b
Mixed	0.629	0.0231	132	0.583	0.675	b	b
Coniferous	0.661	0.0258	132	0.61	0.712	b	b

Table A1.11. Results of pairwise comparisons of mean Bray-Curtis dissimilarity values (emmean) between each trail type at each distance from trail. Results are averaged over the most common vegetation type (mixed/broadleaf). Degrees of freedom (df) determined using the Kenward-Roger method. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in final two columns denote significant differences in mean Bray-Curtis dissimilarity values between quadrats, without adjustments or with the Tukey adjustment for multiple tests.

Distance compared to 10m	Trail type	emmean	SE	df	lower	upper	Diff. (not adjusted)	Diff. (Tukey adjusted)
	Control	0.536	0.0364	221	0.464	0.607	а	а
0	Footpath	0.643	0.0368	228	0.571	0.716	bc	ab
UIII	OHV	0.724	0.0206	213	0.683	0.764	b	b
	Road	0.771	0.0489	223	0.674	0.867	b	b
2m	Control	0.548	0.0364	221	0.477	0.62	а	а
	Footpath	0.611	0.0368	228	0.538	0.683	ab	а
	OHV	0.64	0.0206	213	0.599	0.68	b	а
	Road	0.694	0.0489	223	0.597	0.79	b	а
	Control	0.541	0.0364	221	0.469	0.613	а	а
_	Footpath	0.546	0.0368	228	0.473	0.618	а	а
511	OHV	0.55	0.0206	213	0.509	0.59	а	а
	Road	0.549	0.0489	223	0.452	0.645	а	а

Table A1.12. Results of pairwise comparisons of mean Bray-Curtis dissimilarity values (compared to the 10 m quadrat) for footpaths and OHV trails (emmean) for each vegetation type. Results are averaged over the levels of distance to trail. Degrees of freedom (df) determined using the Kenward-Roger method. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in the final two columns denote significant differences in mean Bray-Curtis dissimilarity values between footpaths and OHV trails, without adjustments or with the Tukey adjustment for multiple tests.

Vegetation	Trail type	emmean	SE	df	lower	upper	Diff. (not adjusted)	Diff. (Tukey adjusted)
Grassland	Footpath	0.38	0.062	94	0.26	0.506	a	а
	OHV	0.55	0.049	94	0.45	0.644	b	b
Shrubland	Footpath	0.78	0.057	94	0.663	0.888	а	а
	OHV	0.65	0.038	94	0.574	0.726	а	а
Mixed	Footpath	0.58	0.062	94	0.458	0.704	а	а
	OHV	0.66	0.024	94	0.609	0.705	а	а
Coniferous	Footpath	0.64	0.057	94	0.525	0.749	а	а
	OHV	0.69	0.027	94	0.641	0.748	а	а

Table A1.13. Results of pairwise comparisons of the mean probability of exotic species presence (emmean) within each vegetation type. Results are averaged over the most common trail type (OHV). Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Different lower-case letters in final two columns denote significant differences in mean probability of exotic species presence between quadrats, without adjustments or with the Tukey adjustment for multiple tests.

Vegetation type	emmean	SE	df	lower	upper	Differences (not adjusted)	Differences (Tukey adjusted)
Grassland	1.00	0.0019	Inf	0.924237	1	а	а
Shrubland	0.96	0.0522	Inf	0.617281	0.9973	ac	ab
Mixed	0.72	0.22	Inf	0.236775	0.9544	с	bc
Coniferous	0.02	0.03	Inf	0.000948	0.251	b	с

Table A1.14a. Results of pairwise comparisons of the mean probability of exotic species present (emmean) at each distance from trail for each trail type. Results are averaged over the most common vegetation type (mixed/broadleaf). Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Intervals are back-transformed from the logit scale. Different lower-case letters in pairwise significance column denote significant differences in the odds ratio of the probability of exotic species present between quadrats, without adjustments or with the Tukey adjustment for multiple tests.

Trail type	Distance (m)	emmean	SE	df	lower	upper	Diff. (not adjusted)	Diff. (Tukey adjusted)
Control	0	0.32	0.34	Inf	0.023	0.907	а	а
	2	0.32	0.34	Inf	0.023	0.907	а	а
	5	0.17	0.23	Inf	0.009	0.829	а	а
	10	0.32	0.34	Inf	0.023	0.907	а	а
Footpath	0	1.00	0.00	Inf	0.854	0.999	а	а
	2	0.91	0.13	Inf	0.297	0.996	а	ab
	5	0.19	0.25	Inf	0.010	0.842	b	b
	10	0.03	0.05	Inf	0.001	0.464	b	bc
	0	1.00	0.00	Inf	0.992	1	а	а
	2	0.97	0.03	Inf	0.795	0.997	bc	bc
υπν	5	0.73	0.18	Inf	0.312	0.943	b	b
	10	0.65	0.20	Inf	0.245	0.917	b	b
	0	0.99	0.03	Inf	0.295	0.999	a	a
	2	1.00	0.01	Inf	0.608	1	ab	a
roau	5	0.93	0.16	Inf	0.107	0.999	a	a
	10	0.78	0.39	Inf	0.040	0.997	а	а

Table A1.14b. Results of pairwise comparisons of the probability of exotic species present (emmean) for each trail type at each distance. Results are averaged over the most common vegetation type (mixed/broadleaf). Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Intervals are back-transformed from the logit scale. Different lower-case letters in pairwise significance column denote significant differences in the odds ratio of the probability of exotic species present between quadrats, without adjustments or with the Tukey adjustment for multiple tests.

Distance	Trail type	Prob.	SE	df	lower	upper	Difference (not adjusted)	Difference (Tukey adjusted)
0.m	Control	0.32	0.33	Inf	0.023	0.907	а	а
	Footpath	1.00	0.0042	Inf	0.854	0.999	b	ab
UIII	OHV	1.00	0.0002	Inf	0.992	1	b	b
	Road	0.99	0.03	Inf	0.295	0.999	ab	ab
	Control	0.32	0.34	Inf	0.023	0.907	а	а
2m	Footpath	0.91	0.13	Inf	0.297	0.996	ab	а
	OHV	0.97	0.03	Inf	0.795	0.997	b	а
	Road	1.00	0.01	Inf	0.608	1	b	а
	Control	0.17	0.23	Inf	0.009	0.829	а	а
5	Footpath	0.19	0.25	Inf	0.010	0.842	а	а
5111	OHV	0.73	0.18	Inf	0.312	0.943	а	а
	Road	0.93	0.16	Inf	0.107	0.999	а	а
	Control	0.32	0.34	Inf	0.023	0.907	а	а
10m	Footpath	0.03	0.05	Inf	0.001	0.464	ac	а
10111	OHV	0.65	0.20	Inf	0.245	0.917	ab	а
	Road	0.78	0.39	Inf	0.040	0.997	а	а
Table A1.15. Results of estimated marginal means of linear trends comparing the slope of the relationship between the probability of at least one exotic species and distance from trail (trend) for the subset data of only footpaths and OHV trails within each vegetation type. Degrees of freedom (df) determined using the Kenward-Roger method. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Bolded 'p-value' indicates significant differences between slopes.

Vegetation	Trail type	trend	SE	df	lower	upper	p-value
Grassland	footpath	-0.000	1.204	401	-2.37	2.37	0.348
	OHV	-1.375	0.833	401	-3.01	0.263	
Shrubland*	footpath	-4.759	1.453	401	-7.62	-1.902	0.013
	OHV	-1.261	0.303	401	-1.86	-0.665	
Coniferous	footpath	-1.171	0.747	401	-2.64	0.298	0.033
	OHV	-3.586	0.946	401	-5.45	-1.726	

\*Shrubland includes shrubland, mixed, and broadleaf vegetation types due to low replication and to avoid unreasonable slope estimates.

Table A1.16. Results of pairwise comparisons (emmeans) of the mean probability of at least one exotic species per transect compared between each vegetation type. Degrees of freedom (df) determined using Kenward-Roger method. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Intervals are back-transformed from the logit scale. Different lower-case letters in pairwise significance column denote significant differences in the mean probability of exotic species present between transects, without adjustments or with the Tukey adjustment for multiple tests.

Vegetation	estimate	SE	df	lower	upper	Diff. (not adjusted)	Diff. (Tukey adjusted)
Grassland	1	9.09E-13	Inf	2.22E-16	1	ab	ab
Shrubland	1	9.08E-13	Inf	2.22E-16	1	а	а
Mixed	1	9.08E-13	Inf	2.22E-16	1	ab	ab
Coniferous	1	9.08E-13	Inf	2.22E-16	1	b	b

Table A1.17. Results of pairwise comparisons (emtrends) of the slope of the relationship between the probability of at least one exotic species per transect and elevation compared between each trail type. Results are averaged over the most common vegetation type (mixed/broadleaf). Degrees of freedom determined using Kenward-Roger method. Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Intervals are back-transformed from the logit scale. Different lower-case letters in pairwise significance column denote significant differences in the mean probability of exotic species present per transect, without adjustments or with the Tukey adjustment for multiple tests.

Trail use type	emmean	SE	df	lower	upper	Difference (not adjusted)	Difference (Tukey adjusted)
Control	2.52	37.2	Inf	-70.3	75.3	а	а
Footpath	10.74	39.8	Inf	-67.3	88.8	ab	ab
OHV	5.36	37.2	Inf	-67.5	78.2	b	b
Road	188.34	16361.2	Inf	-31879	32255.7	ab	ab

Table A1.18. Results of pairwise comparisons of the probability of rare species present (emmean) compared between each trail type. Results are averaged over the most common vegetation type (mixed/broadleaf). Lower and upper confidence intervals for the estimates are included (confidence level = 0.95). Intervals are back-transformed from the logit scale. Different lower-case letters in pairwise significance column denote significant differences in the odds ratio of the probability of rare species present between quadrats, without adjustments or with the Tukey adjustment for multiple tests.

Trail use type	emmean	SE	df	lower	upper	Difference (not adjusted)	Difference (Tukey adjusted)
control	0.4704	0.1148	Inf	0.2646	0.687	а	а
footpath	0.2869	0.1011	Inf	0.13251	0.515	ab	а
OHV	0.2375	0.0552	Inf	0.14627	0.361	b	а
road	0.0655	0.0648	Inf	0.00875	0.358	b	а

## **APPENDIX 2:** Chapter 3 Supplementary Materials

Table A2.1. Results of the indicator species analysis for plots with or without *Botrychium* according to an indicator species analysis with 9,999 permutations. Values include the relative frequency and average relative abundance of species occurring in plots with *Botrychium* absent or present as well as the group each species has maximum indicator value for *Botrychium* (Occurrence- present or absent). Significant indicator species are shown in bold lettering.

Scientific Name	Relative	Relative	Relative	Relative	Occurrence	p-
	(absent)	(present)	(absent)	(present)		value
Abies balsamea	0.647	0.429	0.731	0.269	absent	0.183
Acer glabrum	0.588	0.143	0.908	0.092	absent	0.049
Achillea millofolium	0.824	0.857	0.464	0.536	present	0.659
Actaea rubra	0.353	0.286	0.531	0.469	absent	0.939
Agoseris	0.235	0.143	0.490	0.510	absent	1.000
aurantiaca						
Agoseris glauca	0.118	0.571	0.171	0.829	present	0.029
Agrostis scabra	0.118	0.143	0.407	0.593	present	0.844
Agrostis	0.059	0.000	1.000	0.000	absent	1.000
stolonifera						
Allium cernuum	0.529	0.429	0.602	0.398	absent	0.612
Alnus alnobetula	0.471	0.143	0.781	0.219	absent	0.243
Alnus incana ssp.	0.000	0.143	0.000	1.000	present	0.296
tenuifolia						
Alyssum	0.059	0.000	1.000	0.000	absent	1.000
alyssoides						
Amelanchier	0.765	0.571	0.629	0.371	absent	0.348
alnifolia		0.000	0.644			0.0.00
Anaphalis	0.588	0.286	0.641	0.359	absent	0.370
Anemone	0.412	0 714	0.403	0 597	nresent	0.223
multifida	0.112	0.711	0.105	0.097	present	0.225
Anemone	0.000	0.143	0.000	1.000	present	0.287
parviflora						
Angelica arguta	0.118	0.000	1.000	0.000	absent	0.570
Angelica	0.412	0.571	0.368	0.632	present	0.281
dawsonii						
Antennaria	0.000	0.143	0.000	1.000	present	0.285
alpina						
Antennaria	0.176	0.429	0.490	0.510	present	0.548
howellii						
Antennaria media	0.000	0.143	0.000	1.000	present	0.289

Scientific Name	Relative	Relative	Relative	Relative	Occurrence	p-
	frequency	frequency	abundance	abundance		value
	(absent)	(present)	(absent)	(present)		0.202
Antennaria	0.000	0.143	0.000	1.000	present	0.302
microphylia	0.17(	0.000	1.000	0.000	1 (	0.520
Antennaria	0.176	0.000	1.000	0.000	absent	0.529
parvijolia	0.000	0.142	0.000	1.000		0.207
Antennaria	0.000	0.143	0.000	1.000	present	0.287
	0.252	0.142	0.742	0.259		0.429
Antennaria	0.333	0.145	0.742	0.238	absent	0.428
racemosa Antonnavia nogog	0.252	0.420	0.270	0.620	magant	0.560
Aniennaria rosea	0.333	0.429	0.370	0.030	present	0.360
Antennaria	0.176	0.429	0.265	0.735	present	0.224
umbrinella		0.400	0.4.60	0.501		0.666
Anticlea elegans	0.294	0.429	0.469	0.531	present	0.666
Anticlea	0.235	0.429	0.397	0.603	present	0.421
occidentalis						
Aphyllon uniflora	0.000	0.143	0.000	1.000	present	0.297
Apocynum	0.118	0.000	1.000	0.000	absent	0.567
androsaemifolium						
Aquilegia	0.176	0.286	0.325	0.676	present	0.367
flavescens						
Arabis nuttallii	0.000	0.286	0.000	1.000	present	0.074
Arctostaphylos	0.471	0.429	0.531	0.469	absent	0.861
uva-ursi						
Arnica cordifolia	0.824	0.571	0.613	0.387	absent	0.228
Arnica fulgens	0.000	0.143	0.000	1.000	present	0.288
Arnica latifolia	0.059	0.000	1.000	0.000	absent	1.000
Arnica ovata	0.000	0.286	0.000	1 000	nresent	0.076
Antomisia	0.050	0.200	1,000	0.000	abcont	1.000
Artemisia	0.039	0.000	1.000	0.000	absent	1.000
Artomisia	0.176	0.1/3	0.400	0.510	abcent	1.000
michauxiana	0.170	0.175	0.470	0.510	absent	1.000
Artemisia	0.059	0.000	1 000	0.000	absent	1 000
tridentata	0.057	0.000	1.000	0.000	dosent	1.000
Astragalus	0.059	0.143	0.292	0 708	nresent	1 000
alninus	0.027	0.115	0.272	0.700	present	1.000
Astragalus	0.000	0.143	0.000	1.000	present	0.287
hourgovii	0.000	01115	0.000	11000	present	0.207
Astragalus	0.059	0.000	1.000	0.000	absent	1.000
canadensis	01009	0.000	1.000	0.000		1.000
Astragalus	0.000	0.286	0.000	1.000	present	0.079
vexilliflexus					1	
Balsamorhiza	0.059	0.000	1.000	0.000	absent	1.000
sagittata						

Scientific Name	Relative	Relative	Relative	Relative	Occurrence	p-
	frequency	frequency	abundance	abundance		value
Rerheris renens	(absent) 0.647	(present)	(absent)	(present)	absent	0.373
Retula	0.059	0.000	1.000	0.000	absent	1 000
glandulosa	0.057	0.000	1.000	0.000	absent	1.000
Boechera	0.118	0.429	0.292	0.708	present	0.126
lemmonii					1	
Boechera stricta	0.118	0.000	1.000	0.000	absent	0.564
Bromus carinatus	0.176	0.143	0.523	0.477	absent	0.884
Bromus ciliatus	0.059	0.143	0.215	0.785	present	0.789
Bromus inermis	0.294	0.286	0.507	0.493	absent	1.000
Bromus	0.059	0.143	0.198	0.802	present	0.784
pumpellianus						
Bromus vulgaris	0.118	0.000	1.000	0.000	absent	0.568
Calamagrostis canadensis	0.235	0.000	1.000	0.000	absent	0.283
Calamagrostis	0.000	0.143	0.000	1.000	present	0.295
purpurescens	0.(47	0.420	0.5(7	0.422	-1	0.000
calamagrosiis	0.047	0.429	0.307	0.455	absent	0.009
Calamagrostis	0.059	0.000	1.000	0.000	absent	1.000
stricta						
Calochortus	0.235	0.143	0.712	0.288	absent	0.585
apiculatus						
Calypso bulbosa	0.000	0.143	0.000	1.000	present	0.293
Campanula	0.706	0.429	0.667	0.333	absent	0.231
rotundifolia						
Carex aurea	0.059	0.000	1.000	0.000	absent	1.000
Carex bebbii	0.059	0.000	1.000	0.000	absent	1.000
Carex capillaris	0.000	0.143	0.000	1.000	present	0.293
Carex	0.471	0.286	0.622	0.378	absent	0.571
concinnoides						
Carex deweyana	0.059	0.000	1.000	0.000	absent	1.000
Carex flava	0.059	0.000	1.000	0.000	absent	1.000
Carex geyeri	0.118	0.000	1.000	0.000	absent	0.560
Carex hoodii	0.235	0.286	0.579	0.421	absent	1.000
Carex microptera	0.118	0.143	0.452	0.548	present	1.000
Carex obtusata	0.059	0.143	0.171	0.829	present	0.289
Carex	0.000	0.286	0.000	1.000	present	0.075
pnaeocephala Canor	0.000	0.142	0.000	1.000	magant	0.207
nraparacilis	0.000	0.143	0.000	1.000	present	0.297
P'ucsi ucilis	l				1	1

Scientific Name	Relative frequency	Relative frequency	Relative abundance	Relative abundance	Occurrence	p- value
	(absent)	(present)	(absent)	(present)		, and
Carex raynoldsii	0.000	0.143	0.000	1.000	present	0.285
Carex rossii	0.588	0.429	0.664	0.336	absent	0.408
Carex siccata	0.059	0.000	1.000	0.000	absent	1.000
Castilleja hispida	0.176	0.286	0.475	0.525	present	0.919
Castilleja miniata	0.706	0.429	0.553	0.447	absent	0.528
Castilleja	0.059	0.286	0.121	0.879	present	0.078
occidentalis						
Ceanothus	0.118	0.000	1.000	0.000	absent	0.569
velutinus	0.004	0.000	0.500	0.4==		0.001
Cerastium	0.294	0.286	0.523	0.477	absent	0.891
arvense Congstium	0.000	0.142	0.000	1.000	nragant	0.202
fontanum	0.000	0.145	0.000	1.000	present	0.295
Cerastium nutans	0.059	0.286	0.171	0.829	present	0.133
Chamaenerion	0.882	0.714	0.536	0.464	absent	0.524
angustifolium	0.002	01711	0.000	01101	uosent	0.02.
Chamaenerion	0.059	0.143	0.171	0.829	present	0.281
latifolium						
Cherleria	0.118	0.286	0.331	0.669	present	0.552
obtusiloba	0.500	0.1.10	0.504	0.000		0.4.6
Chimaphila	0.529	0.143	0.794	0.206	absent	0.167
umbellata	0.050	0.000	1.000	0.000		1 000
	0.039	0.000	1.000	0.000	absent	1.000
Cirsium arvense	0.118	0.286	0.198	0.802	present	0.378
Cirsium	0.000	0.143	0.000	1.000	present	0.296
floamanii	0.225	0.286	0.400	0.510	magant	0.042
Cirsium	0.233	0.280	0.490	0.310	present	0.945
Cirsium vulgare	0.059	0.143	0.292	0.708	present	1.000
Claytonia	0.059	0.000	1.000	0.000	absent	1.000
lanceolata	0.009	0.000	1.000	0.000	uosent	1.000
Clematis	0.529	0.571	0.513	0.487	present	1.000
occidentalis					1	
Clintonia uniflora	0.647	0.286	0.680	0.320	absent	0.310
Coeloglossum	0.059	0.143	0.215	0.785	present	0.785
viride						
Collinsia	0.118	0.143	0.407	0.593	present	0.840
parviflora	0.050	0.000	0.000	0.007		0.075
Collomia linearis	0.059	0.286	0.093	0.907	present	0.075
Comandra	0.176	0.143	0.523	0.477	absent	1.000
umbellata						

Scientific Name	Relative	Relative	Relative	Relative	Occurrence	p-
	frequency	frequency	abundance	abundance		value
	(absent)	(present)	(absent)	(present)	1 .	0.550
Corallorhiza	0.118	0.000	1.000	0.000	absent	0.573
maculata						
Corallorhiza	0.118	0.143	0.452	0.548	present	1.000
striata						
Corallorhiza	0.118	0.143	0.382	0.618	present	0.835
trifida						
Cornus	0.235	0.286	0.475	0.525	present	0.926
canadensis						
Cornus	0.059	0.143	0.452	0.548	present	1.000
stolonifera						
Crataegus	0.059	0.000	1.000	0.000	absent	1.000
chrysocarpa						
Cryptantha	0.059	0.000	1.000	0.000	absent	1.000
celosioides						
Cystopteris	0.294	0.429	0.354	0.646	present	0.439
fragilis						
Danthonia	0.059	0.000	1.000	0.000	absent	1.000
intermedia						
Danthonia	0.059	0.000	1.000	0.000	absent	1.000
spicata						
Dasiphora	0.471	0.714	0.368	0.632	present	0.213
fruticosa						
Doellingeria	0.529	0.143	0.742	0.258	absent	0.191
engelmannii						
Draba aurea	0.118	0.286	0.292	0.708	present	0.500
Draba	0.059	0.143	0.382	0.618	present	1.000
lonchocarpa						
Draba paysonii	0.000	0.143	0.000	1.000	present	0.295
Draba reptans	0.059	0.000	1.000	0.000	absent	1.000
Dracocephalum	0.000	0.143	0.000	1.000	present	0.287
parviflorum					1	
Dracocephalum	0.000	0.143	0.000	1.000	present	0.288
thymiflorum					1	
Dryas	0.059	0.143	0.121	0.879	present	0.297
drummundii					1	
Dryas hookeriana	0.000	0.143	0.000	1.000	present	0.294
Drymocallis	0.176	0.143	0.649	0.351	absent	0.655
arguta						
Drymocallis	0.000	0.143	0.000	1.000	present	0.285
glandulosa						
Echium vulgare	0.000	0.143	0.000	1.000	present	0.279

Scientific Name	Relative	Relative	Relative	Relative	Occurrence	p-
	frequency	frequency	abundance	abundance		value
	(absent)	(present)	(absent)	(present)		1.000
Elaeagnus	0.059	0.143	0.407	0.593	present	1.000
commutata	0.471	0.000	1.000	0.000	1	0.050
Elymus glaucus	0.471	0.000	1.000	0.000	absent	0.052
Elymus	0.000	0.143	0.000	1.000	present	0.291
lanceolatus						
Elymus scribneri	0.000	0.143	0.000	1.000	present	0.296
Elymus	0.000	0.143	0.000	1.000	present	0.287
trachycaulus ssp.						
trachycaulus						
Epilobium	0.059	0.143	0.236	0.764	present	0.782
anagallidifolium						
Epilobium	0.059	0.143	0.236	0.764	present	0.787
brachycarpum						
Equisetum	0.235	0.286	0.553	0.447	absent	1.000
arvense						
Equisetum	0.000	0.143	0.000	1.000	present	0.286
fluviatile						
Equisetum	0.000	0.286	0.000	1.000	present	0.081
hyemale						
Erigeron acris	0.000	0.143	0.000	1.000	present	0.302
Erigeron	0.059	0.000	1.000	0.000	absent	1.000
caespitosus						
Erigeron	0.176	0.429	0.265	0.735	present	0.215
compositus						
Erigeron	0.000	0.143	0.000	1.000	present	0.290
glabellus var.						
pubescens						
Erigeron	0.059	0.000	1.000	0.000	absent	1.000
peregrinus						
Erigeron	0.176	0.143	0.523	0.477	absent	1.000
speciosus						
Eriogonum	0.000	0.143	0.000	1.000	present	0.288
ovalifolium						
Eriogonum	0.235	0.000	1.000	0.000	absent	0.276
umbellatum						
Erythronium	0.235	0.571	0.292	0.708	present	0.137
grandiflorum						
Eurybia	0.765	0.571	0.559	0.441	absent	0.599
conspicua						
Eurybia sibirica	0.118	0.429	0.215	0.785	present	0.131
Festuca	0.176	0.286	0.407	0.593	present	0.603
campestris						

Scientific Name	Relative	Relative	Relative	Relative	Occurrence	p-
	frequency	frequency	abundance	abundance		value
E and a m	(absent)	(present)	(absent)	(present)	-1	1 000
Festuca	0.235	0.143	0.602	0.398	absent	1.000
Eastwar	0.050	0.000	1.000	0.000		1 000
Festuca	0.039	0.000	1.000	0.000	absent	1.000
Eastura mubra	0.050	0.000	1.000	0.000	abcont	1 000
Festuca rubra	0.039	0.000	1.000	0.000	absent	1.000
Festuca	0.000	0.143	0.000	1.000	present	0.295
Festuca subulata	0.118	0.000	1.000	0.000	absent	0.558
Fostuca	0.059	0.000	1.000	0.000	absent	1 000
trachynhylla	0.039	0.000	1.000	0.000	ausent	1.000
Fragaria	0.941	1.000	0.497	0.503	nresent	0.955
virginiana	0.941	1.000	0.777	0.505	present	0.755
Gaillardia	0.176	0.143	0.523	0 477	absent	1 000
aristata	0.170	0.115	0.020	0.177	uosent	1.000
Galium boreale	0.765	0.714	0.498	0.502	absent	0.982
Galium triflorum	0.294	0.286	0.517	0.483	absent	1.000
Gentianella	0.235	0.000	1.000	0.000	absent	0.324
amarella						
Geranium	0.176	0.429	0.261	0.739	present	0.215
richardsonii					1	
Geranium	0.412	0.143	0.673	0.327	absent	0.441
viscosissimum						
Geum aleppicum	0.059	0.000	1.000	0.000	absent	1.000
Geum	0.059	0.143	0.292	0.708	present	1.000
macrophyllum						
Geum triflorum	0.059	0.143	0.215	0.785	present	0.787
Glycyrrhiza	0.059	0.000	1.000	0.000	absent	1.000
lepidota						
Goodyera	0.647	0.143	0.805	0.195	absent	0.069
oblongifolia						
Gymnocarpium	0.118	0.000	1.000	0.000	absent	0.574
dryopteris						
Hackelia	0.118	0.143	0.553	0.447	absent	1.000
micrantha						
Hedysarum	0.412	0.714	0.362	0.639	present	0.177
sulphurescens						
Heracleum	0.353	0.429	0.572	0.428	absent	0.991
maximum	0.110	0.000	1.000	0.000	1 .	0.570
Heterotheca	0.118	0.000	1.000	0.000	absent	0.578
VIIIOSA	0.252	0.296	0.526	0.464	alaasst	0.070
Heuchera	0.353	0.286	0.536	0.464	absent	0.960
cylinarica						

Scientific Name	Relative	Relative	Relative	Relative	Occurrence	p-
	frequency	frequency	abundance	abundance		value
11	(absent)	(present)	(absent)	(present)	1 (	0.154
Hieracium	0.471	0.143	0.819	0.181	absent	0.154
albijiorum	0.17(	0.000	1.000	0.000	1 (	0.520
Hieracium	0.176	0.000	1.000	0.000	absent	0.538
Scouleri II: anna is an tuinta	0.225	0.420	0.401	0.500		0.402
Hieracium triste	0.235	0.429	0.401	0.599	present	0.403
Hieracium	0.118	0.143	0.553	0.447	absent	1.000
umbellatum	0.050	0.000	1.000	0.000	1	1.000
Juncus	0.059	0.000	1.000	0.000	absent	1.000
arummonaii	0.706	0.420	0.(41	0.250	1 (	0.000
Juniperus	0.706	0.429	0.641	0.359	absent	0.286
<i>communis</i>	0.17(	0.142	0.(22	0.270	-1	0.004
Juniperus	0.176	0.143	0.622	0.378	absent	0.894
Norizonialis Voologia	0.204	0.142	0.641	0.250	abaant	0.569
Koeleria	0.294	0.145	0.041	0.559	absent	0.308
I athronya	0.471	0.571	0.426	0.574	procont	0.560
Lainyrus	0.4/1	0.371	0.420	0.374	present	0.300
Loucanthomum	0.118	0.286	0.236	0.764	present	0.332
vulgare	0.110	0.200	0.230	0.704	present	0.332
l inaria vulgaris	0.118	0.143	0.354	0.646	nresent	0.847
Linuru vuguris	0.176	0.145	0.523	0.040	present	0.047
	0.170	0.200	0.525	0.4//	present	0.000
Linum lewisii	0.176	0.143	0.712	0.288	absent	0.662
Lithospermum	0.353	0.143	0.832	0.168	absent	0.295
ruderale						1.000
Lomatium	0.176	0.143	0.553	0.447	absent	1.000
dissectum	0.050	0.000	1.000	0.000	1 .	1 000
Lomatium	0.059	0.000	1.000	0.000	absent	1.000
	0.050	0.000	1.000	0.000	1 (	1 000
Lonicera aioica	0.059	0.000	1.000	0.000	absent	1.000
Lonicera	0.412	0.429	0.490	0.510	present	1.000
involucrata	0.500	0.000	1.000	0.000	1	0.010
Lonicera	0.588	0.000	1.000	0.000	absent	0.019
utahensis	0.410	0.142	0.750	0.041	1 /	0.000
Lupinus sericeus	0.412	0.143	0./59	0.241	absent	0.299
Luzula parviflora	0.118	0.000	1.000	0.000	absent	0.562
Maianthemum	0.882	0.286	0.753	0.247	absent	0.019
racemosum						
Maianthemum	0.294	0.571	0.227	0.773	present	0.065
stellatum						
Medicago	0.000	0.286	0.000	1.000	present	0.075
lupulina						

Scientific Name	Relative	Relative	Relative	Relative	Occurrence	p-
	frequency	frequency	abundance	abundance		value
Malian	(absent)	(present)	(absent)	(present)		1.000
melica	0.039	0.145	0.292	0.708	present	1.000
Melica subulata	0.353	0.000	1.000	0.000	absent	0.131
Mencu suburara	0.333	0.000	1.000	0.000	absent	0.131
Menziesia	0.412	0.000	1.000	0.000	absent	0.11/
Jerruginea	0.000	0.296	0.000	1.000	magant	0.072
Micranines	0.000	0.280	0.000	1.000	present	0.075
Mitella braveri	0.050	0.000	1.000	0.000	abcont	1.000
	0.039	0.000	1.000	0.000		1.000
Mitella nuda	0.118	0.143	0.590	0.410	absent	1.000
Moehringia	0.118	0.143	0.452	0.548	present	1.000
lateriflora						
Monarda	0.294	0.143	0.658	0.342	absent	0.620
fistulosa	0.000	0.1.40	0.000	1.000		0.000
Nassella viridula	0.000	0.143	0.000	1.000	present	0.296
Neottia cordata	0.118	0.143	0.553	0.447	absent	1.000
Orthilia secunda	0.529	0.286	0.682	0.318	absent	0.247
Osmorhiza	0.529	0.286	0.673	0.327	absent	0.299
berteroi						
Osmorhiza	0.059	0.143	0.292	0.708	present	1.000
depauperata					1	
Osmorhiza	0.059	0.429	0.121	0.879	present	0.063
occidentalis						
Oxyria digyna	0.000	0.143	0.000	1.000	present	0.284
Oxytropis	0.118	0.143	0.292	0.708	present	0.694
campestris var.					1	
spicata						
Oxytropis	0.059	0.143	0.121	0.879	present	0.292
splendens						
Packera cana	0.235	0.000	1.000	0.000	absent	0.327
Packera	0.471	0.571	0.440	0.560	present	0.561
pseudaurea					-	
Parnassia	0.059	0.000	1.000	0.000	absent	1.000
fimbriata						
Paxistima	0.059	0.000	1.000	0.000	absent	1.000
myrsinites						
Pedicularis	0.294	0.429	0.382	0.618	present	0.529
bracteosa						
Penstemon	0.118	0.286	0.340	0.660	present	0.511
albertinus						
Penstemon	0.588	0.429	0.507	0.493	absent	0.873
confertus						

Scientific Name	Relative	Relative	Relative	Relative	Occurrence	p-
	frequency	frequency	abundance	abundance		value
Donstomon	(absent)	(present)	(absent)	(present)	prosont	0.280
ellinticus	0.000	0.145	0.000	1.000	present	0.289
Penstemon lyallii	0.294	0.143	0.553	0.447	absent	0.806
Perideridia	0.059	0.000	1.000	0.000	absent	1.000
gairdneri						
Phacelia hastata	0.294	0.429	0.472	0.529	present	0.649
Phacelia sericea	0.118	0.286	0.248	0.752	present	0.422
Phleum pratense	0.294	0.571	0.340	0.660	present	0.204
Physaria	0.059	0.143	0.292	0.708	present	1.000
didymocarpa						
Picea glauca	0.706	0.714	0.500	0.500	present	0.999
Pilosella	0.059	0.000	1.000	0.000	absent	1.000
aurantiacum						
Pinus contorta	0.588	0.429	0.540	0.460	absent	0.726
Pinus flexilis	0.176	0.286	0.553	0.447	present	0.886
Platanthera	0.059	0.000	1.000	0.000	absent	1.000
dilatata						
Platanthera	0.000	0.143	0.000	1.000	present	0.292
huronensis	0.050	0.000	1.000	0.000	1 /	1.000
Platanthera orbiculata	0.059	0.000	1.000	0.000	absent	1.000
Platanthera	0.176	0.000	1.000	0.000	absent	0.529
stricta						
Platanthera	0.059	0.000	1.000	0.000	absent	1.000
unalascensis						
Poa abbreviata	0.000	0.143	0.000	1.000	present	0.289
Poa alpina	0.059	0.286	0.171	0.829	present	0.187
Poa compressa	0.059	0.000	1.000	0.000	absent	1.000
Poa interior	0.059	0.000	1.000	0.000	absent	1.000
Poa palustris	0.118	0.143	0.407	0.593	present	0.844
Poa pratensis	0.235	0.286	0.390	0.610	present	0.702
ssp. Pratensis						
Poa secunda	0.000	0.286	0.000	1.000	present	0.084
Podagrostis	0.059	0.000	1.000	0.000	absent	1.000
humilis						
Polemonium	0.059	0.143	0.382	0.618	present	1.000
pulcherrimum	0.110	0.1.42	0.452	0.540		1.000
Polygonum	0.118	0.143	0.452	0.548	present	1.000
Polystichum	0.059	0.1/3	0.202	0.708	nrecent	1 000
lonchitis	0.037	0.175	0.272	0.700	Present	1.000

Scientific Name	Relative	Relative	Relative	Relative	Occurrence	p-
	frequency	frequency	abundance	abundance		value
Dereilur	(absent)	(present)	(absent)	(present)		1.000
Populus balgamifora	0.235	0.145	0.397	0.005	absent	1.000
Daisamijera	0.500	0.296	0.690	0.220	abaant	0.226
ropulus	0.388	0.280	0.080	0.520	absent	0.320
Dotontilla	0.050	0.142	0.282	0.619	nragant	1.000
rolenina	0.039	0.145	0.362	0.018	present	1.000
Dotontilla	0.000	0.142	0.000	1.000	prosont	0.285
1 Olenillu glaucophylla	0.000	0.145	0.000	1.000	present	0.205
Potentilla gracilis	0.225	0.420	0.262	0.620	prosont	0.411
Fotentitia gracitis	0.233	0.429	0.302	0.039	present	0.411
Primula	0.059	0.143	0.121	0.879	present	0.286
conjugens	0.050	0.000	1.000	0.000	1 /	1.000
Prosartes hookeri	0.059	0.000	1.000	0.000	absent	1.000
Prosartes	0.412	0.429	0.507	0.493	present	1.000
trachycarpa						
Prunella vulgaris	0.118	0.143	0.292	0.708	present	0.685
Prunus	0.118	0.143	0.673	0.327	absent	0.842
pensylvanica						
Prunus	0.118	0.000	1.000	0.000	absent	0.572
virginiana						
Pseudoroegneria	0.353	0.286	0.541	0.459	absent	0.910
spicata						
Pseudotsuga	0.235	0.000	1.000	0.000	absent	0.329
menziesii						
Pteridium	0.059	0.000	1.000	0.000	absent	1.000
aquilinum						
Pulsatilla	0.000	0.143	0.000	1.000	present	0.293
nuttalliana						
Pyrola asarifolia	0.294	0.143	0.641	0.359	absent	0.633
Pyrola	0.294	0.000	1.000	0.000	absent	0.271
chlorantha						
Pyrola picta	0.059	0.000	1.000	0.000	absent	1.000
Ranunculus acris	0.059	0.286	0.236	0.764	present	0.197
Ranunculus	0.000	0.143	0.000	1.000	present	0.296
cardiophyllus					I	
Ranunculus	0.000	0.143	0.000	1.000	present	0.293
eschscholtzii					1	
Ranunculus	0.059	0.143	0.215	0.785	present	0.790
uncinatus					1	
Rhinanthus minor	0.235	0.000	1.000	0.000	absent	0.283
Rhodiola	0.059	0.143	0.382	0.618	present	1.000
integrifolia					1	

Scientific Name	Relative	Relative	Relative	Relative	Occurrence	p-
	frequency	frequency	abundance	abundance		value
Rhododendron	0.059	0.000	1 000	0.000	absent	1 000
albiflorum	0.057	0.000	1.000	0.000	dosent	1.000
Ribes hirtellum	0.059	0.000	1.000	0.000	absent	1.000
Ribes inerme	0.000	0.143	0.000	1.000	present	0.288
Ribes lacustre	0.588	0.857	0.517	0.483	present	0.479
Ribes	0.294	0.143	0.523	0.477	absent	0.856
viscosissimum						
Rosa acicularis	0.353	0.429	0.467	0.533	present	0.970
Rosa arkansana	0.118	0.143	0.452	0.548	present	1.000
Rosa woodsii	0.353	0.429	0.465	0.535	present	0.928
Rubus idaeus	0.412	0.714	0.350	0.650	present	0.147
Rubus parviflorus	0.765	0.286	0.726	0.274	absent	0.066
Rumex acetosella	0.000	0.143	0.000	1.000	present	0.291
Sabulina rubella	0.000	0.286	0.000	1.000	present	0.074
Salix bebbiana	0.059	0.286	0.292	0.708	present	0.189
Salix discolor	0.353	0.000	1.000	0.000	absent	0.149
Salix	0.000	0.143	0.000	1.000	present	0.290
drummundiana						
Salix planifolia	0.059	0.000	1.000	0.000	absent	1.000
Salix scouleriana	0.412	0.286	0.622	0.378	absent	0.578
Salix vestita	0.000	0.143	0.000	1.000	present	0.293
Sambucus	0.235	0.000	1.000	0.000	absent	0.331
racemosa						
Sanicula	0.000	0.286	0.000	1.000	present	0.074
<i>marilandica</i>	0.050	0.286	0.226	0.764	nragant	0.102
bronchialis	0.039	0.280	0.230	0.704	present	0.192
Saxifraga	0.000	0.143	0.000	1.000	present	0.296
mertensiana					-	
Sedum	0.294	0.714	0.322	0.678	present	0.088
lanceolatum						
Sedum	0.059	0.143	0.292	0.708	present	1.000
stenopetalum						
Selaginella densa	0.176	0.143	0.553	0.447	absent	1.000
Senecio fremontii	0.000	0.286	0.000	1.000	present	0.077
Senecio	0.000	0.143	0.000	1.000	present	0.297
hydrophiloides	0.050	0.142	0.202	0.700	maggart	1.000
senecio triangularis	0.039	0.143	0.292	0.708	present	1.000
	1	1	1	1		1

Scientific Name	Relative	Relative	Relative	Relative	Occurrence	p-
	frequency	frequency	abundance	abundance		value
Shanhandia	(absent)	(present)	(absent)	(present)	abaant	0.620
Snepherala	0.706	0.371	0.555	0.447	absent	0.030
Silono acquiis	0.000	0.1/13	0.000	1.000	nresent	0.20/
Silene acaalis	0.000	0.143	1.000	0.000	present	1.000
Silene parryi	0.039	0.000	1.000	0.000	absent	1.000
Sisyrinchium	0.000	0.143	0.000	1.000	present	0.284
montanum	0.000	0.1.40	0.000	1.000		0.000
Smelowskia	0.000	0.143	0.000	1.000	present	0.292
americana	0.050	0.000	1.000	0.000	1 /	1.000
Solidago	0.059	0.000	1.000	0.000	absent	1.000
gigantea	0.17(	0.000	1.000	0.000	1	0.521
Solidago lepida	0.176	0.000	1.000	0.000	absent	0.531
var. salebrosa	0.110	0.000	1.000	0.000	1 /	0.570
Solidago	0.118	0.000	1.000	0.000	absent	0.572
missouriensis	0.004	0.400	0.452	0.540		0.(20
Solidago	0.294	0.429	0.452	0.548	present	0.638
multiradiata	0.471	0.200	0.755	0.245	1 4	0.250
Sorbus scopulina	0.471	0.286	0.755	0.245	absent	0.350
Sorbus sitchensis	0.059	0.000	1.000	0.000	absent	1.000
Spinulum	0.118	0.000	1.000	0.000	absent	0.785
annotinum ssp.						
Annotinum						
Spiraea lucida	0.882	0.714	0.517	0.483	absent	0.677
Stellaria crispa	0.059	0.000	1.000	0.000	absent	1.000
Stellaria longipes	0.059	0.143	0.292	0.708	present	1.000
Streptopus	0.235	0.000	1.000	0.000	absent	0.291
amplexifolius						
Symphoricarpos	0.765	0.571	0.628	0.372	absent	0.325
albus						
Symphyotrichum	0.588	0.714	0.468	0.532	present	0.616
laeve					-	
Symphyotrichum	0.000	0.143	0.000	1.000	present	0.299
puniceum						
Taraxacum	0.471	0.714	0.368	0.632	present	0.224
officinale						
Thalictrum	0.941	0.714	0.579	0.421	absent	0.280
occidentale						
Tiarella trifoliata	0.118	0.000	1.000	0.000	absent	0.567
var. trifoliata						
Toxicoscordion	0.059	0.143	0.215	0.785	present	0.784
venenosum						
Tragopogon	0.118	0.143	0.673	0.327	absent	0.848
dubius						

Scientific Name	Relative	Relative	Relative	Relative	Occurrence	p-
	frequency	frequency	abundance	abundance		value
TI : C 1:	(absent)	(present)	(absent)	(present)		0.000
Trifolium	0.118	0.143	0.215	0.785	present	0.680
hybridum	0.110	0.000	0.171	0.000		0.150
Trifolium	0.118	0.286	0.171	0.829	present	0.150
pratense	0.000	0.000	0.000	1.000		0.000
Trifolium repens	0.000	0.286	0.000	1.000	present	0.080
Trisetum	0.176	0.000	1.000	0.000	absent	0.528
canescens	0.0.50	0.000	0.1.11	0.0.50		0.100
Trisetum	0.059	0.286	0.141	0.859	present	0.138
spicatum	0.050	0.000	1.000	0.000	1 /	1 000
Trollius	0.059	0.000	1.000	0.000	absent	1.000
albiflorus	0.110	0.000	1.000	0.000	1 (	0.774
Urtica dioica	0.118	0.000	1.000	0.000	absent	0.//4
Vaccinium	0.235	0.143	0.742	0.258	absent	0.642
caespitosum						
Vaccinium	0.235	0.143	0.694	0.306	absent	0.719
membranaceum						
Vaccinium	0.353	0.000	1.000	0.000	absent	0.134
myrtillus						
Vaccinium	0.235	0.286	0.536	0.464	present	1.000
scoparium	0.005	0.551	0.050			0.100
Valeriana	0.235	0.571	0.270	0.730	present	0.109
sitchensis	0.647	0.1.42	0.500	0.010	1 .	0.067
Veratrum viride	0.647	0.143	0.788	0.213	absent	0.067
Verbascum	0.235	0.286	0.452	0.548	present	0.905
thapsus		0.1.10		1.000		0.000
Veronica	0.000	0.143	0.000	1.000	present	0.289
Veroniag	0.000	0.142	0.000	1.000	nracant	0.284
wormskioldii	0.000	0.143	0.000	1.000	present	0.204
Veronica	0.000	0.143	0.000	1 000	present	0.287
wvomingensis	0.000	0.115	0.000	1.000	present	0.207
Vibernum edule	0.059	0.000	1.000	0.000	absent	1.000
Vicia americana	0.529	0.429	0.563	0.437	absent	0.812
Viola adunca	0.412	0.571	0.500	0.500	present	0.709
Viola canadensis	0.294	0.143	0.641	0.359	absent	0.632
Viola glabella	0.059	0.143	0.121	0.879	present	0.291
Viola orbiculata	0.529	0.286	0.673	0.327	absent	0.283
Xerophyllum	0.059	0.000	1.000	0.000	absent	1.000
tenax						
Zizia aptera	0.000	0.143	0.000	1.000	present	0.292