NON-NATIVE PLANT OCCURRENCE AND HUMAN DISTURBANCE AT FRESHWATER SPRINGS IN ALBERTA, CANADA

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For
Brendon Louis Taras McQuaid
(February 3, 1991 – March 15, 2016)

You are dearly missed, my friend.

ABSTRACT

This thesis investigates the factors that affect non-native plant occurrence at freshwater springs in southern Alberta, Canada, with special focus on the effect of human disturbance, and the life history traits of commonly-occurring native and non-native plant taxa. Non-native species richness and abundance were higher at springs with greater human disturbance, and at springs within regions of the province that support greater land use relative to livestock grazing. Non-metric multidimensional scaling demonstrated that commonly-occurring non-native plant taxa were associated with springs that experienced greater human disturbance. Autecological investigation revealed that both native and non-native plant taxa commonly exhibited life history traits that confer greater tolerance to various types of disturbance, including grazing. Overall, these results demonstrate that springs ecosystems that experience greater human disturbance are vulnerable to invasion by non-native plants, which could reduce biodiversity and ecosystem services provided by these distinctive, insular ecosystems.

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LIST OF ABBREVIATIONS

AEP	Alberta Environment and Parks
ANOVA	Analysis of variance
Elv	Elevation
HI	Human impact score
Lat	Latitude
Lon	Longtiude
msl	Meters above sea level
NMDS	Non-metric multidimensional scaling
SE	Standard error of the mean
SEAP	Springs Ecosystem Assessment Protocol
SIP	Springs Inventory Protocol
sp	Species (singular)
spp	Species (plural)
Q	Discharge (m/s^3)

CHAPTER 1: AN OVERVIEW OF THE ECOLOGICAL IMPACTS OF INVASIVE NON-NATIVE PLANTS AND HUMAN DISTURBANCE

1.1 Biological invasion and the history of invasion science

Biological invasion is the phenomenon in which a species is translocated from its native ecological range to a novel region, often bypassing significant biogeographical barriers, where it then establishes a population and spreads vigorously (Simberloff 2013). While it is possible for a species to expand its range across such barriers naturally, the field of invasion science focuses on species that have been introduced to a new region as a result of human intervention (Mack et al. 2000).

As reviewed by Simberloff (2013), some of the earliest records of non-native plants date back to the 1500s in Europe. In the 17th century, following European colonization, several non-native species were documented in both North America and Europe. Pehr Kalm, a student of Carl Linnaeus, was one of the first people to formally study the non-native plants of North America, conducting his work in the 18th century. During his travels, Charles Darwin noted that non-native plants had almost entirely replaced native plant populations on some of the islands that he visited. Darwin is also credited as one of the first scholars to pose the question as to why some non-native species are able to establish and become invasive while others are unable to survive in the non-native range.

Despite a long history of scientists documenting non-native species, the field of invasion science is relatively young. This field was first introduced to a broader audience in 1958 with Charles Elton’s book, *The Ecology of Invasions by Animals and Plants*, and then experienced substantial expansion during the 1980s. Much of the subsequent work in this field continues to incorporate and develop the central themes that were first developed in Elton’s book (Richardson and Pyšek 2008).

It is difficult to determine the exact number of non-native plants species that have established outside of their native range, but it is estimated that more than 13,000 species have become naturalized (i.e., have developed a self-sustaining population in a novel region) around the globe. Of all the continents, North America supports the greatest number of non-native plants, reflecting extensive colonization activities by Europeans (van Kleunen et al. 2015). The rate of transport of non-native species has grown in proportion to global trade, and it is estimated that at least three non-native species are introduced to a new region per year (Mooney and Cleland 2001).

1.2 Factors influencing invasion success

Invasion occurs in five stages: (1) transport, (2) introduction, (3) colonization, (4) naturalization, and (5) spread (Catford et al. 2009). One or more individuals of a species are transported from their native region (1) and are brought to a new region (2), where they survive (3) and establish a self-sustaining population (4) and subsequently spread through the new region (5). It is during the final stages of naturalization and spread when a non-native may be considered invasive (Catford et al. 2009).

There has been considerable focus on determining the ways in which non-native species negotiate these stages to invade a novel region (Richardson and Pyšek 2006). This effort has led to the development of numerous concepts and hypotheses regarding invasion at all ecosystem levels, as well as the influence of various biotic and abiotic factors within the invaded region. Often these factors are considered in terms of their effect on species invasiveness and site invasibility, where invasiveness considers the traits of the invading species, and invasibility considers the factors of the novel environment that influence its susceptibility to invasion (Richardson and Pyšek 2006).

The invasiveness of a non-native plant is often the product of intrinsic life history traits that confer increased competitive ability within the novel region. Some invasive non-native plants employ more generalist life history traits that confer tolerance to a broad range of environmental conditions (Marvier et al. 2004). Similarly, phenotypic plasticity can contribute to the invasiveness of non-native plants by providing the ability to respond to and tolerate a range of environmental conditions. Both a generalist life history strategy and phenotypic plasticity can allow non-native plants to rapidly expand throughout a new range without a significant lag, which would be expected with facilitation through the evolution of adaptive traits (Pyšek and Richardson 2007; Hulme 2008).

Species invasiveness can develop as the result of adaptive selection for increased growth in the non-native range. Blossey and Notzold (1995) proposed the evolution of increased competitive ability (EICA) hypothesis, which states that the invasiveness of a non-native plant is related to an improvement in its competitive ability that results in a shift in allocation of resources from defence (e.g., against herbivory) to growth and reproduction. Over time, there would be selection for these individuals and this could result in that species becoming invasive.

There is some evidence opposing specific predictions of the EICA hypothesis (Richardson and Pyšek 2006), and strong evidence that non-native plant populations benefit from a lack of natural enemies in the novel range (Simberloff 2013). This observation led to the development of the enemy release hypothesis, where non-native plants are able to invade novel regions due to the absence of herbivores and other natural enemies (Keane and Crawley 2002). Decreased control from those organisms can facilitate the plant's expansion. The EICA and the enemy release hypotheses are not exclusive and although these may not explain the success of all invasive plants, many non-native plant populations have evolved adaptive and competitive traits in the novel range, and some benefit from the absence of natural enemies, increasing invasiveness (Felker-Quinn et al. 2013; Simberloff et al. 2013).

One of the goals of invasion science is to identify a generalized 'invasion syndrome', whereby the traits associated with the successful invasion of one or more non-native species could be used to predict the invasiveness of other non-natives (Perkins and Nowak 2013). This goal has been met with limited success, although there are several traits that recur among invasive plants. For example, non-native plants often exhibit high rates of growth and reproduction, which can allow for rapid population expansion (Pyšek and Richardson 2007). However, these apparently conserved traits still vary across different regions (Pyšek et al. 2012).

The invasibility of a region is another important factor that affects whether a non-native species will become invasive. One of the most widely-studied factors is the biodiversity of the recipient region, which relates to a concept originally proposed in Elton (1958). This concept theorizes that regions with high native species richness and diversity were less susceptible to invasion as a result of the decreased availability of unoccupied niches for incoming non-native species. This concept led to the development of the biotic resistance hypothesis (Mack et al. 2000), which states that an ecosystem with high species diversity and richness is better able to resist invasion due to increased competitive interactions between the incumbent species and the non-native. There has been mixed support for this hypothesis, as it has been observed that ecosystems with high species richness can experience high, low, or variable rates of invasion (Richardson and Pyšek 2006). A meta-analysis of biotic resistance conducted by Levine et al. (2004) demonstrated that competition with native plants does not confer community resistance to non-native plant invasion, but it can reduce the spread of already established non-native plants, thus limiting invasion.

Environmental factors related to the climate and physical geography of a novel region also influence site invasibility. These factors are difficult to generalize for all invasive non-native plants, since the influence of climate and physical geography will vary by species. The native climatic niche of a non-native plant can be used, in some cases, to predict areas within a novel region where the plant may establish successfully. However, it has been demonstrated that some invasive non-native plants are able to occupy climatic niches that are distinct from that of their native range (Broennimann et al. 2007).

1.3 Human disturbance and non-native plant invasion

In addition to environmental factors, there is considerable evidence that disturbance from human activities affects site invasibility (Pyšek et al. 2010; Inderjit et al. 2017). Environmental disturbance is often an important component of an ecosystem, but the addition of human disturbance to the natural regime can have detrimental impacts. Native species within an ecosystem are generally adapted to the natural disturbance regime, and thus the addition of human disturbance can disrupt an ecosystem such that it becomes more susceptible to invasion by reducing biodiversity or altering the abiotic conditions (Moles et al. 2012).

Non-native plants are often more abundant in regions that experience disturbance from human activities, such as in urban areas and agricultural regions, and along transport corridors (Alston and Richardson 2006; McKinney 2008). However, even regions with relatively low human disturbance, such as national parks and other protected areas, can support non-native plants. In national parks in the United States, non-native plant richness strongly correlated with the population size of nearby human settlements by acting as a source of non-native propagules (McKinney 2002).

Human disturbance can facilitate non-native species at all stages of invasion (Inderjit et al. 2017). In the early stages of invasion, human activities may increase the propagule pressure of a non-native species, which refers to number of times a non-native species is introduced to a region (Richardson and Pyšek 2006). For non-native plants, this often occurs deliberately or accidentally as the result of horticultural and agricultural activities (Reichard and White 2001). In the mid- and later stages of invasion, human disturbance may facilitate the establishment of a non-native plant population by removing native species and thereby lowering the biotic resistance of a site (MacDougall et al. 2013), or by aiding the dispersal of established non-native plants throughout a region (Mack and Lonsdale 2001).

1.4 Ecological impacts of invasive non-native plants and disturbance

Invasion of non-native species is widely accepted as one of the greatest threats to global biodiversity, as invasive non-native species can alter ecosystem structure and processes such that the native species cannot survive (McGeoch et al. 2010). Non-native plants can reduce biodiversity in their invaded regions in various ways, including direct and indirect resource competition, altering ecosystem processes, or by combining these effects (Levine et al. 2003).

Simberloff (2013) reviewed several of the ways in which non-native plants directly and indirectly affect native species, including those mentioned below. Non-native plants can directly compete with native plants for resources such as water, light, or nutrients, and indirect competition for pollinator visitation and seed dispersal (Levine et al. 2003). Native plant species can also be excluded through allelopathic effects from non-natives that reduce habitat suitability, or by non-natives facilitating changes in disturbance regimes, such as the frequency and intensity of fires (Levine et al. 2003). Non-native species can also implement changes in ecosystem processes by altering the cycling of nutrients or water availability, thus reducing habitat suitability or resource availability for native species. In some cases, multiple non-native species within an ecosystem may facilitate each other's invasion through mutually-beneficial ecological modifications. This phenomenon is termed 'invasional meltdown', whereby the type and magnitude the ecological impact of each non-native species is increased by their co-occurrence in a region (Simberloff and Von Holle 1999).

In addition to decreasing native biodiversity, invasive species can also alter ecosystem services within a region. Ecosystem services are ecological processes that act to benefit or maintain human society. Charles and Dukes (2007) provide a comprehensive overview of the impacts of non-native species on various ecosystem services, including economic, climatic, cultural, and aesthetic services. For example, non-native plants can affect the growth of crop plants, which can lead to economic losses through reduced food production, and alter environmental conditions by affecting regional processes such as flooding.

In some cases, it is difficult to discern whether invasion is the causal agent of ecosystem change (the ‘driver model’), or if invasion is a covariate of other factors causing change (the ‘passenger model’) (sensu MacDougall and Turkington 2005). While there are demonstrable impacts of non-native plants in ecosystems, sometimes other environmental factors drive changes in native biodiversity and ecosystem services (Didham et al. 2007). This underscores the importance of including environmental factors, especially human disturbance, when studying invasive non-native plants. Because invasive species and human disturbance are generally associated, the direct impacts of either may be impossible to disentangle when describing negative ecosystem changes, and thus it is important to consider the two together.

Because of their potential to degrade an ecosystem, conservation efforts often aim to control or eradicate invasive non-native plants, although this can be quite challenging. Mack et al. (2000) highlights many of the difficulties associated with controlling invasive non-native plants, whereby efforts can be hindered by factors such as propagule pressure from extensive seedbanks and continued introduction, an extensive range through the invaded region, or resistance to chemical or mechanical removal. There has been some success controlling invasive plants by introducing natural enemies from their native region (termed biological control) (Blossey et al. 2001), but it not always a feasible solution due to a lack of effective control agents or because of constraints in time and/or funding to develop these programs (Mack et al. 2000). Due to these challenges, it generally agreed that controlling the non-native plants in the early stages of invasion (i.e., transport, introduction, and colonization) is the most effective way to prevent invasion. Consequently, many conservation strategies are focused on preventing the introduction of non-native species and monitoring established non-native plant populations (Simberloff 2014).

1.5 Invasion of insular ecosystems and freshwater springs

Islands are thought to be more susceptible to non-native species invasion as a result of reduced biotic resistance, since island ecosystems typically support fewer species than mainland ecosystems (Wilson and MacArthur 1967). In addition to reduced biotic resistance, islands often support specialized native biota that may be unable to compete with non-native species, and thus experience accelerated invasion by non-natives and even local extinctions of native species (Sax et al. 2007). In fact, several studies have indicated that, globally, a high proportion of islands support high species richness of invasive non-native plants (Pyšek et al. 2008; Richardson and Pyšek 2012).

As with islands, insular island-like ecosystems are also vulnerable to invasion by non-native plant species (Stohlgren et al. 2003). These insular ecosystems are often resource-rich oases within resource-poor regions, and thus support comparatively high biodiversity. Stohlgren et al. (2003) demonstrated that insular ecosystems in the United States, such as wetland and riparian ecosystems, often support high non-native plant richness. Because these ecosystems are often utilized for resources by humans, they are at increased risk of ecological degradation from disturbance from human activities, which can facilitate non-native plant invasion.

Even more so than wetlands and riparian zones, freshwater springs often support insular island-like ecosystems. Springs are hydrogeomorphic features that form where groundwater emerges at or near the Earth’s surface. Springs occur in locations where geologic formations and processes result in the movement from groundwater from an aquifer to adjacent permeable zones aboveground. The geology of the permeable zone can affect the way in which groundwater emerges, resulting in variable hydrology, chemistry, and geomorphology where springs occur (Springer and Stevens 2009). This variation typically results in the development of unique groundwater-dependent ecosystems surrounding a spring, usually with high biodiversity. Many springs throughout the world support endemic species, and often provide critical habitat for sensitive species, especially in arid regions where water is scarce (Stevens and Meretsky 2008).

In many regions, springs are utilized by humans as a source of water (Stevens and Meretsky 2008). Disturbance resulting from human utilization can alter groundwater availability, modify the surrounding geomorphology, and increase pollution. This can lead to decreased biodiversity and diminished ecological services provided by the spring (Kløve et al. 2014). For these reasons, springs are considered among the most threatened ecosystems on the globe. Globally, springs ecosystems are also understudied, often owing to challenge of mapping aquifers and predicting groundwater movement and emergence (Chenini and Ben Mammou 2010). Because of their insular nature, springs ecosystems may be particularly vulnerable to invasion by non-native plants, especially when subjected to human disturbance. However, very few studies have addressed the how human disturbance affects vulnerability of springs ecosystems to non-native plant invasion.

1.6 Disturbance and non-native plants at freshwater springs in southern Alberta

In southern Alberta, freshwater springs are found throughout the region, and form insular ecosystems that are hotspots of biodiversity that support many native plants, including several rare species (Springer et al. 2015). Differences in the type and extent of land use can lead to variation in the type and extent of human disturbance throughout the province. These differences provided an opportunity to compare non-native plant occurrence across a range of human disturbance levels at freshwater springs.

Using data previously collected on springs in Alberta, the richness and abundance of non-native plants were compared to physical environmental factors and human disturbance across springs in southern Alberta. The life history traits of commonly occurring native and non-native spring taxa were also examined to assess autecological similarities and differences in plant communities at springs. The main predictions of this study were that greater occurrence of non-native plants would be found at springs with high human disturbance, and that commonly occurring non-native plants would possess life history traits conferring tolerance to human disturbance.

This project was undertaken to expand our understanding of how human disturbance and environmental factors affect non-native plant occurrence at springs, and to identify the traits of native and non-native plants that colonize these ecosystems. In addition to growing our understanding of the relationship between human disturbance and non-native plant invasion, this research also aims to provide guidance on the management and conservation of spring ecosystems.

1.7 Thesis framework

This thesis is comprised of four chapters, including an introduction, two research chapters, and a concluding chapter. Note that research Chapters 2 and 3 were written in the form of standalone research papers, and thus contain some overlap of background, theoretical concepts, and methodology.

Chapter 2 investigates the impacts of the physical environment and human disturbance on plant communities at freshwater springs in southern Alberta. The variation in the richness and abundance of native and non-native plant species are compared to differences in response to human disturbance, and geographical and hydrological factors.

Chapter 3 characterizes the plant communities of springs in southern Alberta, using an autecological approach to identify the life history traits of commonly occurring native and non-native plants, as well as the patterns of presence and abundance of these taxa with respect to differences in human disturbance and the physical environment at springs.

Chapter 4 provides the overall conclusions of this project, coordinating the findings from Chapters 2 and 3, and provides insight on ways to conserve biodiversity and ecosystem services found at springs that are at risk of degradation from invasive non-native plants and human disturbance.

CHAPTER 2: HUMAN DISTURBANCE AND PHYSICAL ENVIRONMENT INCREASE OCCURRENCE OF NON-NATIVE PLANTS AT SPRINGS IN ALBERTA, CANADA

2.1 Introduction

Invasive non-native plant species have been shown to be a significant cause of biodiversity loss worldwide (Vilà et al. 2011). Identifying the ecological factors that contribute to occurrence of non-native species is an important step in elucidating the mechanisms that cause non-native species to become invasive (Levine et al. 2003; Inderjit et al. 2017). Recognizing the factors associated with the increased occurrence of non-native plant populations can help in the management of ecosystems in two ways: (1) to keep established populations from becoming invasive, and (2) to prevent establishment in ecosystems that do not yet support non-native populations (Theoharides and Dukes 2007; Early et al. 2016).

The literature investigating factors associated with an ecosystems' potential to support non-native species is extensive, and indicate that the success of non-native plants in the initial stages of invasion is largely dependent on the abiotic characteristics of the novel environment (Richardson and Pyšek 2006; Pyšek et al. 2012). The characteristics of the physical environment that favour occurrence are key in the early stages of non-native plant invasion. In particular, attributes such as geographic location and the underlying hydrogeology provide important influences on non-native plant establishment (Pino et al. 2005). In conjunction with the physical environment, human disturbance is often correlated with successful establishment of non-native species (Pyšek et al. 2010). Human activities such as raising livestock can facilitate non-native plant occurrence by lowering the biotic resistance of a site by creating habitat for colonization through the removal of already established species (Keeley et al. 2003), and by providing a vector for non-native propagules to enter the novel ecosystem (Mack and Lonsdale 2001).

Smaller ecosystems with limited physical extent, such as islands, are thought to be more vulnerable to increased non-native plant occurrence compared to larger, less isolated ecosystems (Richardson and Pyšek 2012), however this concept is still under debate (Pyšek et al. 2008; Vilà et al. 2011). This concept arose from the observation that islands typically have lower species richness and higher occurrences of endemic species compared to mainland ecosystems, which makes them more susceptible to biological invasions (Kier et al. 2009; Rojas-Sandoval et al. 2017). Non-native species often arrive to these islands as a result of deliberate human introductions through agriculture and horticulture (Reichard and White 2001), although accidental introductions also occur (Lehan et al. 2013). When non-native plants are introduced to these ecosystems, they may possess competitive advantages over the native species, or the established population may acquire these traits over time (EICA hypothesis; Blossey and Notzold 1995). These traits may include increased reproductive ability, better resource acquisition, disturbance tolerance, or competitive interactions through vigorous growth or allelopathic effects (see review in Richardson & Pyšek 2006).

Freshwater springs represent insular, island-like ecosystems that are limited in spatial extent, and often differ from the surrounding environment with respect to hydrology, geology, and the associated biota. This is especially true in arid regions, where springs differ considerably from the surrounding areas, and may provide critical habitat and water for local species (Stevens and Meretsky 2008; Huntington et al. 2016).

Depending on the type of groundwater emergence, and physical aspects including local topography and climate, springs often support bands, rings, or patches of vegetation that are distinct from the habitat surrounding the spring. The plant communities found within these springs are typically species rich and often include endemic species (Huntington et al. 2016). In southern Alberta, springs occur across diverse geographic regions and, in many cases, are utilized as a source of freshwater for agricultural activities, such as grazing, as well as for recreational purposes (Springer et al. 2015). In Springer et al. (2015), it was reported that the springs included in that study supported a quarter of Alberta's native flora on an area collectively representing less than 0.001% of the provincial land area.

The aim of this study was to explore how aspects of the physical environment and human disturbance affect non-native plant occurrence at freshwater springs in southern Alberta. The springs surveyed in southern Alberta provides an ideal system to conduct this research, since there are both physical environmental and regional land use differences in this part of the province that may affect the occurrence of non-native plants. The Rocky Mountain zones support forestry, recreation, and tourism; the foothills and parkland regions are utilized for livestock grazing; and the prairie zones support extensive crop production (Downing and Pettapiece 2006). These differences provide variation in the type and intensity of human disturbances, which may act to promote non-native plant occurrence. The geographical variation created by the west-to-east transition from the Rocky Mountains to the prairies results in differences in the hydrogeomophology of springs in this region, including the groundwater emergence type (termed 'discharge sphere') (Springer and Stevens 2009), and the microhabitat surface type. Microhabitat surface types are determined in part by the substrate and collection of water, and may also affect the occurrence of non-native plants species.

With this framework, we compared plant community variables, specifically richness and abundance of non-native and native plant species, to physical geographic factors and human disturbance levels across springs in southern Alberta, following the work conducted by Springer et al. (2015). It was predicted that: (1) non-native species richness and abundance would be highest at springs with the greatest human disturbance, (2) non-native species richness and abundance will be greatest in regions that support the greatest land use, and (3) non-native species would be less abundant in wetter hydrogeomorphic zones that require specialized strategies to survive inundation.

2.2 Methods

2.2.1 Study sites

This study was conducted using vegetation and environmental data collected at 55 springs surveyed in southern Alberta by Springer et al. (2015) from 2008 to 2012. These springs were located between 49°1′41.17″N to 52°3′30.68″N latitude and –109°59′28″W to –115°35′26.8″W longitude and ranged in elevation from 822 to 2048 msl (Figure 2.1). Each spring was surveyed following sampling protocol developed by the Springs Stewardship Institute (Stevens et al. 2016). The springs surveyed were selected based on the availability of data on the location and accessibility of the site during the time of survey. These locations were determined using various provincial sources, including maps published by the Alberta Geological Survey, hydrology maps, regional reports, park managers, non-governmental organizations, and private landowners. These springs were managed by Parks Canada (Banff and Waterton Lakes National Parks), Alberta Environment and Parks (provincial parks, Crown land), the Nature Conservancy of Canada and partners, and private landowners.

2.2.2 Field inventories

The data collected at each site followed the Level 2 spring ecosystem inventory protocols developed by the Springs Stewardship Institute for establishing baseline conditions for future monitoring and management (Stevens et al. 2016). These protocols outline collection procedures for observations and measurements of physical and cultural variables by trained experts to ascertain the ecological condition of the spring. The Springs Inventory Protocol (SIP) was used for the collection of physical and biological characteristics, and the Springs Ecosystem Assessment Protocol (SEAP) for the collection of characteristics pertaining to ecosystem quality and management (Stevens et al. 2016). The Level 2 inventory protocol begins with the identification of the location of the spring, including land ownership details, and then proceeds with documentation of the landscape setting and type of spring, the condition of the spring relative to natural and/or human alterations, georeferencing (e.g., latitude, longitude, elevation), measurements of the annual solar radiation budget, descriptions of microhabitat surface types, identification of plant species and percent cover, identification of invertebrates and vertebrate organisms, descriptions of geomorphology, description and measurement of water discharge, measurement of water quality, and the collection of cultural data, including indigenous, archaeological, and historical usage, and identification and rating of human influences. Only the specific data collection methods for variables used in this study will be elaborated on further.

2.2.3 Physical environmental characteristics

Measurements of elevation (msl), latitude, and longitude were all documented around the point of groundwater emergence at each site. The area (m^2) of each spring was determined based on the amount of land under groundwater influence, based on protocol outlined in Stevens et al. (2016). Within the total spring area, the area of different microhabitat surface types were measured. Microhabitat surface types were identified based on differences in geomorphology, hydrology, substrate, and vegetation within the site (Stevens et al. 2016). The discharge sphere (Springer and Stevens 2009), or classification of groundwater emergence type, was also determined using the criteria outlined in Springer and Stevens (2009). Spring discharge (m^3/s) was measured where possible, and microhabitat surface types were classified within the area of the spring. These were simplified according to the moisture level of the (wet, moderately wet, or dry) due to low sample sizes for some specific microhabitats. Sites were also classified according to the physiographic region (Pettapiece 1986) in which the spring was found to differentiate sites according to variation in the physical landscape relative to geography, biota, and land use. Physiographic regions were included the Rocky Mountains, foothills, parkland, and plains. The parkland region in this study refers to the upland aspen-lodgepole pine transition zone between mixed grass prairie and the foothills zones (Downing and Pettapiece 2006), and is comprised of a combination of natural subregions (Figure 2.1).

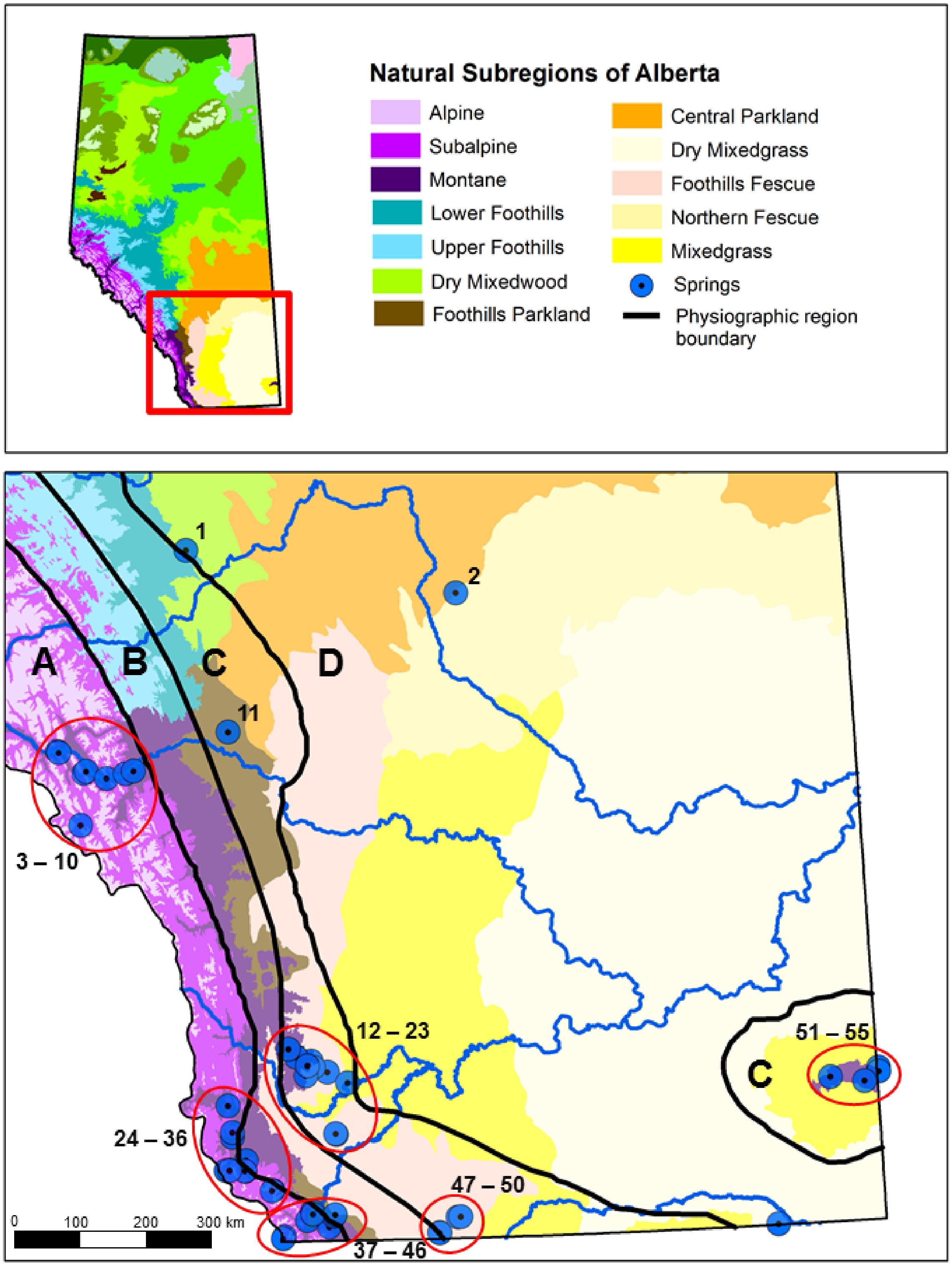

Figure 2.1. Map of 55 springs surveyed by Springer et al. 2015, adapted from the Natural Subregions of Alberta Map prepared by Downing and Pettapiece 2006. The letters identify the physiographic regions: A) Rocky Mountains, B) Foothills, C) Parkland, and D) Plains. Map identification numbers correspond to spring names listed in Appendix A (Table A.1).

2.2.4 Human impact score

The degree of human disturbance at each site was characterized using the Freedom from Human Influences assessment in the SEAP, which assigned a numeric score based on observation the following criteria: apparent surface water quality (clarity); extent of flow regulation/alteration; nearby roads, trails, railroads; evidence of construction; evidence of livestock with grazing or fecal pads; evidence of recreation such as with trails for off-highway vehicles; and adjacent land conditions such as proximity to cultivated fields. Scores of 0 – 6 were assigned, where 0 indicated poor or low site quality and 6 indicated high site quality within each criterion. These scores were averaged to produce a Freedom from Human Influences score for each spring, which was divided by 6 and then subtracted from 1 to produce a human impact score. The human impact score ranged from 0 – 1, with 0 indicating relatively pristine site condition with minimal human disturbance, and 1 indicating severely degraded site condition with extensive human disturbance.

2.2.5 Plant community survey

Sites were surveyed in July or August to characterize vegetation during the interval of maximal foliar cover. All plants growing within the total spring area were identified to the species level where possible, and subsequently assigned status as native or non-native, according to the USDA Plants Database (2017) for the Great Plains or Western Mountains regions. Plant specimens unidentified or identified to the family level only were excluded in these analyses due to the unreliability of assigning nativity status. For the sake of simplicity, the term “species” will be used in lieu of “taxon”, and specimens identified to the genus level are treated as unique taxa.

Species richness values, equivalent to the number of species, were determined for each site for both native and non-native species. Species richness values were also determined for each microhabitat surface type at each spring. Due to differences in the areas of the springs and the different microhabitat surface types, species richness values were transformed to correct for area sampled, whereby species richness represented the number of plant species ÷ $\log_{10}$ of area (Nilsson et al. 1994; Gotelli and Colwell 2001).

The percent cover of each species in each microhabitat was visually estimated for six strata types (aquatic, non-vascular, ground, shrub, mid-canopy, and tall canopy). These values were summed across strata types to produce cover index values for all native and non-native species within each microhabitat. With multiple strata, the overall cover values could exceed 100%. The weighted cover index for native and non-native species at each site was calculated by taking the sum of the cover index in each microhabitat and then multiplying that sum by the area of the spring.

2.2.6 Statistical analysis

Pearson product-moment correlations were calculated using SPSS v. 21 (IBM 2012) to assess the linear relationships between various environmental factors and the plant community variables listed in Table 2.1. Significant correlations between plant community traits and combinations of environmental factors were analyzed using multiple linear regression with both forward and backward model selection using Akaike’s Information Criterion (Bozdogan 1987) using the base *lm* package incorporated in R (R Core Team 2016).

One-way analyses of variance (ANOVA) were conducted, comparing native and non-native plant richness and cover across physiographic region, spring discharge sphere, and microhabitat surface type moisture level, with significant differences identified with Tukey's HSD post-hoc test using the *lm* package in R (R Core Team 2016). Where the assumptions of the one-way ANOVA were not met, Kruskal-Wallis non-parametric H tests were conducted (Kruskal and Wallis 1952), with pairwise significant differences identified using the Kruskal-Wallis multiple comparison test using the *pgirmess* package in R (Giraudoux 2016).

2.3 Results

A total of 526 unique plant taxa were identified across the 55 springs surveyed in southern Alberta, Canada. Of those observed, 66 (12.5%) were identified as non-native and 460 (87.5%) were native to the province. For each spring surveyed, numbers of individual plant species ranged from 0 to 18 non-native species and 9 to 90 native species. The maximum number of species observed at a particular spring was 101 (11 non-native, 90 native), and the minimum number of species surveyed was 10 (1 non-native, 9 native).

All Pearson's product-moment correlations generated from the bivariate correlation are presented in Table 2.1. Among physical environmental factors, elevation was positively correlated with longitude and spring discharge, and negatively correlated with human impact score. Latitude was positively correlated with longitude and human impact score. Comparing physical environmental factors to plant community variables, non-native richness was negatively correlated with elevation, and positively correlated with human impact score; non-native cover index was negatively correlated with elevation and longitude, and positively correlated with human impact score; native species richness was positively correlated with elevation, and negatively correlated with latitude; and native species cover index was negatively correlated with human impact score. Among plant community variables, non-native species richness was positively correlated with non-native cover index, and negatively correlated with native cover index; native species richness was positively correlated with native species cover; and non-native and native cover indices were negatively correlated.

Table 2.1. Pearson product-moment correlations between independent environmental factors and dependent plant community variables inventoried at freshwater springs (n=55) in Alberta, Canada. Statistically significant patterns are distinguished using two levels of confidence: bold for $p < 0.05$, bold and underlined for $p < 0.01$. Red and blue text indicate positive and negative correlations, respectively.

		Lat	Long	Area	Discharge	Human impact score	Species richness		Cover index	
							Native	Non-native	Native	Non-native
Elevation (msl)		-0.204	**0.413**	-0.061	**0.275**	**-0.346**	**0.308**	**-0.310**	0.032	**-0.389**
Latitude[†]			**0.358**	0.196	0.213	**0.267**	**-0.300**	-0.011	-0.188	0.015
Longitude[‡]				0.217	0.185	-0.129	0.124	-0.141	0.050	**-0.435**
Area (m^2)					0.023	0.203	-0.159	0.066	-0.051	-0.060
Discharge (m^3/s)						-0.038	-0.151	-0.139	-0.089	-0.094
Human impact score							-0.215	**0.347**	**-0.378**	**0.384**
Richness	Native							0.042	**0.299**	-0.190
	Non-native								**-0.409**	**0.573**
Cover	Native									**-0.362**

[†] Latitude increases south to north.

[‡] Longitude increases east to west.

Table 2.2. Multiple linear regression analyses of relationships between plant community variables and environmental factors. Row values represent the variables in the equation generated from multiple linear regression analyses of the form $y = \beta_0 + \beta_i x_i + \ldots + \beta_n x_n$, where β_0 is the intercept, $\beta_{i\text{-}n}$ are the coefficients of the predictive independent environmental factors $x_{i\text{-}n}$ of plant community variables y.

Plant community variables (y)		Intercept (β_0)	Environmental factor coefficients ($\beta_{i\text{-}n}$)				Adjusted r^2
			Elevation (msl)	Latitude	Longitude	Human Impact Score	
Species richness	Non-native	3.70	-0.0015	-	-	3.48	0.13
	Native	43.26	0.0050	-1.51	-	-	0.12
Cover index	Non-native	578.44	-	-	-5.10	39.79	0.27
	Native	99.15	-	-	-	-109.15	0.13

The physical environmental site variables included in the forward and backward model selection process for the multiple regression analysis were as follows: elevation and human impact score for non-native species richness; elevation and latitude for native species richness; elevation, longitude, and human impact score for non-native cover index; and elevation, longitude, and human impact score for native cover index. The equations of the best fit models selected to predict non-native and native species richness and cover index and their coefficients of determination based on multiple linear regression analysis are presented in Table 2.2. Non-native species richness was best predicted by elevation and human impact score (adjusted $r^2 = 0.13$), native species richness was best predicted by elevation and latitude (adjusted $r^2 = 0.12$), non-native cover index was best predicted by longitude and human impact score (adjusted $r^2 = 0.27$), and native cover index was best predicted by human impact score (adjusted $r^2 = 0.13$).

The results of the one-way analyses of variance comparing non-native and native species richness and cover across site physiographic region are presented in Figure 2.2. Springs in southern Alberta were located in four physiographic regions: Rocky Mountains, foothills, parkland, and plains. Non-native species richness was significantly different across these physiographic regions ($F_{3,51} = 6.96$, $p < 0.001$), with significantly higher non-native species richness in the parkland region compared to the foothills (Figure 2.2A). The assumptions of the ANVOA were not met for the non-native cover index data, so both an ANOVA and a Kruskal-Wallis H test were run to compare non-native cover index across physiographic region, and both tests returned significant differences (ANOVA: $F_{3,51} = 9.10$, $p < 0.001$; Kruskal-Wallis: $H = 26.97$, $df = 3$, $p < 0.001$). Tukey's HSD post-hoc analysis of the ANOVA result showed significant differences between the parkland region and the Rocky Mountains and foothills regions, while the post-hoc analysis of the Kruskal-Wallis result demonstrated a difference between the parkland and Rocky Mountain regions only. Figure 2.2B indicates the results given by the Kruskal-Wallis analysis, although this figure shows mean non-native cover, rather than the median. Native species richness and cover index were not significantly different across physiographic regions (richness: $F_{3,51} = 0.22$, p = 0.88; cover index: $F_{3,51} = 1.66$, p = 0.19; Figure 2.2A and B).

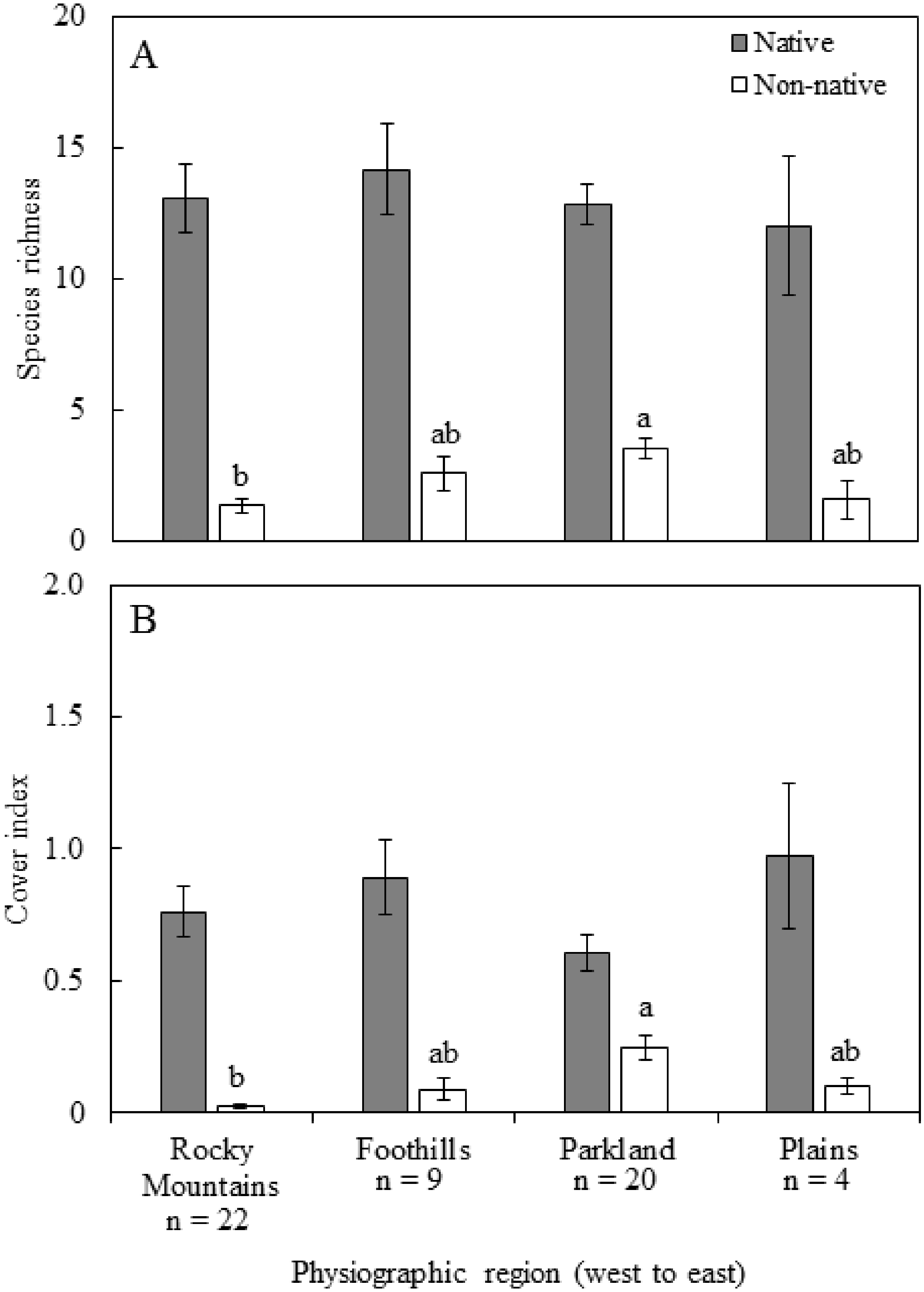

Figure 2.2. Mean (± SE) A) species richness (spp/log(m^2)) and B) cover index of non-native and native plants at freshwater springs across physiographic regions in Alberta, Canada. Letters indicate statistically significant differences. Sample sizes of springs in each region are indicated on the x-axis.

The results of the analyses of variance comparing non-native and native species richness and cover indices compared across springs' discharge spheres are presented in Figure 2.3A and B. Only springs classified as helocrene (n = 13), hillslope (n = 28), rheocrene (n = 7), and limnocrene (n = 4) were included in these analyses, as the other discharge spheres (cave, hanging garden, and gushet) were only observed once. Non-native species richness and cover index were not significantly different across discharge sphere (richness: $F_{3,48} = 0.24$, $p = 0.87$; cover index: $F_{3,48} = 0.67$, $p = 0.57$). Native species richness and cover index were also not significantly different across discharge sphere (richness: $F_{3,48} = 1.43$, $p = 0.25$; cover index: $F_{3,48} = 0.24$, $p = 0.87$).

Within each spring, non-native and native species richness and cover index were compared across the relative moisture level of microhabitat surface types (wet, intermediate, and dry). The assumptions of ANOVA were not met for any plant community variable, so both the one-way ANOVA and Kruskal-Wallis H-test were run. Note that the results presented in Figure 2.4 are means (± SE) with significance assigned according to the results of the Kruskal-Wallis analysis. Non-native species richness was significantly different across moisture levels (ANOVA: $F_{2,187} = 5.16$, $p = 0.007$; Kruskal-Wallis: $H = 21.07$, $df = 2$, $p < 0.001$). Tukey's HSD post-hoc and Kruskal-Wallis multiple comparisons post-hoc analyses identify significantly higher non-native species richness in dry compared to wet microhabitats, and intermediate compared to wet microhabitats (Figure 2.4A). Native species richness was significantly different across moisture levels (ANOVA: $F_{2,187} = 4.41$, $p = 0.013$; Kruskal-Wallis: $H = 11.44$, $df = 2$, $p < 0.001$). Tukey's HSD post-hoc and Kruskal-Wallis multiple comparisons post-hoc analyses indicated significantly higher native species richness in dry compared to wet microhabitats (Figure 2.4A). Non-native cover index was significantly different across moisture levels (ANOVA: $F_{2,187} = 8.96$, $p < 0.001$; Kruskal-Wallis: $H = 36.29$, df = 2, $p < 0.001$). Tukey’s HSD post-hoc identified significantly higher non-native cover in the intermediate compared to dry, intermediate compared to wet, and dry compared to wet microhabitats, while Kruskal-Wallis multiple comparisons post-hoc identified significantly higher non-native cover in intermediate compared to wet and dry compared to wet microhabitats (Figure 2.4B). Native cover index was significantly different across moisture levels (ANOVA: $F_{2,187} = 10.03$, $p < 0.001$; Kruskal-Wallis: $H = 23.29$, df = 2, $p < 0.001$). Tukey’s HSD post-hoc and Kruskal-Wallis multiple comparisons post-hoc analyses identified significantly higher native cover in dry compared to wet and intermediate compared to wet microhabitats (Figure 2.4B).

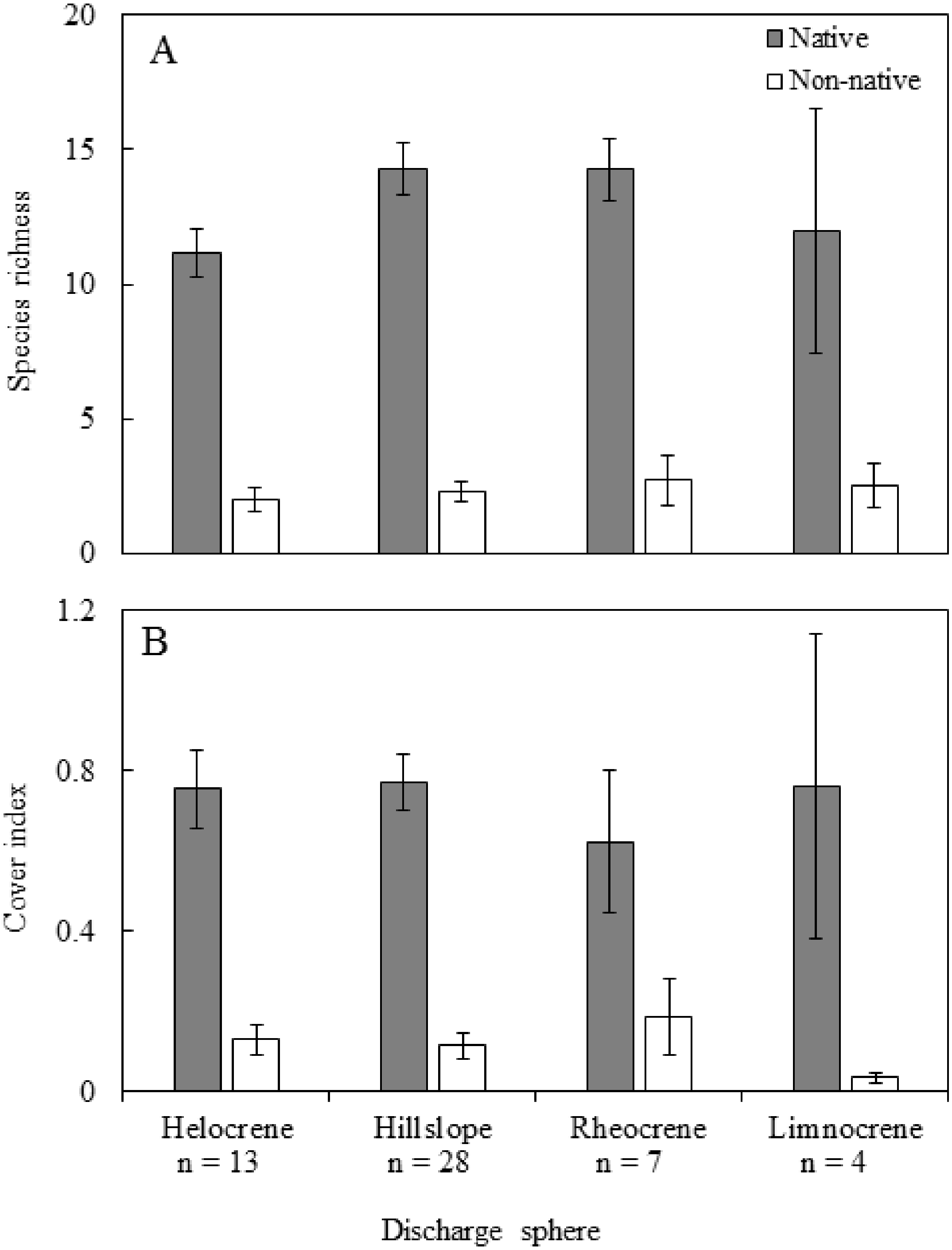

Figure 2.3. Mean (± SE) A) species richness (spp/log(m^2)) and B) cover index of non-native and native plants at freshwater springs across spheres of discharge in Alberta, Canada. Discharge spheres are arranged in order from least confined (helocrene/marsh) to most confined (rheocrene/creek, limnocrene/pool) groundwater emergence. Sample sizes of springs in each classification are indicated on the x-axis.

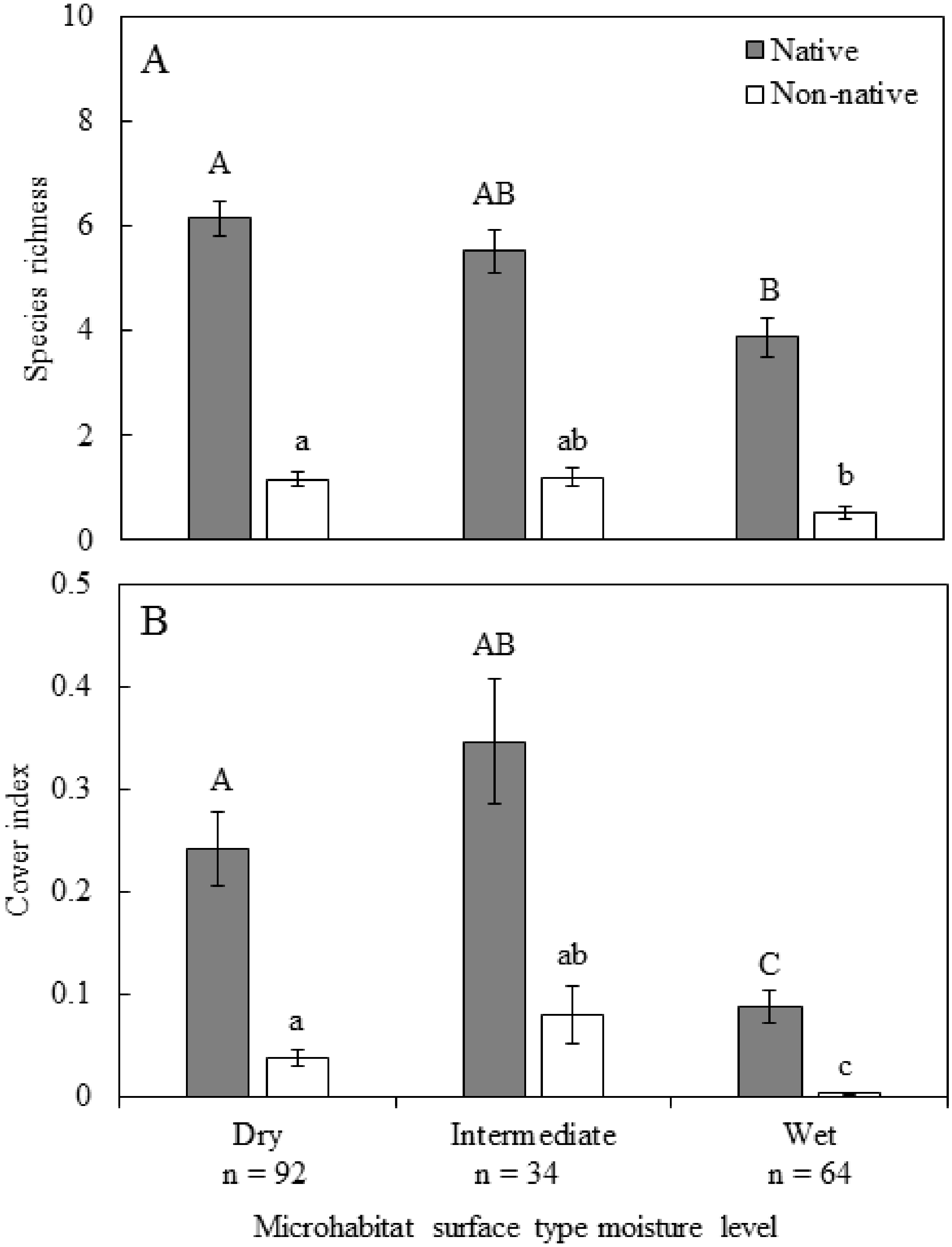

Figure 2.4. Mean (± SE) A) species richness (spp/log(m^2)) and B) cover index of non-native and native plants at freshwater springs across microhabitat surface type moisture level classifications in Alberta, Canada. Letters indicate statistically significant differences (upper case for natives and lower case for non-natives). Sample sizes for microhabitats in each category are indicated on the x-axis.

2.4 Discussion

This study investigated patterns of native and non-native species richness and abundance (cover index) in plant communities around freshwater springs in southern Alberta, Canada. The patterns explored relative differences in human disturbance, physical geography, and hydrogeomorphic features to investigate factors that affect the invasibility of springs by non-native plants.

The analyses demonstrated the nature and strength of relationships between plant community variables and physical environmental factors (Table 2.2). Non-native species richness and abundance were higher at springs with higher human impact scores, indicating that human disturbance increased non-native plant occurrence, which supported the first prediction of this study. This is a common pattern in other systems, where an increase in both the richness and abundance of non-native plant species are associated with a broad range of human activities (Catford et al. 2009; Pyšek et al. 2010; Inderjit et al. 2017). Human disturbance also decreased native plant abundance, with human impact score accounting for 13% of the variation in native cover index. The decline in native plant abundance at sites with greater human disturbance is another common theme in prior studies (reviewed in Mack et al. 2000). This trend is of concern for springs in southern Alberta, since reliance on groundwater is anticipated to increase over the following decades (AEP 2014), and this could increase stress on spring ecosystems (Kløve et al. 2014). Given that springs in arid and semi-arid regions often act as refugia for wetland plant species, increased human disturbance at these sites could result in the eventual loss of regionally rare or threatened wetland plants (Kløve et al. 2011).

Elevation and longitude were both significant predictors of non-native plant establishment at springs, where non-native richness decreased with elevation, and non-native abundance decreased with longitude (Table 2.2). Elevation and longitude are correlated in southern Alberta, with the high-elevation Rocky Mountains in the west transitioning to low-elevation prairie in the east, which may account for the observed patterns in non-native plant occurrence. The results of the one-way analyses of variance and Kruskal-Wallis test support this pattern, as non-native species richness and cover index were significantly lower at Rocky Mountain springs relative to parkland region (Figure 2.2). These results support the second prediction, as non-native plant occurrence follows patterns of land use in the province. Springs surveyed within the Rocky Mountain region were largely within National Parks (Banff and Waterton Lakes) and provincial wildlands, which are managed to reduce human impacts in part to conserve the increased biodiversity in these areas (Downing and Pettapiece 2006; AEP 2014). The decreased occurrence of non-native plants is likely the result of management of these areas that aims to reduce human disturbance. National Parks, for example, often experience lower rate of species invasion as a result of reductions in human disturbance (Foxcroft et al. 2011). There is evidence that the preservation of the natural disturbance regime of an ecosystem may also reduce non-native plant occurrence, which may also account for this pattern, as protected areas are generally managed to promote natural disturbance regimes, like controlled burns (Alpert et al. 2000).

In contrast, the parkland physiographic region is subject to high human disturbance, particularly though livestock activities, with many areas in this region allocated to cattle grazing (Downing and Pettapiece 2006; AEP 2014). Disturbance from livestock has been linked to increased non-native plant occurrence: animals can act as vectors for non-native plant propagules via zoochory (Chuong et al. 2016), and promote spread of non-native species by reducing the abundance of native species, thereby increasing invasible areas (Kimball and Schiffman 2003; Brooks et al. 2006). Cattle may also selectively avoid grazing on unpalatable non-native plants which, when combined with the removal of native species, can facilitate rapid invasion of the grazed area by the non-native species (DiTomaso 2000). Interestingly, the facilitation of non-native plant invasion can lead to the degradation of grazing land where the abundance of unpalatable non-native species is increased such that livestock can no longer gain sufficient nutrients at that site (Duncan et al. 2004). At springs in the Mojave Desert, USA, Fleishman et al. (2006) found a correlation between grazing intensity and the non-native plant occurrence, where the richness and cover of non-native plants were greatest at moderate and high levels of grazing.

Surprisingly, the plains physiographic region, which is the eastern-most and lowest elevation region in the province, did not support the greatest richness and abundance of non-native plant species (Figure 2.2). This region is subject to intensive crop production, and much of the native grasslands have been replaced by patches of monotypic crop stands. Croplands provide a continuous source of non-native propagules, increasing propagule pressure, which is strongly correlated with the successful establishment of non-native plant populations, especially in the early stages of invasion (Alston and Richardson 2006; Catford et al. 2009). Given this trend, it is somewhat surprising that the plains region did not support the greatest non-native species abundance, though this may be due to the low number of plains region springs (n = 4).

Relative to land use trends, it was interesting that native species richness did not vary across the physiographic regions, despite apparent associations with elevation (positive) and latitude (negative) (Figure 2.2A). It is possible that, while these trends were statistically significant, there is no strong biological effect of these factors on plant communities. In general, species richness in the Northern Hemisphere tends to increase with decreasing latitude toward the Equator (Kreft and Jetz 2007). Native species abundance declined with greater human disturbance, although this relationship is not reflected in land use differences across physiographic regions in the province. This might relate to the intensity of disturbance, as opposed to the type of disturbance. No significant difference in human impact score was detected across the physiographic regions (Figure 2.2B), but the types of disturbance do change (Downing and Pettapiece 2006).

There were differences in non-native plant occurrence across microhabitat surface type moisture levels, where richness and abundance were significantly higher in dry compared to wet microhabitats. This pattern provides support for the prediction that wetter microhabitats would support fewer non-natives. Hydrophytic plants require specialized adaptations to tolerate substrate saturation or inundation (Catford et al. 2011). This environmental factor influenced both non-native and native plant species, where the wettest microhabitats supported the lower richness and abundance of plants (Figure 2.4). The increased occurrence of non-native and native plants in the dry and intermediate microhabitats may also be the result of a trade-off between water stress tolerance and physical barriers within colonizable spaces. Plants that colonize these intermediate microhabitats are likely more tolerant of stress from near-inundation, thus reducing competition with more generalist species that might display limited flood tolerance. With a reduction in generalist species, the inundation-tolerant species are able to increase in abundance within these surface types because there is no physical barrier to increasing cover as there would be with colonizing more wet microhabitats, such as pools, where plant abundance would be constrained by barriers such as water depth.

Overall, the results of this study demonstrate that both the physical environment and the extent of human disturbance influence the richness and abundance of non-native plants at freshwater springs in southern Alberta. In order to best manage springs for long-term biodiversity and ecosystem services, conservation efforts should focus on limiting human disturbance, especially in regions with extensive land use for livestock grazing. Springs support distinctive, biodiverse landscape features and are highly deserving of increased recognition and protection in southern Alberta, as is the case in many regions across Canada and worldwide.

CHAPTER 3: LIFE HISTORY TRAITS OF NATIVE AND NON-NATIVE PLANTS AT FRESHWATER SPRINGS IN ALBERTA, CANADA

3.1 Introduction

Invasion by non-native plants can have deleterious ecological consequences in the habitats that they invade (Pyšek and Richardson 2010; Vilà et al. 2011; Simberloff et al. 2013). These species have been associated with the loss of native species, thus reducing the native biodiversity of the invaded region, and can also disrupt ecosystem services (Simberloff 2014). In many regions, the removal of invasive plants is virtually impossible (Blossey et al. 2001; Genovesi 2005), and thus preventing the spread of these species is often more effective in controlling invasion (Simberloff et al. 2013). In order to prevent the spread of non-native plants, it is important to know which characteristics facilitate their ability to invade an ecosystem (Lloret et al. 2005; Pyšek and Richardson 2007).

Invasive plants are often ecological generalist species that are capable of growing under a broad range of habitat conditions, and often display high tolerance to disturbance and exhibit prolific of reproduction (Sciance et al. 2016). Numerous studies have attempted to determine a suite of traits can be used as predictors of the invasiveness of any particular plant species (reviewed in Pyšek and Richardson 2007). These studies typically examine the traits of plants that have already successfully invaded a region, often comparing these traits to those of plants native to the region. Some studies also included examinations of environmental or abiotic traits of the invaded region (Lloret et al. 2005). However, there has been limited consensus, and it has been recognized that species' traits may only partially explain invasion success (Dupré and Ehrlén 2002; Pyšek et al. 2009).

Despite the difficulty in predicting the invasiveness of a particular species, managing invasive plants is important for conserving the structure and function of vegetation communities. As such, strategies to discourage invasion should be developed. Based on previous work, the most effective approach involves integrating information of specific biotic traits of non-native species and introduction history within the environmental context of the invaded ecosystem (reviewed in Simberloff et al. 2013).

Freshwater springs constitute ecosystems at high risk of plant invasion due to their insular nature as small, island-like ecosystems (Stevens and Meretsky 2008; Kløve et al. 2014). The risk of invasion of non-native plants is typically greater in regions with high human disturbance (Mack and Lonsdale 2001; McKinney 2002; Pyšek et al. 2010), and springs are often utilized by humans for a variety of industrial and recreational purposes (Stevens and Meretsky 2008; Springer et al. 2015). Springer et al. (2015) surveyed 55 springs across southern Alberta, Canada and found that those ecosystems supported a quarter of the plant taxa found within the province on less than 0.001% of the provincial land area. In addition, springs in the province that are outside of protected areas may be subjected to disturbance from livestock grazing, and it was shown in the previous chapter that the occurrence of non-native plants was greater at springs with high human disturbance. While reducing or eliminating these types of disturbance would likely reduce invasion at springs in southern Alberta, understanding the traits associated with non-native plants found in these ecosystems would also help identify species that could become invasive so as to monitor their spread.

Using the springs surveyed by Springer et al. (2015), this study aimed to explore and characterize some of the traits that are associated with invasiveness among common non-native plants found at these springs. This study also sought to characterize the traits of native plants at the springs, in an effort to assist in future monitoring efforts by providing a list of spring taxa and of prospective traits for other plant species that may occur at other springs in Alberta or elsewhere in western Canada. Subsets of the most commonly observed native and non-native taxa were investigated for life history traits and introduction history, as well as the physical environmental factors of springs that support those taxa. It was predicted that non-native taxa would exhibit traits associated with greater disturbance tolerance and generalist life history strategies, and that native taxa would be largely hydrophyte specialists.

3.2 Methods

3.2.1 Inventories of springs

These investigations were undertaken using data collected from 55 springs surveyed in southern Alberta from 2008 to 2012, as introduced in Springer et al. (2015). The springs surveyed were located between 49°1′41.17″N to 52°3′30.68″N latitude and –109°59′28″W to –115°35′26.8″W longitude, and ranged in elevation from 822 to 2048 msl (see Chapter 2, Figure 2.1).

Data were collected on the physical and biological characteristics of each spring, including documenting and measuring site elevation (msl) and geographic location (latitude and longitude) at or near the point of groundwater emergence, the area (m^2) of the spring, and groundwater discharge (m^3/s). All present plant taxa were identified, and their percent cover quantified.

The Springs Ecological Assessment Protocol (Stevens et al. 2016) was used to identify and quantify the extent of different human disturbances using the Freedom from Human Influences assessment. Observations of the following criteria were made: apparent surface water quality (clarity); extent of flow regulation/alteration; nearby roads, trails, railroads; evidence of construction; evidence of livestock with grazing or fecal pads; evidence of recreation such as with trails for off-highway vehicles; and adjacent land conditions such as proximity to cultivated fields. A score of 0 – 6 was assigned to each criteria, where 0 indicated poor site quality and 6 indicated good site quality within each criterion. These scores were averaged across all criterion to produce a Freedom from Human Influences score for each spring. This score was then divided by 6 and then subtracted from 1 to generate a human impact score from 0 – 1, where 0 indicated a relatively pristine spring with little evidence human disturbance, and 1 indicated degraded spring condition with evidence of extensive human disturbance.

3.2.2 Vegetation surveys and taxa selection

Springs inventories were conducted during the months of July or August during the interval of greatest foliar cover. All plants present within the spring area were identified. Any unknown specimens collected for future identification. The percent cover of each taxon was visually estimated for six strata types (aquatic, non-vascular, ground, shrub, mid-canopy, and tall canopy), and were then summed across strata to generate a cover index value for each plant taxon at each spring (Chapter 2, subsection 2.2.5).

The plant lists from each site were combined to create a master list of all plant taxa observed across all springs surveyed, and then grouped according to genus. To select the most commonly observed plants, these were sorted by the numbers of occurrences across all springs. From this, the top quartile was nine and this subset of plant taxa was used in the following analysis.

3.2.3 Non-metric multidimensional scaling

To investigate patterns of the presence/absence and abundance of plant taxa at these springs, non-metric multidimensional scaling (NMDS) ordinations were undertaken using PC-ORD v.6 (McCune and Mefford 2011), using Sørensen's distance calculation in two dimensions with a maximum of 250 iterations, a stability criterion of 0.00001, and a step length of two, with varimax rotation applied. The environmental variables used in the NMDS procedure were selected using Pearson's product-moment correlation to determine the variables associated with the richness and abundance of native and non-native plant taxa (Table 2.1 in Chapter 2). The variables included were elevation (msl), latitude, longitude, spring discharge (m/s^3), and human impact score.

Two matrices were developed for presence/absence and cover index values for the most commonly observed taxa. In cases where multiple species within the same genus were surveyed at the same spring, cover index values for each species were summed to produce one cover index value for that genus.

3.2.4 Autecology

To characterize the traits of commonly occurring plants at springs, a subset of the eleven most commonly observed taxa was selected from the taxa used in NMDS ordination, split evenly between non-native and native plants (n = 22, Table 3.1). The life history traits were selected according to their potential to contribute to establishment success, and included guild (growth form), longevity, flowering phenology, pollination strategy, fruit or seed type, seed dispersal mechanism, vegetative reproduction ability, and tolerance to disturbance. For non-native taxa only, the approximate time of introduction and the region of origin of species within each genus were also documented. Information on these traits was collected for each of the taxa of interest where available from regional field guides, the USDA Plants database (USDA 2017), and from prior reports. The wetland indicator status of species within each taxon was also noted (USDA 2017). The proportion of taxa exhibiting each particular life history trait was calculated. If a taxon included species that fit more than one type of life history trait (e.g., biennial and perennial), that taxon was counted under each trait. The proportion of taxa exhibiting a particular trait were also subdivided according to their status as native and non-native.

3.3 Results

The taxa master list included a total of 526 taxa (460 native, 66 non-native). The top quartile of most commonly observed plants included 74 taxa that were surveyed a minimum of nine times across 55 springs in southern Alberta. Of these taxa, 63 were native and 11 were non-native (Appendix B, Table B.1).

The results of the NMDS ordinations are presented in Figure 3.1. In both ordinations, elevation and spring discharge provided the strongest correlations with spatial arrangement of taxa. The presence/absence ordination of taxa in spring space is presented in Figure 3.1A. Human impact score and longitude were associated with axis 1, and latitude and spring discharge were aligned with axis 2. The cover index ordination of taxa in spring space is presented in Figure 3.1B. Human impact score and longitude were aligned with axis 1, and latitude and discharge were aligned with axis 2. In both the presence/absence and cover index ordinations, non-native taxa tended to cluster along the human impact score vector (Fig 3.1). This clustering is most distinct in the presence/absence ordination, with the spatial mean of the non-native taxa aligned closely with the human impact score vector. Native taxa did not show any obvious clustering patterns in either the presence/absence or cover index ordinations, where the both the spatial means of native taxa are near the origin of the environmental vectors (Fig 3.1). In both ordination spaces, the spatial means of the native and non-native do not share any spatial overlap.

The taxa explored in the autecological analysis are listed in Table 3.1. Plants within the genus *Carex* (sedges) were the most commonly observed native taxa, with a total of 101 observations of at least 32 species. The next most common taxon surveyed was the genus *Juncus* (rushes), observed 67 times with at least 11 unique species identified. The most commonly observed non-native taxon was the genus *Cirsium* (thistles), which were observed 40 times, with at least two species identified. The non-native taxa were not as diverse as the native taxa in terms of species membership, with three being the greatest number of species identified within a taxon, which was found for the genera *Trifolium* (clovers) and *Rumex* (sorrels).

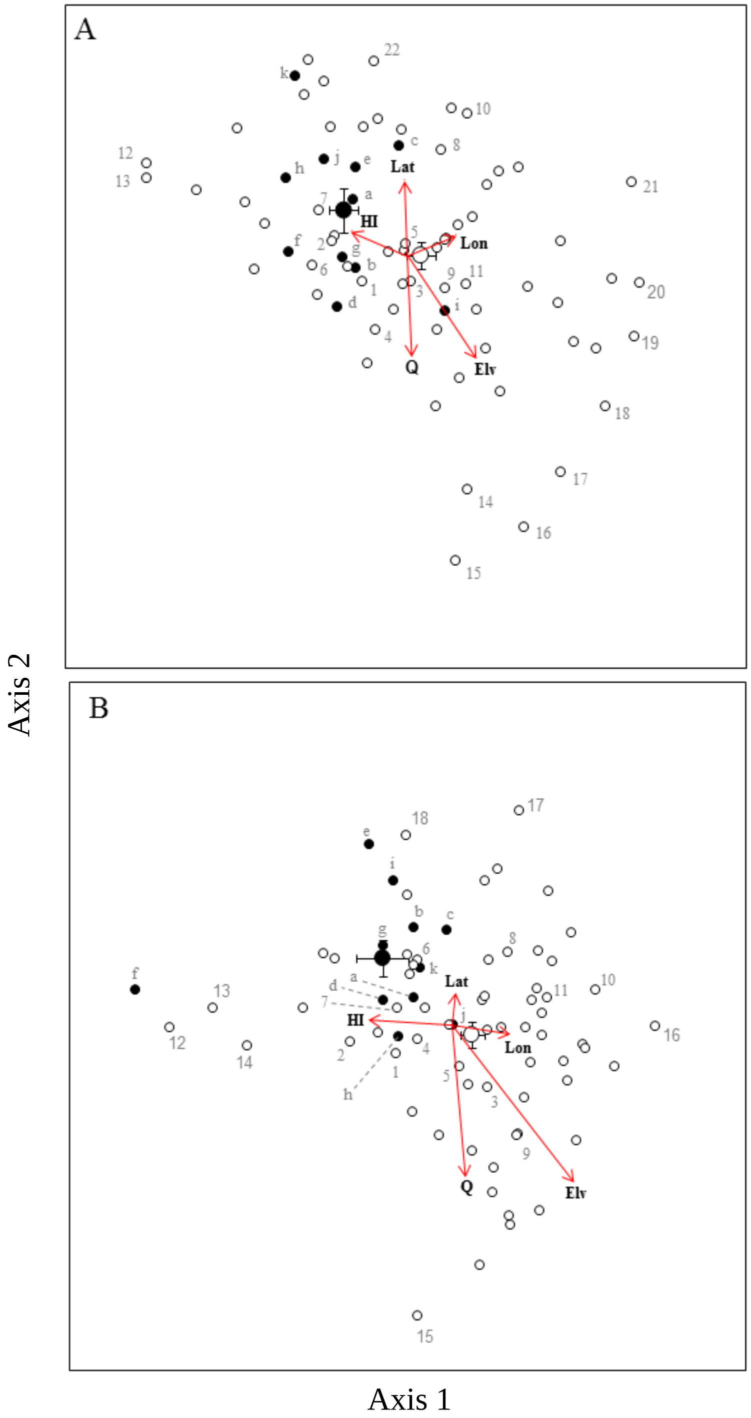

Figure 3.1. Non-metric multidimensional scaling of the A) presence/absence and B) cover index of the most commonly observed plant taxa non-native (black, n = 11) and native (white, n = 63) at 55 springs in Alberta, Canada. Large circles represent mean (± SE) position of non-native and native taxa in ordination space. Red arrows represent vectors for environmental factors through the ordination space (Elv = elevation msl, Lon = longitude, Lat = latitude, HI = human impact score, Q = spring discharge m/s^3). Numbers and letters in correspond to the taxa characterized in the autecological analysis in Table 3.2. Numbers >11 correspond to taxa listed in Appendix B (Table B.3).

Table 3.2 summarizes the proportion of taxa exhibiting particular life history traits of interest, as well as the proportion of those that were native and non-native. The majority of taxa surveyed were either forbs or graminoids, and all but one exhibited perennial growth. Most taxa flowered during spring, with relatively equal proportions among natives and non-natives, and most employing either wind or insects as pollination vectors. Two non-native taxa, *Taraxacum* (dandelions) and *Medicago* (medicks), were capable of autogamous fertilization. The majority of taxa produced achenes. Zoochory, or animal-assisted seed dispersal, was the most common mechanism of seed dispersal, with 64% of taxa employing this mechanism, split evenly among natives and non-natives. More than half of these taxa were capable of vegetative reproduction, through rhizomous or stoloniferous growth, or clonal suckers.

Each of the 22 taxa surveyed exhibited at least one trait conferring disturbance tolerance, including resistance to drought, inundation, and grazing, association with primary successional habitats, or growing in disturbed soils. Because grazing is a common form of type disturbance in southern Alberta (AEP 2014), and is associated with increased occurrence of non-native plant species (see Chapter 2 Results), this category was broken down to look at traits associated with disturbance from grazing: grazing tolerance and herbivory defence. Roughly half of the taxa sampled exhibited tolerance to grazing and, of those, almost 80% were native. The majority of taxa sampled were not documented as having structural or phytochemical defences against herbivory, but those that did were exclusively non-native. These defences included sharp spines on leaves, and phytochemicals such as coumarins and saponins in leaves.

Table 3.1. Life of the most commonly observed plant taxa at 55 springs in Alberta, Canada. Species included in this table were observed a minimum of three times, and are listed in order of most frequent occurrence. NMDS codes refer to the characters presented on Figure 3.1. All species are listed in the Appendix B (Table B.2).

NMDS code	Times observed	Genus	Species
Native (n = 11)			
1	101	*Carex*	*microptera, utriculata, aquatilis, pellita, aurea, nebrascensis, praegracilis*
2	67	*Juncus*	*balticus, ensifolius, longistylus, drummondii, nodosus*
3	50	*Equisetum*	*arvense, laevigatum, hyemale*
4	47	*Epilobium*	*ciliatum, clavatum*
5	47	*Salix*	*bebbiana*
6	35	*Achillea*	*millefolium*
7	32	*Potentilla*	*fruticosa, gracilis*
8	32	*Rosa*	*acicularis, woodsii*
9	31	*Geum*	*aleppicum, macrophyllum, rivale*
10	31	*Populus*	*balsamifera, tremuloides, trichocarpa*
11	29	*Galium*	*boreale, triflorum*
Non-native (n = 11)			
a	40	*Cirsium*	*arvense, vulgare*
b	36	*Phleum*	*pratense*
c	33	*Taraxacum*	*officinale*
d	32	*Poa*	*pratensis*
e	26	*Bromus*	*inermis*
f	19	*Rumex*	*acetosa, crispus, stenophyllus*
g	16	*Trifolium*	*pratense, repens*
h	10	*Medicago*	*lupulina*
i	10	*Plantago*	*major*
j	9	*Melilotus*	*albus, officinalis*
k	9	*Tragopogon*	*dubius*

Table 3.2. Life history traits of the commonly observed native (n=11) and non-native (n=11) plant taxa at 55 springs in Alberta, Canada. Native and non-native proportions are based on the total proportion of taxa (n=22) exhibiting a particular life history trait.

Life history trait		Proportion		
		Total	Native	Non-native
Guild	Forb	0.64	0.43	0.57
	Graminoid	0.23	0.40	0.60
	Shrub	0.09	1	0
	Tree	0.05	1	0
Longevity	Annual	0.27	0.17	0.83
	Biennial	0.32	0.14	0.86
	Perennial	0.96	0.52	0.48
Flowering phenology	Spring	0.68	0.47	0.53
	Summer	0.41	0.56	0.44
Pollination strategy	Autogamous	0.09	0	1
	Insect	0.59	0.54	0.46
	Wind	0.46	0.40	0.60
Fruit/seed type	Achene	0.41	0.56	0.44
	Capsule	0.23	0.80	0.20
	Caryopsis	0.14	0	1
	Legume	0.14	0	1
	Nutlet	0.05	1	0
	Sporangia	0.05	1	0
Seed dispersal mechanism	Anemochory	0.36	0.50	0.50
	Hydrochory	0.18	0.50	0.50
	Unassisted	0.09	1	0
	Zoochory	0.64	0.43	0.57
Vegetative reproduction	Yes	0.64	0.57	0.43
	No	0.36	0.38	0.63
Grazing tolerance	Yes	0.46	0.78	0.22
	No	0.55	0.25	0.75
Herbivory defence	Yes	0.18	0	1
	No	0.82	0.58	0.42

Of the non-native taxa surveyed, 8 of 11 included species with upland or facultative upland wetland indicator status, indicating a preference for drier habitats. Of the native taxa sampled, those species exhibited a wider range of wetland indicator statuses, from obligate wetland to facultative upland. No species within the native taxa sampled were obligate upland species.

3.4 Discussion

This study sought to characterize the environmental and autecological traits of native and non-native plant taxa growing at springs in southern Alberta. This study also aimed to identify traits of common non-native plants, as well as to identify the traits of native plants at commonly grow at springs in Alberta. It was predicted that non-native taxa would be associated with human disturbance and would possess more generalist, non-specialized life history traits, and that native taxa would tend to be more specialized hydrophytes.

The NMDS ordination found that non-native taxa presence and abundance were associated with springs that had greater human impacts more than any other environmental trait (Figure 3.1). This pattern supported our prediction, as human activities are often the vectors through which non-native plants enter novel ecosystems (Mack and Lonsdale 2001). This result ties in with the findings of the autecological survey, which found that most non-native taxa possessed some degree of tolerance to habitat disturbance (Table 3.2). Surprisingly, there were only small proportion of non-native taxa that demonstrated specific tolerance to disturbance from livestock. Because livestock production is pervasive form of disturbance in southern Alberta, it was expected that common non-native plants would have specific traits to cope these activities, such as increased vegetative growth in response to herbivory (Blossey and Notzold 1995).

However, only a small proportion of the taxa exhibiting grazing tolerance or herbivory defences were non-native. There were other traits that confer tolerance to disturbance at springs with greater human impacts, such as the ability to produce a taproot or an extensive root, which would contribute to these plants’ ability to tolerate greater disturbance.

Both native and non-native taxa tended to be entirely, or partially, perennial (Table 3.2). A review on the traits that confer invasiveness to plants by Pyšek and Richardson (2007) indicated mixed results, where both short-lived (annual, biennial) and long-lived (perennial) life history strategies have been associated with increased invasiveness. This review suggested that annual and biennial plants may be more abundant in the early stages of invasion due to the increased allocation of resoures to reproduction (Pyšek et al. 2003), where results from Sutherland (2004) suggest that perennial plants tend be more successful in the later stages of invasion. With respect to springs in southern Alberta, the perennial non-native plants may be more likely to invade over time and might warrant greater monitoring, compared to the annual and biennial non-native taxa.

At springs with greater disturbance from livestock grazing, the ability to utilize animals as seed dispersers would be an advantage for non-native taxa, and may account for their association with human impacts. Zoochory has been identified in other studies as a common trait among non-native plants, although any mode of seed dispersal that is efficient will affect invasion ability, though this trait is environment-dependent (Pyšek and Richardson 2007). In southern Alberta, zoochory likely represents an efficient mode of seed dispersal for non-native springs plants, as livestock production is abundant in this part of the province, and many springs are utilized as a source of water for livestock (AEP 2014; Springer et al. 2015).

There were no obvious patterns of clustering of native plant taxa observed in either the presence or abundance NMDS ordinations, where all native taxa were apparently distributed evenly among all environmental vectors in ordination space. This result suggests a lack of specialization among native taxa that commonly occur at springs in Alberta, with respect to traits related to the environmental factors included in the ordinations. The autecology survey demonstrated a variety of life history strategies employed by common native plant taxa, and like the non-native taxa, traits conferring disturbance tolerance were common among the taxa sampled. The ability to tolerate disturbance among native taxa may be related to the nature of springs as magnets for native herbivores. Springs are sources of freshwater for many animals, including vertebrate and invertebrate herbivores (Stevens and Meretsky 2008; Springer et al. 2015). As such, native springs plants would likely have experienced selective pressure for increased disturbance tolerance from native wildlife such as deer and elk that graze and trample on these plants.

Four of the most commonly observed native taxa (*Carex*, *Juncus*, *Achillea*, *Potentilla*) clustered along the human impact score axis of the presence NMDS ordination, possessed tolerance to grazing, and are able to colonize disturbed soils. These characteristics constitute shared traits between commonly observed native and non-native taxa at springs. This is an interesting result relative to the concept of weedy species, which are those plants that are considered to be a nuisance, but may be native or non-native (Colautti and MacIsaac 2004). These disturbance-tolerant native taxa could also increase in abundance at springs with increasing human activities alongside non-native taxa, constituting concern for biodiversity within these sites. Recently, there has been some attention paid to aggressive native species within habitats that may have negative impacts on biodiversity within these regions (Marrs et al. 2013). These invasive native plants have to potential to be as detrimental as non-native invaders within the site (Marrs et al. 2010), and should thus be monitored by ecosystem managers as well.

This study has characterized some of the traits of commonly occurring plants at springs in southern Alberta, and highlights similarities and differences among native and non-native taxa. This serves as a tool to be used in future botanical inventories of springs to predict the taxa or traits of taxa that may be present. With respect to management, these findings demonstrate that disturbance tolerance is a common trait among commonly occurring native and non-native plants. The results also demonstrate that springs tend to support more plants with more generalist life history strategies, with respect to reproduction and disturbance tolerance. However, the native plant taxa tended to be facultative and obligate wetland species, while the non-native taxa tended to be upland and facultative wetland species, which suggests that native springs plants tend to be hydrophytic specialists, while the non-native plants are more tolerant of dry soil conditions.

These findings highlight springs as ecosystems that may experience high levels of human disturbance and disturbance from native herbivores, and thus support taxa that are adapted to those environments. Those that are interested in the management and conservation of springs for conserving biodiversity and ecosystem services should pay special attention to both native and non-native taxa with greater tolerance to disturbance, as these plants may pose a long-term threat to the continued functionality of these rare and distinctive ecosystems.

CHAPTER 4: RESEARCH SUMMARY AND SYNTHESIS OF DISTURBANCE AND NON-NATIVE PLANTS AT FRESHWATER SPRINGS

4.1 Human disturbance and non-native plants at springs in Alberta, Canada

The purpose of this project was to expand our understanding of how the occurrence of non-native plants at springs ecosystems was affected by human disturbance and environmental conditions, and to characterize the traits of commonly-occurring non-native plants found at springs in Alberta, Canada. Due to the insular, island-like nature of springs ecosystems, it was expected that they would be susceptible to invasion by non-native plants. I predicted that the occurrence of non-native plant species would be the greatest at springs that experienced increased disturbance from human activity, and that commonly-occurring non-native taxa plants would possess life history traits that conferred tolerance to disturbance, which would allow those taxa to become especially common at springs in regions of higher human disturbance. The traits of commonly-occurring native plants were also determined, thus allowing for the assessment of similarities and differences among the life history traits of the common plants at springs in southern Alberta.

In Chapter 2, it was demonstrated that increased non-native plant richness and abundance at springs were associated with greater human impact scores, and with springs that emerged within the parkland physiographic region. These findings agree with the ordinations conducted in Chapter 3, which demonstrated that non-native taxa tended to occur in association with springs with greater human impact scores. Together, these results indicated that non-native plants are closely associated with disturbance from livestock grazing in Alberta. The results in Chapter 2 also demonstrated an association between environmental condition and non-native plant occurrence, where non-native plants tended to colonize drier microhabitat surface types. This result agrees with the autecological analysis conducted in Chapter 3, which revealed that plant species within commonly-occurring non-native taxa favoured drier upland habitats, compared to the native taxa surveyed, of which there were more obligate and facultative wetland species. The autecological analysis in Chapter 3 demonstrated that both native and non-native taxa exhibited traits that would be expected of generalist growth strategies, including the ability to exploit multiple pollination and seed dispersal vectors, tolerance of colonize disturbed soils, and the ability to reproduce vegetatively.

With the current projections of global climate change, Alberta is expected to increase its demand on groundwater resources (AEP 2014), which means that some springs may experience decreased discharge over time. Changes in the hydrological regime of a spring could result in changes to that ecosystem which may favour invasion. For example, a decrease in the availability of water to these ecosystems would likely result in changes to biodiversity, specifically decreasing the occurrence of obligate wetland plants. While many of the commonly occurring native and non-native plants surveyed in this work are likely to continue to thrive under these conditions, the loss of species that require abundant water could lead to decreased biotic resistance in the ecosystem, and thus facilitate non-native plant invasion. In addition to decreased biodiversity, changes to the hydrological regime could also alter the invasibility by providing more available ground for colonization. Under these circumstances, the potential of any established non-natives plants to become invasive would increase.

Efforts to effectively monitor changes in non-native plant occurrence at springs would require repeated surveys of the conditions of the springs of interest. As with any ecosystem, springs will experience environmental changes over time. This fact was exemplified by revisits to Turtle Mountain Sulfur Spring, a spring that was surveyed in 2009 by Springer et al. (2015). This spring was originally classified a limnocrene (i.e., pool-forming) spring, emerging adjacent to the Crowsnest River in the Rocky Mountains (Figure 4.1A). The spring-fed pool was created as the result of beaver dam, which blocked the flow of water from the spring to the Crowsnest River. However, in 2013 the Crowsnest River experienced a significant flood that likely resulted in structural damage to the beaver dam. The damage to this dam no longer sequestered the emergent groundwater, which now forms a channel that flows into the Crowsnest River (Figure 4.1B and C).

This change resulted in an increase in availability of dry ground for vegetative colonization, and a subsequent change in the plant community composition (Figure 4.1). In 2015, there was extensive colonization of the newly-available ground by the non-native grass *Phragmites australis* (Figure 4.1B). In 2017, however, the cover of *P. australis* was reduced, and there was an increase in the cover of the native cattail *Typha latifolia* (Figure 4.1C). During the initial survey of this spring in 2009, neither *P. australis* nor *T. latifolia* were observed, and now both species are abundant at this site. Given a thorough resurvey of this spring, it is likely that many of the plant species that were previously observed would be present at different abundances, if present at all. As well, this spring had a human impact score of 0.56, suggesting moderate human impacts due to its close proximity to an active railway and major highway. It is possible that, given greater human disturbance, that this spring may have continued to support a large population of non-native plant species. While the magnitude of this change is somewhat anomalous, given the generally static nature of springs ecosystems (Stevens and Meretsky 2008), it highlights the importance of long-term monitoring of springs for assessing environmental changes that may facilitate non-native plant invasion.

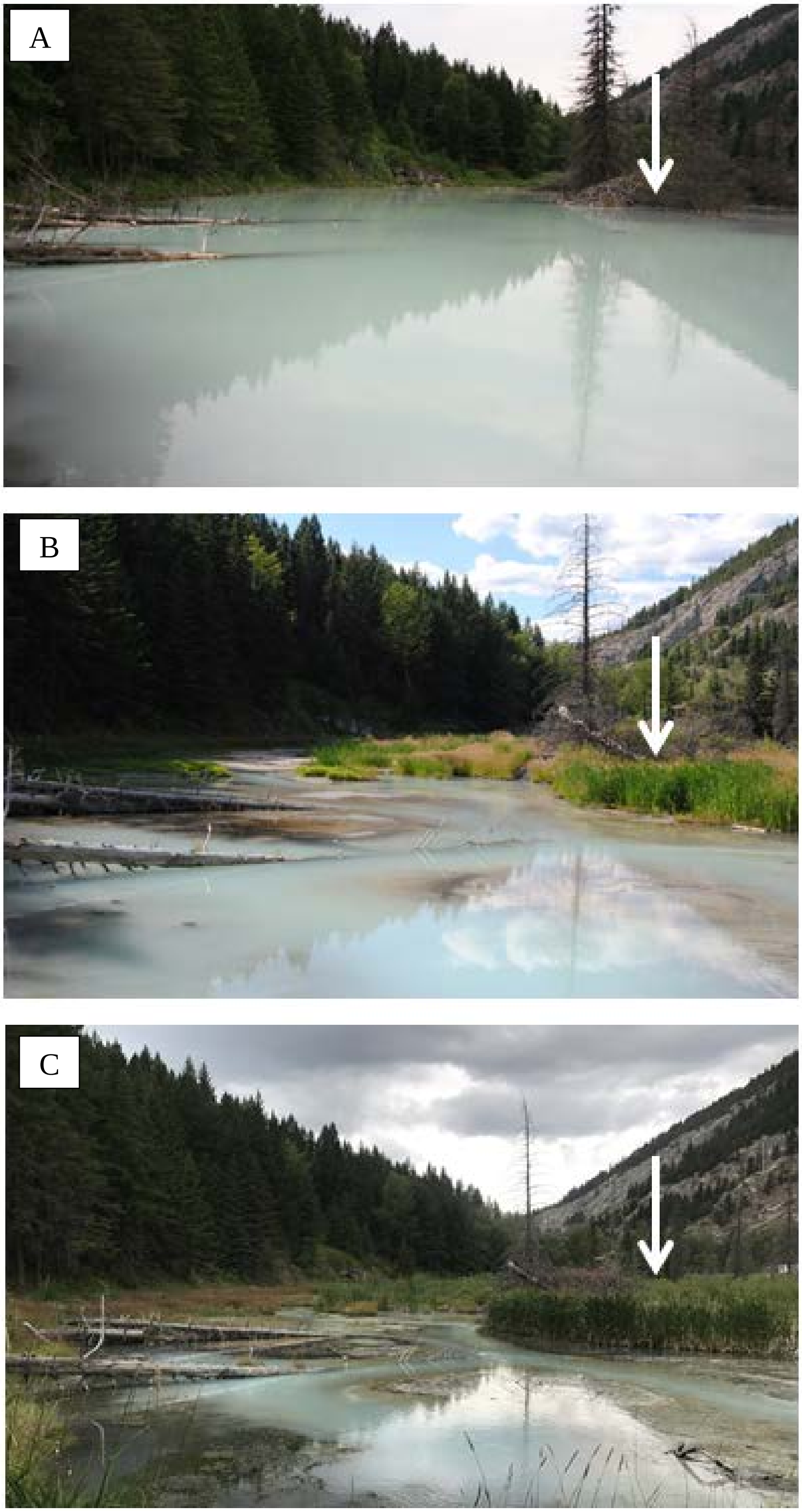

Figure 4.1. Turtle Mountain Sulfur Spring on A) July 27, 2009, B) July 23, 2015, and C) August 13, 2017. Successive photographs show difference in spring ecosystem before and after the removal of a beaver dam behind the photographer. Arrows indicate areas that experienced shifts in plant community composition and abundance.

4.2 Future prospects and suggestions for management

In order to best protect the ecological integrity of springs, improvements must be made to the study and monitoring of these ecosystems. An important step in this process will be to conduct more effective mapping of the locations of springs, as these landscape features are poorly mapped in most of the world (Stevens and Meretsky 2008). The use of GIS technology has been demonstrated as an effective tool for mapping springs (Chenini and Ben Mammou 2010), and represents a promising way in which these ecosystems may be mapped throughout the globe.

Given the understudied nature of springs, there is a need for the development and implementation of standardized protocols for assessing and monitoring these landscape features. The protocols (Stevens et al. 2016) use for the collection of data analyzed in this thesis could be utilized by ecosystem managers, as they can be used for initial surveys, as well as for long-term assessment. Long-term data collection following a standardized protocol would allow for comparisons of many different variables at springs. For those ecosystem managers that are interested in preserving biodiversity, monitoring efforts should focus on minimizing human disturbance at springs that support rare or endemic plant species. For springs on private land, especially those used for livestock production, minimizing human disturbance will present a challenge, but could be achieved by providing alternative water sources, such as piping part of the spring flow to a drinking trough, or by erecting barriers that limit access to the spring, in addition to continued monitoring.

Any newly-introduced non-native plant with high tolerance for natural and human disturbance should be monitored if found growing at a spring, as those traits could allow that species to invade in response to various changes in the disturbance regime. The surveys conducted by Springer et al. (2015) provide a baseline for comparison of changes in the biotic and abiotic conditions of these springs over time, and the results of this thesis demonstrate how human disturbance is linked with non-native plant occurrence, and as well as the traits of commonly-occurring native and non-native plants. Together, these results can be used to help inform future management strategies for springs in southern Alberta.

Springs are unique ecosystems that provide significant ecological value, and they are at risk of degradation from human disturbance and non-native plant invasion. Environmental stewards in Alberta, and worldwide, should recognize springs as hotspots of biodiversity, and as ecosystems that provide important resources and services for humans. Especially in the face of a changing climate, future conservation and management plans for springs should focus on efforts that preserve the ecological integrity of these unique ecosystems and educate society on their intrinsic value. These efforts to will allow for the preservation of springs ecosystems, and will help ensure that springs persist as important, valued features of the landscape for future generations to come.

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APPENDIX A

Table A.1. Identification number and corresponding name of 55 springs surveyed in Alberta, Canada (Chapter 2, Figure 2.1).

Map ID	**Spring name**	**Map ID**	**Spring name**
1	Raven Brood Trout Station Spring	41	Waterton Spring Creek Spring
2	Soap Hole 1	42	Waterton Willow Spring
3	Upper Middle Hot Springs	43	Waterton Camp 142 Spring
4	Cave and Basin Upper Spring	44	Wishing Well
5	Grassi Lakes Spring	45	Belly Gushet
6	Canmore Sulfur Spring	46	Birdseye Bench Spring
7	Railside Spring	47	Whiskey Gap Meadow
8	Many Springs 1	48	Whiskey Gap Spring
9	Willow Rock Campground Spring 1	49	Sandstone Ranch Spring
10	Watridge Karst Spring	50	Sandstone Eyrie Spring
11	Big Hills Spring	51	Kennedy Coulee Spring
12	Heath Creek Cutbank Springs	52	Nichol Spring
13	Douglas-fir Coulee Springs	53	CHPP Graburn Creek 2
14	Beaver Creek Parsnip Spring	54	Reesor Spring
15	Carlton Springs	55	Border Spring
16	The Big Spring		
17	Nadeau House Springs		
18	Poplar Bluff Springs Upper		
19	Price Hutterite House Springs		
20	North Field Springs		
21	Walker Farm Springs		
22	Metzler Wall Spring		
23	Metzler Ravine Spring		
24	Turtle Mountain Sulfur Spring		
25	Adanac Owt Springs		
26	Adanac Eno Springs		
27	Beaver Mine Springs 1		
28	Red Chair Springs		
29	Jellyroll Springs		
30	South Wetland Pond Springs 1		
31	Moosejaw Springs		
32	Sandboil Springs		
33	BSNA Ephemeral Springs 1		
34	Bovin Outlet Springs		
35	Bovin Cienega Springs		
36	Bovin Cascade Springs		
37	Cameron Hillslope Spring		
38	Akamina Trail Spring		
39	Blakiston Seep		
40	Buffalo Springs		

APPENDIX B

Table B.1. List of 74 plant taxa included in NMDS ordinations of the presence and abundance of native (n = 63) and non-native (n = 11) taxa at 55 springs in Alberta, Canada.

Taxon
Non-native
Bromus
Cirsium
Medicago
Melilotus
Phleum
Plantago
Poa
Rumex
Taraxacum
Tragopogon
Trifolium
Native
Abies
Achillea
Actaea
Amelanchier
Argentina
Arnica
Artemisia
Betula
Calamagrostis
Campanula
Carex
Castilleja
Chamerion
Cornus
Deschampsia
Elaeagnus
Eleocharis
Elymus
Epilobium
Equisetum
Erigeron
Fragaria
Galium
Geranium
Geum
Glyceria
Hackelia
Heracleum
Hordeum
Juncus
Juniperus
Lathyrus
Lonicera
Maianthemum
Mentha
Mimulus
Mitella
Osmorhiza
Packera
Parnassia
Penstemon
Picea
Platanthera
Polygonum
Populus
Potentilla
Prunus
Pyrola
Ranunculus
Ribes
Rosa
Rubus
Salix
Senecio
Shepherdia
Solidago
Spiraea
Symphoricarpos
Thalictrum
Urtica
Veronica
Vicia
Viola

Table B.2. Complete list of the most commonly observed plant taxa at 55 springs in Alberta, Canada. NMDS codes refer to grey letters and numbers in Chapter 3 ordinations (Fig 3.1).

Family	**Genus**	**NMDS code**	**Plant taxon**	**Times observed**
Asteraceae	*Cirsium*	a	*Cirsium arvense*	26
			Cirsium sp.	7
			Cirsium vulgare	7
Poaceae	*Phleum*	b	*Phleum pratense*	31
			Phleum sp.	5
Asteraceae	*Taraxacum*	c	*Taraxacum officinale*	33
Poaceae	*Poa*	d	*Poa pratensis*	24
			Poa sp.	7
			Poa compressa	1
		e	*Bromus inermis*	18
			Bromus tectorum	1
Polygonaceae	*Rumex*	f	*Rumex sp.*	15
			Rumex acetosa	2
			Rumex crispus	1
			Rumex stenophyllus	1
Fabaceae	*Trifolium*	g	*Trifolium sp.*	8
			Trifolium pratense	4
			Trifolium repens	3
			Trifolium aureum	1
	Medicago	h	*Medicago lupulina*	6
			Medicago sp.	2
			Medicago sativa	2
Plantaginaceae	*Plantago*	i	*Plantago major*	10
Fabaceae	*Melilotus*	j	*Melilotus alba*	4
			Melilotus officinalis	4
			Melilotus sp.	1
Asteraceae	*Tragopogon*	k	*Tragopogon dubius*	8
			Tragopogon sp.	1
Cyperaceae	*Carex*	1	*Carex sp.*	16
			Carex utriculata	11
			Carex microptera	11
			Carex aquatilis	10
			Carex pellita	10
			Carex aurea	9
			Carex disperma	3
			Carex nebrascensis	3
			Carex praegracilis	3
			Carex pachystachya	2
			Carex atherodes	1
			Carex athrostachya	1

Family	**Genus**	**NMDS code**	**Plant taxon**	**Times observed**
			Carex bebbii	1
			Carex canescens	1
			Carex capillaris	1
			Carex flava	1
			Carex gynocrates	1
			Carex interior	1
			Carex lenticularis var. dolia	1
			Carex mertensii	1
			Carex nigricans	1
			Carex norvegica	1
			Carex phaeocephala	1
			Carex podocarpa	1
			Carex raynoldsii	1
			Carex sartwellii	1
			Carex scirpoidea	1
			Carex simulata	1
			Carex sprengelii	1
			Carex stipa	1
			Carex umbellata	1
			Carex vaginata	1
			Carex xerantica	1
Juncaceae	*Juncus*	2	*Juncus balticus*	27
			Juncus ensifolius	12
			Juncus	7
			Juncus longistylis	5
			Juncus drummondii	4
			Juncus nodosus	3
			Juncus alpinoarticulatus	2
			Juncus bufonius	2
			Juncus stygius	2
			Juncus castaneus	1
			Juncus confusus	1
			Juncus vaseyi	1
Equisetaceae	*Equisetum*	3	*Equisetum arvense*	34
			Equisetum	7
			Equisetum laevigatum	5
			Equisetum hyemale	3
			Equisetum scirpoides	1
Onagraceae	*Epilobium*	4	*Epilobium ciliatum*	29
			Epilobium	14
			Epilobium clavatum	4
Salicaceae	*Salix*	5	*Salix sp.*	31
			Salix bebbiana	11

Family	**Genus**	**NMDS codes**	**Plant taxon**	**Times observed**
			Salix discolor	2
			Salix arctica	1
			Salix exigua	1
			Salix maccalliana	1
Asteraceae	*Achillea*	6	*Achillea millefolium*	35
Rosaceae	*Potentilla*	7	*Potentilla fruticosa*	11
			Potentilla gracilis	10
			Potentilla	7
			Potentilla diversifolia	2
			Potentilla norvegica	1
			Potentilla rivalis	1
	Rosa	8	*Rosa acicularis*	12
			Rosa	10
			Rosa woodsii	9
			Rosa arkansana	1
	Geum	9	*Geum aleppicum*	11
			Geum macrophyllum	9
			Geum	5
			Geum rivale	4
			Geum triflorum	2
Salicaceae	*Populus*	10	*Populus tremuloides*	13
			Populus trichocarpa	12
			Populus balsamifera	4
			Populus	2
Rubiaceae	*Galium*	11	*Galium boreale*	21
			Galium triflorum	7
			Galium	1

Table B.3. List of supplemental native plant taxa identified on the NMDS ordination plots of the presence and abundance of commonly observed non-native and native plant taxa at 55 springs in Alberta, Canada in Chapter 3 (Fig 3.1).

NMDS Code	**Family**	**Genus**	**Species**
Figure 3.1 A (presence/absence)			
12	Cyperaceae	*Eleocharis*	*palustris, quinquefolia*
13	Poaceae	*Hordeum*	*jubatum*
14	Asteraceae	*Arnica*	*cordifolia, fulgens, latifolia, sororia*
15	Pinaceae	*Abies*	*lasiocarpa*
16	Saxifragaceae	*Mitella*	*breweri, nuda, pentandra*
17	Asteraceae	*Senecio*	*hydrophiloides, triangularis*
18	Caprifoliaceae	*Lonicera*	*dioica, involucrate, utahensis*
19	Apiaceae	*Osmorhiza*	*berteroi, depauperata, occidentalis*
20	Ranunculaceae	*Actaea*	*rubra*
21	Cornaceae	*Cornus*	*canadensis, sericea*
22	Cupressaceae	*Juniperus*	*communis, horizontalis*
Figure 3.1 B (cover index)			
12	Poaceae	*Hordeum*	*jubatum*
13	Cyperaceae	*Eleocharis*	*palustris, quinquefolia*
14	Polygonaceae	*Polygonum*	*bistortoides, douglasii, erectum, ramosissimum, vivparum*
15	Scrophulariaceae	*Penstemon*	*albertinus, confertus, fruticosus*
16	Pinaceae	*Picea*	*engelmannii, glauca,*
17	Asteraceae	*Artemisia*	*absinthium, frigida, ludoviciana*
18	Rosaceae	*Prunus*	*virginiana,*